The Birth and Spread of Plants

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THE
BIRTH AND SPREAD
OF PLANTS

by

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Contents

Preface

The contents of this book are mainly quite new material, representing the most important final results of the work that has occupied the writer for most of his mature life—leisure to 1915, and almost all the time since. Portions have been published in Age and Area (1922), *and in* The Course of Evolution (1940), *and in many papers.*

As a boy he became interested in distribution by reading the works of his granduncle William Swainson (p. 294) and by looking at his collections of shells which we had at home. Gradually he went over to botany, the line of his great-grand-father (cf. p. 295), helped by the masterly teaching of Prof. S. H. Vines and Sir Francis Darwin at Cambridge, and stimulated by a remark of one of our leading distributionists, that distribution seemed to be almost beyond the range of the human intellect. The accidental loss of his better eye also helped in this direction, and drove him into distributional work, while at the same time the illogicality of the common conception of natural selection was coming home to him very strongly with his work in the tropical forests and rivers, and the phenomena of endemism.

Gradually he found that distribution worked to a great extent upon an arithmetical basis, and his first work was published in Age and Area. *By this time his method of using the subconscious was largely perfected (cf. p. 248), and deductions from age and area were continually appearing, quite unexpectedly. Finding that when tested upon the facts (a work requiring much time and labour) they invariably proved correct, and that illustrations could always be easily found in any taxonomic* *work, he acquired great faith in this method, and began to collect facts for a book upon evolution and geographical distribution. As it became too large for convenience, he published the evolutionary part of it under the title* The Course of Evolution, *and gave a further eight years of work to the present book.*

Much help has been given by many people, to whom the writer's acknowledgments are given below.

J. C. WILLIS.

Les Terrages, avenue des Alpes.
Montreux, octobre 1948.

Postscript to Preface and Aknowledgements

The above preface was written when the author was nearing the completion of the book. Then two unfortunate accidents combined with the effects of increasing age to reduce his capacity for work to about a quarter. He takes the opportunity allowed by this small space to express his warmest thanks to Prof. Baehni for his patience in the delay of publication, and his kindly help in many ways; also to Mlle Dubugnon and to Dr Weibel, for much help. J.C.W.

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The writer is deeply indebted to the following among others. To the Government of Switzerland for allowing him to live and to do research in so healthy and so beautiful a place as is Montreux. To the City of Geneva, which has given him the hospitality of its Conservatoire de Botanique, and of the journal *Boissiera* published by it, from which this book is a reprint. To Drs. B. P. G. Hochreutiner and Ch. Baehni, successively Directors of the Conservatoire and Botanic Gardens, for their ungrudging and kindly help, and for the use of the great library at the Conservatoire, in which much of the material of this book has been collected. To Mlle Dubugnon, secretary of the Conservatoire, and to Dr. Weibel and other members of the staff.

To Dr. W. Robyns, Director of the Botanic Gardens at Brussels, who was very helpful, especially in allowing me the use of their great library, in which I spent a few days in many different journeys to and from London. To Sir David Prain, Sir Arthur Hill, and Sir Edward Salisbury, successively Directors of the Royal Botanic Gardens at Kew, and to Drs. Cotton, Fischer, Hutchinson, and Turrill in the great herbarium, who were all of great assistance in many ways.

And to many other friends, especially to Mrs. Howe, the well-known traveller and author, to the late Mr. John Murray of the Indian Educational Department, to Prof. Brooks, Mr. G. Udny Yule, and my daughter Mrs. Anderson at Cambridge, to Mr. I. H. Burkill at Leatherhead, to Prof. Small at Belfast, to my cousin J. P. de Chanaz, Mr. H. Davidson, and the late Dr. C. Balfour Stewart at Montreux, and others.

Finally, for the early stages of the work, to the staffs of the institutions of which the writer had once the honour to be the Director, at Peradeniya (Ceylon) and at Rio de Janeiro, in both of which he had full opportunity for the study of vegetable life in the tropics.

Introduction

Except in places where conditions are too extreme for growth, the world is covered with vegetation, usually showing much variety of density and form. Many problems are thus set before us. Why, how, where, and when did all these forms arise, and why, how, whence, and when, did they settle in the spots that they now occupy? Complete answers to all these complicated enquiries obviously involve great and varied knowledge of many branches of science, and can only result from long inductive study.

The present work is an attempt to answer some of these questions, in part at least, and to show that inductive methods may be applied here, as elsewhere in science, with promising results. The earlier history of many of these problems lies in the realm of evolution, the later in that of ecology, which has now become an almost independent science. Geographical botany, or geographical distribution, properly so called, has to fill up the gap in knowledge between these two, and to trace the how and the why, the whence and the when, of the movements of plants from the time of their conception and birth.

Each species (or other form) seems to have been born in some small and definite locality, in which there were certain conditions of life at the moment of birth, and they were of necessity adapted to these, or they could not have survived. It is in fact almost certain that this local adaptation to the birthplace must have been derived from the immediate ancestor, from which they showed at times a definite structural divergence, sometimes enough to give to the offspring a different taxonomic position, whether varietal, specific, generic, or even higher. This change probably happened under some special stress of conditions, which involved some genic change or rearrangement.

Obviously one of the first things that must be known, if one is to work out these problems satisfactorily, is how plants began life, or how and why, where and when, they were evolved. The pre-Darwinian view was that they were created for the localities where they were found. Some, the "successful" ones, had enlarged their area of distribution, some, the "unsuccessful", had lost some of it. With the coming of the Darwinian theory that evolution went on in response to gradual improvements in adaptation made by slow structural alteration, the creed of "Darwinism" sprang up, and FLEEMING JENKIN's criticism being accepted, it was assumed that species began upon considerable areas, rather than upon small ones. This view of the matter has been altered with the work of the writer and of others. Under it, it became usual to look upon things of very small areas as "relics" of former vegetation, the remains of things once covering large spaces. Endemics, though there are numerous exceptions, especially near those regions that were affected by the ice of the glacial periods, proved to be in general young beginners as species or genera. Their numbers, starting with a single leader at the top of a family, increase downwards, slowly at first, and then very rapidly in the smaller ones near the foot, ending there with a great proportion of ones, usually well above one third of the whole total. They thus form the familiar "hollow curve", for the number of possible parents increases at every stage, and the offspring must necessarily begin as "ones". The curve shows in many different kinds of distribution, for example that of farmers'surnames both in BRITAIN and in SWITZERLAND (*Evol.*, p. 35). On the same page are the figures of sizes of genera in the *Monimiaceae*, showing how they form the hollow curve, and one may see it in many tables in this book, for example the *Ranunculaceae* on pp. 30-1, or the many in *AA* or *Evol.*

The universal display of hollow curves was fatal to the idea of general relicdom. It showed that the formation and dispersal of endemics represented in nearly all cases simply the earliest stages in the history of individual species or genera. They began in one place, or possibly sometimes more than one, and their dispersal followed simple arithmetical lines, the area occupied, and the size (number of species) increasing with the age. From these two laws of age and area, and age and size, the third, of size and space, follows automatically, the three forming what we have called the laws of ASA, which are universal, and are fundamental in distribution. Area and size are simply functions of the time elapsed, but of course their rate of operation varies with the type of plant, and one can only use closely related and similar things for comparisons.

The leader of a family (its largest genus) seems to carry with it the potentialities of all the characters that may later appear in that family (and at times in other families also), but which characters shall appear seems to be largely determined by outside conditions. Divergence of structural character usually appears in one or more of the characters at every mutation, and may be said to be the mark of evolution. It becomes less marked, but more frequent (by reason largely of increasing numbers), as time goes on, and we come downward from the rare and great divergences that separated such things as ferns and mosses, or conifers and flowering plants.

Our work also indicates clearly that evolution, as we have already shown in *Evol.*, works *downwards* from larger divergences to smaller, and not, as hitherto supposed, in the upward direction. The leader of a family (its largest genus, as a rule) is the first to appear, and is early followed by the leaders of tribes, these by leaders of sub-tribes, and so on down to sub-species. Dichotomous divergence appears at every mutation, but with a gradually decreasing emphasis. We have therefore called this law the law of DDM, or dichotomous divergent mutation, and we look upon these four laws of ASA and DDM as those which have chiefly guided the appearance and the dispersal of the various plants that cover the world. Evolution, which seems as if it might be electrically controlled (thus accounting for divergence) seems to be more or less completely independent of selection. Structural changes rarely have any serious adaptational importance, and distribution goes on in a more or less mechanical way, with little reference to adaptation or selection, but with the importance of these increasing as time goes on, and the ground gets more and more occupied by a variety of plants. The vital factors, unimportant in early days, assume great importance in the last stages of distribution.

As the deductions which the author formed from these four fundamental laws, largely by aid of the subconscious, always proved to be correct, within reasonable limits, when tested on the actual facts, the writer's confidence in the general correctness of his work has been much strengthened. For example, it was deduced that the early mutations of the leader of a family should tend largely to head large divisions of that family, and the same in the case of a genus. This proved to be an almost universal law, which is illustrated here by many tables (list in Index under Leaders). Incidentally, it shows how taxonomic division, which must of necessity follow the structural divergences, is not, and cannot be, always quite natural, in the genetic sense. Coming downwards, the divergences diminish, and close relationship is more easily made out, while parent and child, at the top of a family, may easily be separated by a divergence of sub-family rank.

In this book we have not tried to apply any of our conclusions to the animal world. But that they may probably be so applied, perhaps with some necessary alterations or modifications, is very likely. We have seen in *AA*, p. 200, that the principle of the hollow curve seems to apply to zoology as well as to botany, and this seems to render it likely that the other more or less mechanical laws which we have worked out for the vegetable kingdom will also apply to the animal; but this question must be left to the zoologists.

Some interesting facts, again, are brought out in the section upon island floras in Chap. XIII. The *Rubiaceae* are obviously one of the oldest families in the world, and especially in the tropics, and it is very striking to see the way in which the leader of the family, and the leaders of the sub-groups, are so marked a feature in the floras of islands in the warmer parts of the world, where in general the island floras must be among the oldest of all. There are 13 genera of *Rubiaceae* in the SEYCHELLES, and they include seven leaders of tribes, one of which is *Psychotria*, the leader of the whole family. Of the other six, five are either second or fourth in one of these tribes, and there is only one small genus (of MALAYA) that can possibly be put down to accidental introduction, most likely by water. Other tropical islands show the same kind of thing. CEYLON, a much more recent island, shows eleven leaders, eighteen genera from second to ninth in their tribes, and sixteen smaller ones. This phenomenon, which is a rule in tropical islands, seems to the writer a final and striking proof of the origin of sub-families, tribes, genera, and species by the downward evolution that he has postulated for 40 years, and makes a little change in our methods of viewing the phenomena of the plant world.

Many other things of interest have come up in the course of this work, and it is evident that the acceptance of our conclusions will open up many new avenues for research. In the first chapter, for example, a number of new problems appear in regard to the British flora, and much the same may be said of most of the other chapters. Perhaps the most obvious thing that needs detailed and far-reaching investigation is the incidence of characters, with its diminishing emphasis as one comes down from the far past to more recent times. This, with the evidence that we have given of the probable commonness of polyphyly, and of the very frequent occurrence of the same character in widely separated places, rather indicates that the evolutionary tree requires a good deal of pruning, not to say coppicing. The facts suggest that there are some important discoveries to be made in the region of genetics.

There are many directions in which useful work may be done. Once one has become used to treating evolution the other way round, so to speak, one realises that many subjects need a considerable revision to bring them into line again with evolution in its new aspect. In this connection, it is worth while to read the chapter in *AA* by Dr GUPPY on p. 101, especially his remarks upon p. 104, and the sentence on p. 105, where he says that " new and unexpected fields of research will be opened up all around him ".

The writer, who will reach 81 in the following February (1949), and is now too old for hard work, has collected great masses of statistics during his lifetime, and if good secretarial help can be obtained, hopes to put them into good shape, and to leave copies to the great botanical institutes of the world, with a view to saving labour in the future. Revision, and not first collection, will be all that they will need.

CHAPTER I

The flora of Great Britain

The presentation of our subject being somewhat new, it may be well to begin with a well-known flora. BRITAIN has, by various estimates, about 100 families, 475 genera, and 1500-2000 species. Where not cultivated, it is covered by different ecological communities of plants (122), composed of many species, varying in abundance from dominant to very rare. No taxonomic relationship shows among them any more clearly than if they had been chosen at random, unless, as at times, two or three members of a genus or family occur together. Climate varies; the soil may be rich or poor in humus, in lime, and in other things, and may differ in degree of humidity, acidity, and consistency. It may bear different types of vegetation, such as trees, shrubs, or herbs, causing different conditions at ground level, and so on.

Under these various conditions, one may get moors, fens, heaths, woods, chalk-pastures, sand-dunes, &c, each having its own type of flora, one often differing widely from another in its composition. In any one country there are usually many types of situation, so that there is a large total flora, the local flora varying from place to place with the communities that there occur. The composition of the latter finally depends upon the total flora, for they are made up out of it, or out of such of it as occurs within reasonable distance, by natural selection of the most suitable, just as the inhabitants of a village are made up from their various qualifications of suitability, chiefly that of having been born and brought up among the conditions there prevailing. Ecology studies the local conditions, the location and composition, of these communities, while distribution proper studies the total floras, with their composition, sources, and origin, a study long left neglected.

Even in a complete and "closed" community, the composition will not always remain the same. Sooner or later, and largely as a result of the continued growth in the same spot of the same plants, soil changes will appear, bringing about changes in relative abundance, some species even disappearing, perhaps, some new ones appearing, so that a species that has long lived near by without being able to join the community may now get its chance to move forward. Probably, on the whole, in large areas (where there are usually many communities), and in long time, each species of a total flora may get a chance of spreading that does not differ so very much from that of others. But one must not forget that the early comers will have the first chance at becoming accustomed to new conditions, and so will have the first chance with yet others before the communities are fully made up, and will thus become the most widely spread of all (" the early bird gets the worm "; " to him that hath shall be given ").

Such ecological changes may occur in what are comparatively short periods, while the movement of species over large areas may take up what are relatively geological periods. Ecology deals with recent events, and variation under local conditions, distribution proper with slow and on the whole steady movements spread out over long periods, during which several ecological changes may occur at the same place. Evolution creates the plants, while distribution studies the way in which they move about the world. These two necessarily go together, while ecology studies the way in which the plants settle in any given spot after arrival. The distribution of plants upon the large scale cannot be intelligently visualised without a proper knowledge of the way in which they came into being. If, for example, a given plant proved to have been independently born in two quite different places, any study based upon the idea that it had only begun in one would be rendered of much less value.

Most often, perhaps, a plant will travel with the community to which it belongs. This will travel as a whole so long as the conditions remain fully favourable to all its members, but as probably no two species have just the same functional adaptability, the community will gradually become altered, some species dropping out, their places being often taken by newcomers, to whom the altered conditions are now suitable. But these changes do not involve any structural change or adaptation, unless a new mutation should happen to coincide with them, and even then there is no reason to look upon it in the light of an adaptation. Such a change will probably involve a slight adaptational change, but it must not be serious, or the species may be killed out by natural selection as soon as it arrives.

If the junction with the continent were once at the southeastern part of BRITAIN, as seems probable, plants arriving there would find little or no immediate change in conditions, but to go thence to the north or west they would have to become suited to different soil and climate. That this is possible is shown by the figures in the *London Catalogue* (11th ed.), which give with great accuracy the distribution of every British species into the " vice-counties ", the more natural divisions made by H. C. WATSON, who began this work, to replace the political counties. Owing to its geological formation, and its nearness to the ATLANTIC, BRITAIN differs so much in different parts that species that occupy many must have become suited to them by some functional or internal process as they moved about. The number of vice-counties in BRITAIN, not including IRELAND, is 112, and the mean is 56.5.

As the chief illustration of this chapter let us take the well known family *Ranunculaceae*. One is very apt to fall into the slipshod habit of saying that the family is well represented and well distributed in BRITAIN. What one really means is that some, but not all, of its genera and species are so. Taking the vice-county figures, and placing a bar at the mean point of 56.5, one gets as the dispersal of its species :

Distribution of Ranunculaceae in Britain

Anemoneae			*Helleboreae*		
Clematis		49	Caltha	112	21
Thalictrum	76	39 38 30 6 4	Helleborus		33 19
Anemone	109	19	Trollius	66	
Myosurus		46	Aquilegia	65	
Ranunculus	112 112 112 112 112 112 104 97 93 87 87 83 76 75 71 62 57	55 51[1] 16 13 10 4 3 3	Aconitum		9
			Actaea		5

Average dispersal: *Anemoneae* 61. *Helleboreae* 41.1.

Of the 43 species 21 are below the mean, and the family average, 57.3, is just above it, while if *Ranunculus* were removed, it would fall to 41. The next table gives the species above-below and the family average, for various large families:

Large families in Britain

Below mean dispersal			*Above mean dispersal*		
Cruciferae	23/35	Av. 49	Ranunculaceae	22/21	Av. 57.3
Caryophyllaceae	32/36	50	Compositae[2]	64/48	58
Leguminosae	34/38	52	Labiatae	33/21	60
Umbelliferae	28/31	55			
Liliaceae	7/22	32	Total	Dicots	236/230
Orchidaceae	16/28	42		Monos	81/123
Gramineae	58/73	53			

Most of these large families, regarded by the old school as very "successful", thus show dispersal rather below than above the mean, especially in Monocots, where the only ones above are a few small families like *Lemnaceae* (water

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[1] A gap like this is common in large genera; in the first fifteen it averaged 33, or more than the ten or fifteen one might expect. Its meaning is not clear (? a narrowing of the isthmus at some time).

[2] Small Hieracia omitted.

plants) or *Dioscoreaceae* (one species). We shall come upon a good many marked differences between Dicots and Monocots (*cf*. Index).

If one accept the view, put forward in *Age and Area*, that small dispersal means late arrival, rather than lack of adaptation, one will not expect any family with many species to be much above the mean, though one of late arrival may well be below it.

One of the first things that one notices in the British (or other European) flora is the great number of the large subfamilies and tribes that are represented. Of the three in *Ranunculaceae* the only one not represented is the unimportant group of the *Paeonieae*, whose leader, *Paeonia*, occurs in the centre and south of FRANCE. We shall return later to the consideration of this phenomenon, which is hardly what one would expect under selection. There is little evidence to show that adaptation takes any serious part in the distribution. Recent work seems to show that a species that is polyploid may be more rapidly distributed than one that is not, but one would hardly, upon present evidence, consider this as adaptation.

The " unsuccessful " British families that have only one genus and one species each, show the dispersal : above the mean 112, 112, 108, 105, 93, 93, 89, 89, 86, 78, 78, 73, 70, 68, 64, 62, 59, and below the mean 41, 26, 23, 12, 8, 7, 6, 6, 3, 2. Thus 17 are above and only 10 below the mean, and the average of 60 is about the same as that of the large families quoted above. There is no evidence for any inferiority in dispersal. The two 112s are *Hedera*, a small genus, and *Oxalis*, a very large. The division between successful and not so must be, if anywhere, within the genus or species. But as success in one country is usually accompanied by success in others, where there is not too great a difference in conditions, the solution of the problem by reference to natural selection is not possible, and it is simpler to adopt that offered by age and area, which puts down distribution to age rather than to adaptation, abandoning the theory that the latter governed dispersal over large areas and long time. Under the Darwinian theory there is no production of new forms without the urge of adaptational improvement, and the new forms kill out their predecessors. Under the theories that we advocate here (**156**), adaptation to its place of birth is born with a new species, and is rather functional than structural, if at all the latter in most cases. Those not born with it are killed out. With the adaptation itself must go a certain amount of adaptability, to enable the organism to withstand the continual small changes of conditions, and this adaptability enables it to spread to a greater or less distance from its birth place. The ancestors are not necessarily killed out.

The current theory, that dispersal is due to adaptation acquired by gradual structural evolution, uses what HUXLEY termed " the verbal anodynes by which the discomfort of ignorance is dulled ", but cannot explain the facts. To what is *Ranunculus*, or any of its species, really adapted? Reference to a couple of British floras shows that they inhabit " ponds, ditches, running streams, deep still waters, rivers, marshes, salt-marshes, wet places, sandy shores of lakes, bogs, thickets, pastures, meadows, cornfields, waste places, woods, bushy places, and most of all cultivated places and slovenly farms ". How did they become suited to all these places, except by the passage of time? To suit what conditions were they really evolved? What made some species so " successful ", some so unsuccessful? Why is the genus so cosmopolitan? Why did it need so many species (it has about 325)? Our solution is simply that it is an old genus, and that its older (more widely dispersed) species have therefore had time to adapt themselves functionally to many different conditions. HUTCHINSON (68) calls it " the most primitive of herbaceous Dicotyledons "; it was probably a very early arrival in EUROPE, where it is conspicuous in the far north, and also goes very high in the ALPS, where, as *R. glacialis* near the summit of the FINSTERAARHORN, it is at the greatest height recorded for any plant in SWITZERLAND (4270 m., or over 14.000 feet) (**113**). It *may* even have been born originally somewhere in northern EURASIA.

How did the common buttercups like *repens* become so suited to cultivated places, when they must be much older than cultivation? They must just have happened to suit them, or have become functionally, not structurally, adapted to them. But what adaptation caused them to become the most widespread of the buttercups? To what were they *really* adapted, and for what, upon the Darwinian plan, were they evolved ? In Bentham's *British flora*, six buttercups are marked abundant, and eight are not. The distribution of these in the *world* is :

Abundant in Britain	*Not*
1. North temperate, Australia	1. North palaeotemperate
2. North temperate	2. North palaeotemperate
3. North temperate	3. North palaeotemperate
4. North palaeotemperate	4. Mediterranean, W.Europe
5. Europe and western Asia	5. Europe and W. As.
6. Europe and western Asia	6. Europe or part of it
	7. Europe or part of it
	8. Europe or part of it

The distribution abroad of the abundant species is much greater than that of the others, and this, so long as one works with groups of allied species, proves to be a general rule, that is practically fatal to the supposition that wide spread depends upon adaptation. This interesting fact was discovered long ago in the flora of Ceylon, where the writer found that " the most widely distributed species in Ceylon, *on the average*, are those that show a distribution abroad to a greater distance than merely to Peninsular India; then follow those that only reach the peninsula, and the least widely distributed in Ceylon are those that are found in Ceylon only " (*Age and Area*, p. 60). These last, known as endemic species, are hardly noticeable in northern Europe. " This graduation of areas... showed not only for the grand total, but also for every family of 14 or more species... nothing but a mechanical explanation would serve. Natural selection could not act on all plants alike with even pressure. " (*l.c.*, p. 61). This phenomenon is so universal that it may be termed a law of distribution, and called the law of " first come, first served ", or " to him that hath shall be given ".

The abundant species in Britain, as their distribution is so wide, must on the average have come from far away, and so, if they had any structural adaptation, they must have brought it with them. But to carry structural adaptation from a country A that will also suit B, C, D or E seems strange, though if it is only structure that is carried, it probably makes little or no difference. The species could not have survived unless it had adaptation to start with, and it would acquire local adaptation as it travelled. But in so doing it does not necessarily alter its structural characters at all, the adaptation being primarily functional. The physiologists have long told us that structure and function are largely independent.

There are many *Ranunculi* with wide dispersal in BRITAIN. Six, the largest number in any single genus, reach the maximum possible of 112, but the average for the whole genus is but 68.7, because other and younger species continued to arrive in BRITAIN until the final separation.

It is of interest to note that the other ten British genera make up a list of localities not much inferior to *Ranunculus* itself—woods, open woods, moist copses, thickets, hedges, cornfields, chalk and limestone pastures, stony pastures, mountain pastures, parks, riverbanks, moist meadows, the sides of ditches, marshes, alpine bogs, sandy shores, chalk hills, dry limestone soils, waste places, old walls, ruins, &c. Similar variety may be found in other large families and genera in BRITAIN.

Evolution. DARWIN's great work, which unfortunately is not called by his name, has shown beyond any doubt that plants and animals owe their great variety of structural form to an evolution that has been going on since the beginning of life. It was originally intended to deal with it also in this work, but it became too bulky, and was published in 1940 as *The Course of Evolution,* where a summary of conclusions will be found on p. 191. In 34 crucial testcases between the Darwinian theory of progress by selection of small structural variations that possess adaptational value, and the pre-Darwinian theory that I have accepted and have called the theory of divergent mutation, I have shown that the evidence is almost overwhelming in favour of the latter. Under this theory, a single mutation, usually very divergent from the parent form, may give rise, at one step (not gradually as under Darwinism) to a new form, of family, generic, specific, or varietal rank. This reverses the course postulated by Darwinism, going from family down to species, not the other way. But if this be so, it is clear that selection cannot have controlled it, unless it work in some recondite way at present unknown, and it is simpler to take the view that

" evolution and natural selection are probably to a great extent independent, and they work at right angles to one another with (in plants at any rate) little mutual interference ". Evolution is evidently " working upon some definite law that we do not yet comprehend ", and the mutations " cause structural alterations, which may, but by no means necessarily must, have some functional advantage attached. If such an advantage appear in the mutation, natural selection will likely allow it to survive. There is no necessary reason why the immediate ancestor should die out ". " Evolution is no longer a matter of chance, but of law. It has no need of any support from natural selection. It thus comes into line with other sciences which have a mathematical basis. The theory of natural selection has been trying to work it backwards ". Or, in the words employed by YULE and the writer (159) " inasmuch as all families, both of plants and animals, show the same type of curve, whether graphic or logarithmic, it would appear that in general the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan. "

In plants, divergent mutation seems to hold very generally. A species with alternate leaves may give rise to one with opposite, or a 5-merous flower to a 4-merous. But as the species of a genus increase, the later tend to fill up the gaps between the earlier, making the divergences less distinct. The early, clearly marked species or genera have most descendants, and tend to become the heads of sub-genera, or tribes. In my work upon the *Podostemaceae* (*Evol.* p. 21), where under as completely uniform conditions as are known, evolution has yet produced the most divergent set of characters known (*cf.* the pictures in 148), I came to the conclusion that, at least under certain circumstances, evolution must go on, whether there be any adaptational reason for it, or not. Such extreme cases of divergence as those just quoted offer no grip to selection, nor could it bring them to perfection as it is usually shown, for as this was approached, the urge would rapidly fall off, till the time needed for the finishing touches would rise to infinity. (*Cf.* Testcase X, *Evol.*, p. 114).

These objections also apply to gradual development by small mutations in series, each altering one feature, unless one abandon selection, and consider these as controlled by some general law. One might get *Myosurus* from *Ranunculus* in two such mutations, one changing the head of carpels to a cylinder, the other giving the petal a tubular base. But there is no adaptational reason for the existence of *Myosurus*, which might ensure that one of these was followed by the other. Probably mutations that change a genus are very rare, but as YULE showed (**158**), one new species, formed anywhere upon the globe, once in 15-30 years, is probably enough to account for all that are known, so that the chance of such an one being recognised is practically *nil*.

But if evolution proceeds upon these lines, adaptation must take a place completely different from that so far assigned to it (**136, 156**). A species born in this sudden way, if not so far adapted to the place of birth as to be able to survive and reproduce, will at once be killed out by natural selection, so that any species that survives may be looked upon as adapted to the place where it grows. How far it can spread from there will depend mainly upon the time available, and its adaptability to new conditions. As this adaptability will presumably centre upon the conditions under which it was born, while that of its parent will centre upon some other place, it *may* be able, once established (which will take a long time, during which the parent may get a long start), to travel more rapidly than its parent, and may even at times pass the latter in its progress. We shall return to this subject below.

Age and Area. If then, evolution was largely independent of any urge from adaptational improvement, as seems highly probable, the latter can have but little influence upon dispersal and some more mechanical explanation must be found. That which the writer proposed, and which he found to cover most of the phenomena of distribution, as yet simply the subject of vague speculation, he called *Age and Area* (*AA*), which may be briefly indicated in the phrase "the most widely dispersed plants, *each in its own circle of affinity*, and taken in groups of ten to cancel individual variation, are the oldest, the least so the youngest". Age in itself effects nothing, but it allows the time for the various active factors in distribution to produce their effects. If in a long time and a large space, one factor produce an effect 1, then in twice the time it will probably produce 2, and the same thing for the resultant of all the factors. In reality it will probably be not quite so simple, on account of the way in which all the conditions are liable to vary.

It was found for CEYLON, NEW ZEALAND, and elsewhere, that those species were the most widely distributed in a country which had the widest distribution outside, while the local or endemic species had the smallest areas, working always with averages of ten allied species, and comparing with allied. Wides, as I called the first named, showed a decrease in number in any country from large areas down to small, endemics an increase. " The facts call for a mechanical explanation, and the most reasonable seems to be that area occupied on the average increases with age, independently of the origin of the species. "

The system in space to which the earth belongs affords a good illustration. The sun may represent the original genus of the family, split off from an older and larger genus. The planets represent further new genera, split off from the sun, the furthest out being the oldest and " covering " the largest area, the nearest to the sun being the youngest with the smallest area; and the satellites of the planets in the same way may represent the species derived from the genera.

" I called this hypothesis by the convenient jingle of age and area, and from the very first I was careful to point out that this result was only strictly true when *averages* of about 10-15 *allied* species were taken (*AA*., pp. 61-2, and seq.). " What has really surprised me ....is that the figures that have been given in many papers, by myself and others, show such clear and unmistakeable results that it is evident that mere age of species is a much more important factor in... distribution than we had been inclined to suppose... one can make so many predictions... especially within comparatively small areas, and find them correct within such small limits, that it is evident that mere age is a very important factor indeed, and consequently that distribution, when one works with groups of species and over enormous periods of time, is a much more mechanical phenomenon than we had been inclined to think ". One could therefore make predictions upon this simple basis. " For example, the flora of the outlying islands of NEW ZEALAND, being in general derived from the same sources as that of the main islands, must be composed of species that were among the earliest arrivals, in their own affinity groups, in NEW ZEALAND, and should therefore... be very widespread there. This proved to be the case in a very striking manner, the species of the islands ranging on the average nearly 300 miles further in NEW ZEALAND than the species that did not reach the islands... Other predictions were equally successful... Age and area has been applied in this manner in over 90 cases without a failure... "

Some people seem to think that the argument just given has been vitiated by the fact that if one have a large space of land, such as must probably have existed when the CHATHAMS, AUCKLANDS, &c formed part of NEW ZEALAND (cf. the soundings, **140,33:** 479), covered by large or small circles of distribution, and then cut out a piece, say the CHATHAMS, that piece will obviously have more in proportion of the large than of the small circles. This is in reality the same argument as mine, and does not affect the prediction in the least. Nor does it in any way give any support to the theory that dispersal was due to the adaptation. It rather implies that the dispersal was more or less equally divided over the whole area, and makes no reference to the fact that the species must have reached NEW ZEALAND from the north, south, or west, while these islands are to the east in the case of the CHATHAMS, the chief island group. It shows that the same results as I obtained can be reached in other ways, but it does not give any evidence to show that my explanation is not correct, nor to show that dispersal depended upon adaptation. How did the NEW ZEALAND species get the adaptation to suit the CHATHAMS, unless they just acquired it upon the way across from NEW ZEALAND? This, and the general mechanical way of distribution, is what I am contending for, and the many ways in which similar results can be arrived at, such as by counting names in the telephone book, or hotels at different places in BRADSHAW, or the heaps of sand made by the holes in a sieve stretched in different degrees by a blow in the middle, the sizes of the stones in a heap of gravel, and so on and so on, that have been brought up in the endeavour to prove that my results are valueless or accidental, all go to show the same thing. The important point about the hollow curves is that every family shows the same curve when of more than just a few genera, and as that curve when expressed in logarithms is a close approach to a straight line, its origin is due to a growth of those families upon the formula

1 — 2 — 4 — 8 — 16 — 32 — 64 — and so on

a formula which is somewhat difficult to reconcile with any system of growth by the selection of chance variations of adaptational value.

Though the notion that an older species should occupy more space than a younger one seemed almost axiomatic, the publication of *Age and Area* in 1922 was met with great opposition, and the principle was not accepted. This was perhaps because it was a direct contradiction of the Darwinian theory of evolution by gradual structural adaptation. As this was applied to distribution, it implied that species might be divided into " successes ", which were expanding, or had expanded, their areas of dispersal, and " failures ", which were contracting, or had contracted, theirs. The well known curves showed the weakness of this supposition, for where, upon an evenly running curve with the " successes " at one end and the " failures " at the other, could one draw a line indicating which was which? But if we abandon this notion, we may take in its place the supposition that allied species, say in groups of ten to cancel irregularities, will react to outside influences in the same general way as other groups allied to the first. Incidentally, the notion of a multitude of failures, exceeding the successes, does little credit to nature's capacity for turning out good work, which in other sciences has been so well brought out in the last twenty years.

Size and Space. Any table in which genera of the same family are arranged in order by the (world) numbers of their species, as for example that upon p. 30, shows that the larger genera, taken in groups as usual, show larger dispersal areas than the smaller. On the whole, the larger the genus, the larger the area (law of size and space). While the first three *Anemoneae* are cosmopolitan, and the fourth in both hemispheres, the genera below them show decreasing areas, and the small ones at the foot are quite local. The *Helleboreae* show the same thing, but they *begin* at a lower level. This law appears to be of universal application, and is a great obstacle to supporters of dispersal by adaptation. Why should better adaptation need more species?

Comparing the first 25 British genera with more than 200 species in the world with the first 25 with less than 50, we find the average dispersal to be 97 to 65 vice-counties. In the larger ones there are 11 at 112, in the smaller 3. Of the 101 Dicots that reach 112,78 are at least North Palaeotemperate in dispersal, while 12 more cover most of Europe and western Asia, leaving only 11 for anything smaller. If in the British flora we average the number of vice-counties in which the most dispersed, the second most, &c species occur, in genera with different numbers of species, we get :

Distribution in Britain of genera of various sizes

Genera of	Average dispersal									
One species in Britain	62									
Two	80	36								
Three	95	60	27							
Four	92	63	37	15						
Five	102	80	47	23	13					
Six to ten	101	76	61	44	27	18	18	9	5	2
Over ten	108	97	88	81	74	67	53	48	37	&c to 1
	Monocots									
One	43									
Two	77	36								
Three	76	35	6							
Four	90	61	34	18						
Over four	111	105	92	75	60	49	&c			

It is clear that the dispersal of the first species of any British genus goes on the whole, in Dicots and Monocots alike, with the local size of the genus *in Britain*, which in turn goes largely with the size in the world. This agrees with the law of size and space, but cannot be fitted into any adaptational scheme. And the second, third, and other species show a similar rise in dispersal from small to large. At the same time the larger genera show their species closer together, with a much greater proportion of very small dispersal. In *Ranunculus*, for example, we have seen the dispersals of the species on p. 10; in *Hypericum* they are 111 106 102 101 91 80 77 63 | 48 5 5 4; in *Trifolium* 112 112 110 109 105 98 85 72 67 60 | 42 25 21 18 12 1 1 1 1; in *Salix* 111 110 107 105 104 103 95 93 62 62 | 38 35 35 35 22 18 12 11 10 8 4 3 3; while *Carex* has 32 above the mean and 42 below it, thus made up 53 52 48 45 44 40 38 34 32 32 25 24 20 19 19 17 16 15 15 14 12 12 11 7 6 6 4 3 3 3 3 2 2 1 1 1 1 1 1. How are all these tails of very local species in big genera to be explained upon the Darwinian supposition? The great bulk of the very local species occur, as we shall presently see with regard to endemics, in the largely represented genera, where there would be more arriving at the last minute, so to speak, and not in those with few species. This just reverses what one would expect under the theory of selection by adaptation, where small and local things are failures and relics.

The genera in the first half of the British flora that have species found in one vice-county only are *Fumaria*, *Arabis*, *Draba*, *Thlaspi*, *Viola*, *Dianthus*, *Arenaria*, *Sagina*, *Trifolium*, *Ornithopus*, *Rubus*, *Alchemilla*, *Sorbus*, *Cotoneaster*, *Saxifraga*, *Tillaea*, *Epilobium*, *Lonicera*, *Senecio*, *Carduus*, *Centaurea*, and *Hieracium*, a list with hardly a small or a local genus. Even without *Senecio* (2000 spp.) they average 186 in world size. It is the big genera that contain the bulk of the species of small dispersal. Of genera over four species, 92% show a species (or more) with dispersal less than 25, of genera with four 73%, genera with three 65%, and with two only 46%. The locally larger genera overlap the locally smaller at both ends—very wide and very local dispersal, a result that we should expect if dispersal be mechanical. The larger genera have their species closer together, as we saw in the table on p. 20, owing to the greater speed at which species spread as the genus gets older. If the big genera really owed their success to adaptation, one would have to explain why so few of their species succeed. The 42 *Carices* in the tail of that genus only average 16 vice-counties each; why are there so many below the mean of the " unsuccessful " genera? If species arrived in BRITAIN by reason of adaptation, rather than by the mere chance of relative age, and of nearness or the reverse, there would hardly be such numbers below 10. The most reasonable explanation of the great numbers of local species in the big genera is that they are the most recent arrivals in Britain.

The dispersal in Britain of the small species of *Rubus* and *Hieracium* sets a somewhat awkward problem before the supporter of the older views upon dispersal. Why, of 237 *Hieracia* below the mean, and 118 *Rubi* (just half as many) are there 41 to 1 in one vice-county only, while in two the numbers are 28/3, the *Rubi* continually gaining till at 19 they go ahead of the *Hieracia*. The latter stop at 39, except for one at 111, while between these figures there are 25 *Rubi*, and the average dispersal is 28 for a *Rubus* and only 7 for a *Hieracium*. These are distinctions too clear to be ignored, and suggest that some kind of evolution of small varieties is actually going on, more recently in *Hieracium* than in *Rubus*, and also perhaps that the same, or approximately the same, mutation may take place in more than one locality. How at present these phenomena are to be explained without calling in age, as (29) and others have done, is not easy to see. And why, too, are there so many different taxonomic divisions of these genera represented?

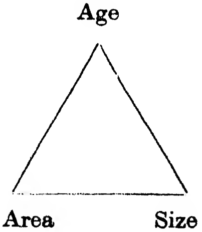
The larger the genus in Europe, and therefore, as a little investigation will show, usually the larger in Britain also, the smaller will be the gaps in time of arrival between its species. If from the last table we take these gaps, and arrange them in the same way, we get :

Gaps between times of arrival of species, as expressed by the number of vice-counties reached

	Dicots	Monocots
Genus of one species	Nil	Nil
two	44	41
three	35 33	41 29
four	29 26 22	29 27 16
five	22 33 24 10	Over, 17 13 6 4
6-10	25 15 17 17	
over	11 9 7 7	

a very fair indication that the prophecy was correct, showing the diminution of gaps from small genera to large.

The laws of ASA, or the Triangle of Distribution. Taking together the principles just discussed, it is clear that age goes with area, and so does size with space (area). It therefore follows that size goes with age. Age represents the resultant of all factors that are active, showing its results in size of genera, and the space that the genus occupies. Taking allied groups of ten to cancel out irregularities, the results will be very similar, and may be expressed in a triangle. An old genus will have many species, and occupy much space; a genus with many species will be old, and cover much area; a genus occupying much space will be old and have many species. To save space, we shall in future call these the laws of ASA.



The basis, then, upon which our subject will be dealt with, is largely that indicated in the two preceding books, *Age and Area*, and *Evol.*, and we hope to show that by the application of the inductive method promising results may be obtained, which give hopes that the vast, and at present confused and unorganised mass of facts that makes up geographical distribution proper, as distinguished from its offshoot ecology, may be gradually reduced to something like order.

If these arithmetical rules hold generally, it should be possible to make successful predictions about the dispersal of the plants of a country, testing them afterwards upon the facts. It may be worth while to give another instance or two. For example, it is clear that if dispersal is thus mechanical, there should probably be a good many species in the British flora that have reached 112, and " have no more worlds to conquer ", whereas if BRITAIN had been large enough, they would have reached various figures beyond 112. In other words, there should be an accumulation of old species at 112, and perhaps another at 111 of species that for example reached the ORKNEYS, but were too late for the SHETLANDS. The figures show as follows, but one must not suppose that the whole flora of the SHETLANDS, for example, shows dispersal of 112, for many are missing in one or more vice-counties further south, thus showing only a dispersal of 111 or less.

Distribution of most widely dispersed species in Britain, showing accumulations at the top

Vice-counties reached	Dicots	Monocots	
112	101	29	(18 grasses)[3]
111[1]	23	15	8
110[2]	13	10	3
109	15	5	—
108	11	4	2
107	14	1	1
106	6	4	1
105	13	2	2
	Total 196	70	(35 grasses)

After the first two, or three in the Monocots, the numbers begin to vary up and down in the irregular way that one would expect, but there is a very definite accumulation at 112, and a smaller, but noticeable one, at 111. The Monocots also seem to show a tendency to accumulate at 110, as if many of their older species had not even been in time to reach some far outlying islands of BRITAIN. The excess of Dicots at 112 is greater than that of the Monocots. Half the Monocots at 105 or more are grasses, and even more at 111 and 112. A large proportion of the dominant and abundant species in the various plant associations also come into these figures, so that the species concerned must evidently appear in many associations.

One may see this accumulation of species at the top of a column elsewhere and often. Thus in the HAWAIIAN IS. (62)

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[1] SHETLANDS, or sometimes outer HEBRIDES, the most usual omission.

[2] ORKNEYS also, most usual omission.

[3] And 4 *Carex*, 3 *Juncus*, and one each of *Iris*, *Potamogeton*, *Scilla*, and *Sparganium*, a list which gives an idea of the kind of country open to colonisation by the earliest Monocotyledons.

41 of the 581 local or endemic species occur on all the islands and there is a smart fall to the 8 that only occur on six islands, from which the numbers go steadily up, being 11 on five, 55 on four, 80 on three, 113 on two, and 273, or 47% of all, on one island only. Evidently the oldest endemics of all accumulated at the top, having nowhere further to go. Incidentally this seems to indicate that the group of islands was cut off very early.

It is evident that the figures of local distribution in Britain, put together with such painstaking labour by Watson and his successors, bid fair to prove of great value and importance in further study of dispersal.

Supposing that we take the sizes *in Britain* of those families that contain any species that reach 112, and place them in order, with the larger numbers rounded to the nearest five, we get, for Dicots only :

125 80 75 70 70 60 55 55 45 30 30 25 20 20 20 15 15 15 10
10 5 5 5 5 4 3 1 1 Total 874 spp.

Average 31 per fam., while the families with no 112s, but reaching 105-111, show

20 20 20 20 12 12 10 6 3 3 2 1 1 Total 130.

Average 10 (Small varieties of *Rubus* and *Hieracium* omitted).

If one note for each genus of the British flora the highest dispersal shown by any of its species, one gets a list of the figures at which each genus comes in. Of the 71 genera of Dicots that reach 112, 46, or 64.8%, belong to the *Compositae* (with 14), *Caryophyllaceae* and *Labiatae* (6 each), *Leguminosae* (5), *Cruciferae*, *Rosaceae*, and *Scrophulariaceae* (4 each) and *Umbelliferae* (3), a list of very large families which we shall find appearing again below in quite other connections (pp. 69—71 for instance).

By the rule of age and area, the most widely dispersed genera in Britain should be the oldest, which again, by the rule of age and size will be the largest, whether in Britain or even in the world. The genera with species reaching 112 are on the whole the largest in Britain, and show an average size (*Dict.* figures) of 160 species in the world. Those reaching 101-11 average 119, those reaching 91-100 average 71. The next lot, 61-90, is brought up by the presence of three enormous genera, *Aster*, *Astragalus*, and *Salvia*, to 85, but the genera from 31-60 only show 56, and those from 1-30 36 in the world. Clearly dispersal is largely dependent upon size in the *world*, a fact which puts " adaptation " very much out of court.

As the present British flora probably entered chiefly at the south-east, one will expect to find, in such an association as that of chalk-pasture, which is there very common, that it is very numerous, and that its most prominent species have a very wide dispersal. A glance at (122), p. 176, will show that the number of species (146 of them) is very large, and so is the dispersal in Britain. The 91 dominant, abundant, and frequent species average 93 vice-counties, the 17 locally dominant &c average 67, both high figures. No fewer than 36 out of the 91 show a dispersal of 112 (shown by only 130 species in all).

A remarkable example of how greatly the species in any given community are determined by their range and commonness within Britain is furnished by the arctic-alpine grassland above 2000 ft. (600 m.) (122, p. 300). To have been able to reach that height in the far north, these 48 plants (list B, not including A) must evidently be very old in Britain, so that one will expect them to be widely dispersed there.

Dispersal of flora of arctic-alpine grassland in Britain

Distribution	Dicots	Monocots
112 v. c.	20 [1]	6 (5 grasses and a Carex)
102-11	9	10 (2 grasses, 4 Carices, one each of Orchis, Juncus, Luzula and Scirpus)
and Antennaria dioica (89) Viola lutea amoena (21)		and Avena pratensis (76)

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[1] *Ranunculus* (6 British spp. at 112), *Cerastium* (2), *Sagina*, *Linum*, *Oxalis*, *Trifolium* (2), *Lotus*, *Potentilla* (2), *Heracleum*, *Scabiosa*, *Bellis*, *Achillea* (2), *Taraxacum*, *Leontodon*, *Veronica* (5), *Euphrasia*, *Thymus*, *Plantago* (2), and two spp. of *Rumex* (4). Thus no less than 36 (out of a Dicot total of 101) show 112, so must be among the oldest of the old in Britain.

List A of the same habitat, the "Highland" species, on the other hand, only shows dispersals of 29,112 (*Festuca ovina*), 22, 40, 20, 20, 8, 20, 14, 20, 20, the usual figures for the dispersal of Highland species, which have not recently climbed from below.

The average dispersal of the 48 species in list B is 107, or very high indeed. The composition of the list of Monocots is worth study.

We may get a rough idea of the variation of conditions under which the members of the various communities grow, by taking the space devoted to them in the Index of (122). Taking only the genera in A and B, those mentioned once only in the index have an average dispersal of 67, twice of 83, 3-6 times of 84, 7-10 times of 95, and more than that of 101.

Outlying genera the largest. As BRITAIN lies at the edge of what has long been the ATLANTIC coast of EUROPE, with deep water beyond, one may make another important prediction about its flora. By the theory of evolution that we have set out, the oldest genera of a family will start at or towards its centre (the oldest of all of course at the very centre), and thus will on the whole be the first to reach the outer boundaries of the present distribution of the family, though at times, as we have suggested, the first genus may be overpassed by some younger one better suited to the conditions in that direction. In other words the most outlying genera of a family will tend to be its oldest or largest in the world. Of the 100 families in BRITAIN, it is therefore of considerable interest to find that this is the case in nearly three quarters. No less than 71 families are headed each by its largest genus in the world, while 10 more are headed by the second or third. This, as we shall see, is not an isolated phenomenon, but is universal.

The supposed operation of adaptation. If the adaptation theory worked as it is supposed to do, it is evident that a slight difference like that between two allied varieties would be ample to ensure that evolution should go on. Why then should one find generic differences at all, and still less why larger ones? Yet these large differences are obviously a part of nature's scheme in evolution. As upon the Darwinian supposition they must have some adaptational value, it is supposed that there must still be competition to widen the gaps between species until they become generic. But as differences become greater and more distinct the higher one goes, this would imply that the competition also increased, whereas it is in reality the other way. There may be great competition between two bootblacks, especially if their stands be near together, but not between a cabinet minister and a stationmaster, nor between a bootblack in LONDON and one in BRISTOL. Natural selection is primarily an individual phenomenon; A may win here, B there, but *all As do not defeat all Bs,* though there has in recent years been a recrudescence of this fallacy. There are no super-species. Had insect organisation been carried further, man would have had little chance, and as it is, a vast amount of skill and labour has to be expended in warring with them. Cotton, to take only one instance, is a vast industry in AMERICA, yet in different years from 10 to 25% of all the labour expended upon it goes to feed boll-weevil and other troublesome insects. Taking the world as a whole, we have estimated that labour equal to that of 30 millions of men is occupied in feeding noxious insects. It is well to remember such things when we pride ourselves too much upon our civilisation.

It is hard to conceive of competition between two species of buttercup *as a whole,* though it may be fierce between one individual of A and one of B. One is compelled to realise that distribution is individual, taking little or no account of the structural characters of the competitors, so long as they are not very unlike. Ecological distribution shows the same thing. What is there in the structure of any of them, that should make *Lythrum Salicaria*, *Epilobium hirsutum*, *Sonchus palustris*, *Lysimachia vulgaris*, and *Typha angustifolia* become members of a reed-swamp association (122, p. 191) There is nothing in their structure to show what kind of habitat they affect, and they show great structural variety, even to the distinction of Dicot and Monocot. No evidence can be brought to show that distribution is seriously affected by structural differences. When one looks into the simple facts of distribution, they are soon found to clash hopelessly with the Darwinian explanation based upon adaptation. There is no reason whatever to suppose that species of plants fight as units.

The tribes of Ranunculaceae. As we cannot describe the whole family of *Ranunculaceae* as being numerous, widespread, and successful in BRITAIN, let us go a step lower to the tribes, taking them from the *London Catalogue* 11th ed. for the figures. *Anemoneae*, which include *Ranunculus*, have 35 species, occupying in all 2135 vice-counties, against 8 *Helleboreae* in 330, an average of 61 against 41.1; both differences are too great to be accidental. If we call the *Anemoneae* the more successful, we must explain why some of them are rarer than any *Helleboreae*, though the *top* four are much superior to the uppermost *Helleboreae* in dispersal. But this fact, which by age and area implies that in this family the achene (the mark of *Anemoneae*) is older than the follicle (that of *Helleboreae*), flatly contradicts the current view, that the follicle is the older form. It would be very difficult to change an achene into a follicle by gradual changes, while a change in the other direction is possible; but to mutation, which we are here upholding, either way seems equally possible. It is clear that all the achene-bearers are not superior to all the follicle-bearers, and so far as I know, it is not possible to find a group, all whose members are superior to any of those of a related group. The simplest way to explain these contradictions is to adopt a supposition like age and area, for which abundant evidence has been adduced. It simply says that the lower genera in each list are on the whole younger than the upper, and therefore have smaller numbers and less dispersal. And one may ignore in this respect the structural differences between them, to which one cannot attach any adaptational value. But this of course is the negation of Darwinism. (*Cf.* also Testcase XV, Achenes and Follicles, in *Evol.*, p. 124).

We shall now give two tables of the genera in these great tribes, arranged in order of size, with their distribution, following it later with the hollow curves produced by plotting the numbers graphically.

Ranunculaceae; distribution and sizes of genera, Anemoneae

Size			
300	Ranunculus	Br.	Cosmopolitan
220	Clematis	Br.	Cosmopolitan
130	Anemone	Br.	Cosmopolitan
75	Thalictrum	Br.	N. Temp., Natal
18	Viorna (Clematis p. p.)		N. Am.
10	Adonis	Fr.	N. palaeotemp.
10	Oxygraphis		N. As., N. Am.
10	Clematopsis (Clematis p. p.)		Madag., trop. Afr.
7	Myosurus	Br.	N. and S. temp.
7	Naravelia (Clematis p. p.)		Indo-malaya
7	Rhopalopodium (Ranunculus p.p.)		W. S. Am.
6	Knowltonia (Anemone p. p.)		South Africa
6	Trautvetteria		Japan, N. Am.
4	Barneoudia (Anemone p. p.)		Chile, Argentina
4	Hamadryas		Antarctic Am.
3	Halerpestes (Ranunculus p. p.)		N. Am.
3	Leucocoma (Thalictrum p. p.)		N. Am.
2	Anemonanthea (Anemone p. p.)		N. temp.
2	Capethia		W. S. Am.
1	Aiolon (Anemone p. p.)		N. Am.
1	Arcteranthis (Oxygraphis p. p.)		N. Am.
1	Aspidophyllum		Peru
1	Beckwithia (Ranunculus p. p.)		California
1	Gampsoceras (Ranunculus p. p.)		Asia Minor
1	Kingdonia		W. China
1	Kumlienia (Oxygraphis p. p.)		N.W. Am.
1	Laccopetalum (Anemone p. p.)		Peru
1	Paroxygraphis		Sikkim
1	Piuttia (Thalictrum p. p.)		Himalaya
1	Stipularia (Thalictrum p. p.)		Himalaya
1	Sumnera (Thalictrum p. p.)		N. Am.
1	Syndesmon (Anemone p. p.)		E. N. Am.
1	Viticella (Clematis p. p.)		Europe

33 genera, 838 spp. Average 25.

Genera reaching Britain are marked Br., reaching France only, Fr. All British genera are found in France also.

Distribution and sizes of genera, Helleboreae

Size			
175	Delphinium	Fr.	N. temp.
110	Aconitum	Br.	N. temp.
75	Aquilegia	Br.	N. temp.
20	Caltha	Br.	N. and S. temp.
20	Isopyrum	Fr.	N. temp.
16	Nigella	Fr.	Medit., Eur.
15	Actaea	Br.	N. temp.
15	Helleborus	Br.	Medit., Eur.
12	Cimicifuga (Actaea p. p.)		N. temp.
12	Trollius	Br.	N. temp.
10	Coptis		N. temp., arctic
10	Consolida (Delphinium p. p.)		E. Medit.
7	Eranthis	Fr.	Medit., As.
5	Callianthemum		Mts. Eur., C. As.
5	Enemion (Isopyrum p. p.)		E. As., N. Am.
4	Paraquilegia		S. C. As.
2	Asteropyrum (Isopyrum p. p.)		China
1	Anemonopsis		Japan
1	Bodiniera		China
1	Calathodes (Trollius p. p.)		Himalaya
1	Chrysocoptis (Coptis p. p.)		N.W. Am.
1	Komaroffia (Nigella p. p.)		Turkestan
1	Leptopyrum (Isopyrum p. p.)		C. As.
1	Paropyrum (Isopyrum p. p.)		Turkestan, N.W. Himalaya
1	Semiaquilegia (Isopyrum p. p.)		Japan
1	Souliea		China
1	Urophysum (Isopyrum p. p.)		Szechyan (China)
1	Xanthorrhiza		Atl. N. Am.

28 genera, 524 spp. Average 18.7

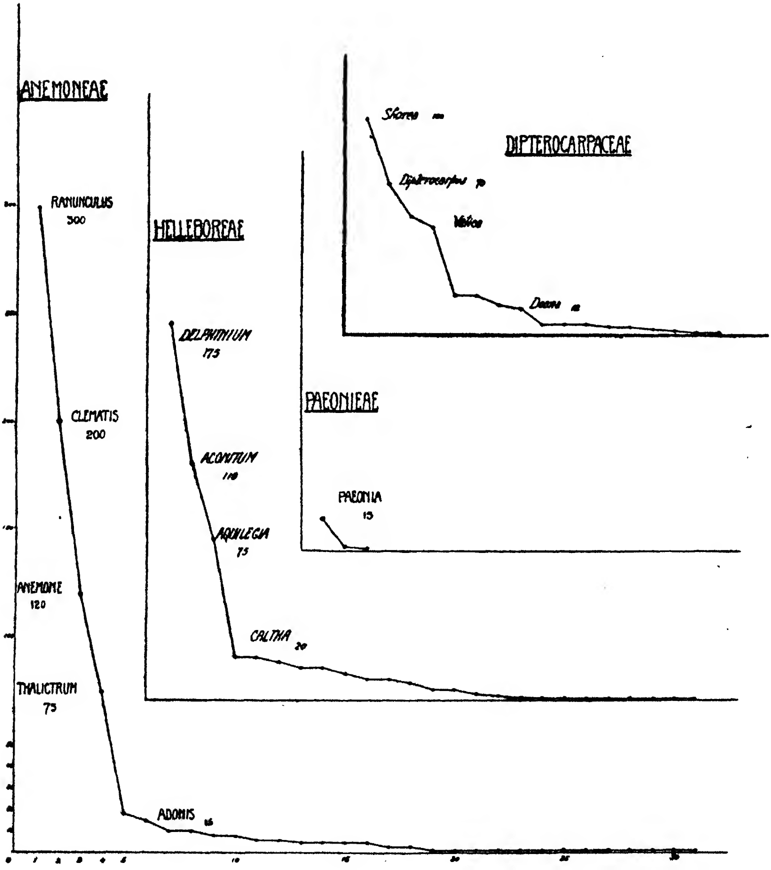
This table is of interest in various ways. One observes at once the extraordinary parallelism of the two sub-families, both in sizes of genera and in areas of distribution. Each list, as we shall see, gives a hollow curve. More than half the total have three species or less in one list, five or less in the other. The larger the number of possible parents, the larger tends to be the number of ones and twos, for these small genera are slow in getting established and in increasing their numbers.

The genera are from my *Dictionary*, with such revision as has been done up to date. Many people do not accept them all as genera, but each represents a group which has been regarded as a somewhat separate group of species, and that is all that really matters in this connection, for we have no definition, but only a description, of a genus. Each lot are probably the descendants of a mutation which we usually describe as somewhat larger than usual. The lists are admittedly not quite up to date, but as COCKAYNE said years ago, in a letter to the writer, "all recent systematic work simply makes age and area stand out more clearly", inasmuch as almost all recent additions to the list are at or near the bottom, thus making the hollow curve more evident. For example, the new genera of *Acanthaceae* in two recent supplements to the *Index Kewensis* are 14/1 and 3/2. Most of the new and small genera are formed by splitting off from the older, so that they are in general satellites, not relics.

Each surviving species started with adaptation to its surrounding conditions, or it could not have survived. It must at the same time have had some range of adaptability, to resist the continual changes in conditions from day to day. Its further distribution would then depend upon how far this adaptation and adaptability would carry it, and how long a time had been available in which to spread. To these must of course be added the great retarding influences of barriers of every kind, as described in *Age and Area*, chaps. II-V.

The exceptions in the table are easily understood with a little thought. *Delphinium*, for example, is much larger than *Caltha*, which reaches both hemispheres, but probably arose a long way from any easy connection to the south, and was perhaps a very slow traveller, or had unusually small adaptability. It is to cancel out irregularities of this kind that even allies must be taken in groups.

HOLLOW CURVES SHOWN BY SUB-FAMILIES OF RANUNCULACEAE
AND BY FAMILY OF DIPTEROCARPACEAE



Let us now turn these two lists into graphic curves in the usual way, by the numbers of species in the genera, and add to the two British sub-families the third, *Paeonieae*, composed of *Paeonia* with 15 in EUROPE, ASIA, and NW AMERICA, and *Glaucidium* with 2 in CHINA and JAPAN. We have shown in *Evol.*, p. 84, that they cannot be regarded as equal in rank to the other two sub-families. The mutation that split off *Paeonieae* was a " larger " one than usual, combining two characters, fleshy ovary wall and loss of honey leaves, which may at times be seen singly in other *Helleboreae*, so that *Paeonieae* presumably came from this group, rather than from *Anemoneae*, as is suggested by the key on p. 85 in *Evol.* This again at once suggests what will be considered later, that a family may possess what one may term a set of characters for kaleidoscopic use.

Size and space shows best in the vertical, age and area in the horizontal direction, in these curves. The smaller and the least dispersed genera are at the bottom right hand end of the curve, the larger and the most dispersed at the top left hand end. Darwinism, as we have been pointing out for many years, is quite helpless to explain these curves, which show, as do many other facts that we have brought up, that if dispersal depends upon adaptation, that adaptation must be generic. But if so, why does the genus need so many species to cover the greater variety of conditions into which greater dispersal takes it?

To show how the hollow curve is formed, let us just consider the possible future growth of the *Paeonieae*. If a new genus form by splitting off from either of the other two, it will necessarily be a " one ", and as 15 + 1 is more than twice 2 (the size of *Glaucidium*), the curve will at once be a hollow one. As each new genus begins as a one, and its early stages will be very slow, there will be an increasing number of ones at the bottom of the curve, while at the top, as the genera grow larger, and thus increase the number of their species in an expanding ratio (on account of the increase in the number of potential parent species), the positions of the genera on the curve will become continually further and further apart, thus lengthening the curve at that end also. (Cf. Testcases III and IV *Evol.*, p. 95, especially the reference to gaps between genera on p. 97.)

Most of the genera split off in the tables, and given as

X, p. p., are from large ones, like *Clematis*, *Anemone*, or *Delphinium*. In the *Anemoneae*, the larger and older group, there are 18 such, and the average size of the parents (*now*) is 145; in the younger group these figures become 8 and 47. The parents in the older group have grown more than those in the younger, of course, on the whole. But this splitting of new genera from older ones by mutations that are larger than usual is exactly the process of evolution that the writer has proposed in his book *The Course of Evolution*, 1940, and is a process that can not be reconciled with the theory of selection upon adaptational (and structural) improvement. It surrounds each genus of importance, which represents some mutation of long ago, with a group of smaller satellites, the result of more recent mutations. As the group thus formed increases in number and size, it goes through the stages of more and more definite recognition. The Supplements to the *Index Kewensis* show clearly how continually new and small genera, usually ones, are being split off from the larger genera. The relic explanation is thus continually being made to look more and more improbable.

All over the northern hemisphere, *Anemoneae* and *Helleboreae* occur together, the former (the larger and older group) always on the whole the best represented. There is little evidence for any dying out of genera or species, *once they have covered an area sufficiently large* for it to be very unlikely that the whole genus or species should be killed out by some geological or other catastrophe. Up to the present time, the evidence of fossils has been interpreted in a way suitable to the current theory of the course of evolution, and they have been looked upon mainly as ancestors, or ancestral relatives, of things now existing. But age and area makes clear that things with small areas of dispersal are in general young themselves, while any descendants to which they have given rise will be younger still, and will occupy smaller areas, usually well within the range of the first. It follows, therefore, that it is entirely unsafe to regard a fossil with small area as being the ancestor of any now existing form—if the small area is all that it has ever occupied, then its descendants, if any, will also be extinct. As most fossils of flowering plants, with which alone we are at present concerned, are known only from comparatively small areas, this discounts very much any evidence to be derived from them as to ancestry. They are far more probably sidelines of evolution that have died out completely, not from any lack of adaptation, but on account of some misfortune that has overtaken them.

The migration to and fro that has marked the floras nearer to the poles, probably more than those in the tropics, seems often to have resulted in the extinction of small genera that could not get away quickly enough, while in the case of large genera only species would be destroyed. Water plants, with fewer species and larger ranges, would be less likely to suffer in this way. These extinct genera may then be found as fossils, but cannot be regarded as ancestral to anything now living, for their descendants, if any, would occupy lesser areas than themselves, and would be destroyed also. Thus the larger genera might go on as before with reduced numbers, while small and local ones might disappear altogether; the larger ones would increase again, and produce a new crop of small descendants.

In this connection it is of interest to read the account of the Pliocene flora of BRITAIN by Mrs REID (105-6). Of the 37 families mentioned, 28 are headed, as regards world size, by the following genera: *Acer*, *Atriplex*, *Betula*, *Carex*, *Ceratophyllum*, *Cornus*, *Elatine*, *Euphorbia*, *Galium*, *Hippuris*, *Hypericum*, *Myriophyllum*, *Naias*, *Nymphaea*, *Polygonum*, *Potamogeton*, *Potentilla*, *Quercus*, *Ranunculus*, *Rhamnus*, *Sagittaria*, *Salix*, *Solanum*, *Sparganium*, *Ulmus*, *Urtica*, *Valeriana*, *Viola*, all of them heading the families at the present day, and the largest (or largest available so far north) genera in them. The other nine, with the genera that now replace them, are: —

Old heads	*Present dispersal*	*New Heads*	*Present dispersal*
Centaurea	one at 112,11 others	Senecio	two 112,9 other
Circaea	106	Epilobium	one 112,11 oth.
Corema	only reaches Spain	Empetrum	73
Heracleum	112	Eryngium	55,9
Hypecoum	only to S. France	Corydalis	94
Menyanthes	110	Gentiana	97
Stachys	two 112,4 others	Salvia	64,6, one Channel Is.
Stellaria	112, 111, 111, 109, &c	Silene	104, 80, 60, 53, &c
Veronica	five 112, many othr.	Pedicularis	two 112 only

None of the second column appear at all in Mrs REID's list, though all of them are the numerical heads of their families, now found in BRITAIN, where most of them have evidently been later arrivals, as shown by their smaller distribution, than those in the first column. They appear to have been passed on the way from the south by younger genera, thus affording full support to the views that I have here brought forward, that such things can and do happen. In the cases of *Corema* and *Hypecoum*, the old genus has not again come so far north as BRITAIN, a fact which may mean slow dispersal, or slow adaptation to the colder climate, or which might mean that the climate was not so warm as formerly.

In considering such a list as this, with its 87 genera, none with more than a few species (largest *Carex* 8, *Ranunculus* 6, *Rumex* 5), one must not forget that coming from one locality, it probably does not represent more than a few, or even one, of the associations of plants that grew in the country at the time. Suppose that at some future date a deposit of the association now growing upon chalk grassland (122, p. 176) is unearthed. It is so large an association that one would be apt to think that one had made a good " haul ", yet it would in reality be less than 10% of the flora of the country, and one would not find the following families at all :

Berb., *Nymph.*, *Papav.*, *Crucif.*, *Franken.*, *Portul.*, *Elat.*, *Hyper.*, *Malv.*, *Tili.*, *Geran.*, *Aquif.*, *Celast.*, *Rham.*, *Acer.*, *Saxi.*, *Dros.*, *Hippur.*, *Halor.*, *Callit.*, *Lyth.*, *Onagr.*. *Cucurb.*, *Aral.*, *Corn.*, *Caprif.*, *Valer.*, *Eric.*, *Pyrol.*, *Plumb.*, *Ol.*, *Apoc.*, *Polem.*, *Conv.*, *Solan.*, *Lentib.*, *Verb.*, *Chenop.*, *Polygon.*, *Arist.*, *Thymel.*, *Elaeag.*, *Loranth.*, *Euph.*, *Ulm.*, *Mor.*, *Urtic.*, *Myric.*, *Bet.*, *Fag.*, *Salic.*, *Empetr.*, *Ceratoph.*, nor *Amaryll.*, *Diosc.*, *Lili.*, *Typh.*, *Sparg.*, *Ar.*, *Lemn.*, *Alism.*, *Butom.*, *Scheuch.*, *Potamog.*, *Erioc.*, or 65 families in all out of the 99 of the British flora. And not only would one not find these families, nor anything to head them, but one would not find such genera as *Potentilla*, *Eryngium*, *Pedicularis*, *Gladiolus*, *Juncus*, or *Panicum*, genera actually heading families in BRITAIN. This point has been somewhat neglected in regard to fossils.

Ranunculaceae are " the most primitive type of herbaceous Dicotyledons " (68, p. 94), and *Ranunculus* itself is usually looked upon as very primitive, yet it is cosmopolitan in its dispersal and has more species than any other of the family, being only passed by about 60 genera in the flora of the world. How did it come to reach almost all of such outlying islands as CEYLON, NEW ZEALAND, and the HAWAIIANS, in which last it is the only genus of the family? How did it go so far north, and to such heights in the mountains? If so old, why has it not been killed out by some more recent and better "adapted" type? Wide dispersal is usually put down to "the possession of some advantage that enables it to spread", but no one has ever been able to suggest such, especially as it must evidently be generic. Even the supporters of selection are compelled to call in age, as DARWIN did (**29**, pp. 358-9), though they reject age and area, which is a direct contradiction of "Darwinism". They also try to have a foot in either camp by explaining small genera as relics (failures) or as local adaptations (successes), thus showing our lack of real knowledge and understanding.

The explanation of the distribution of the *Ranunculaceae*, and if so, of other families also, to and in BRITAIN, where the flora is so recent that there has not been enough time for the formation of many endemic forms (that is, forms so recent that they have had neither time nor opportunity to get beyond the frontier), thus rests very largely upon the mechanical explanations that we have indicated. In any given small area of a country, at any given time, the local distribution is largely determined by the local conditions that there exist, working upon the actual flora that has so far arrived in the country and within reasonable distance of the area concerned. Gradually, in the course of time, natural selection picks out from this those species whose inherited or inborn adaptation and adaptability make them most suitable to whatever conditions may there be found. Supposing that a species arrived at the British frontier with some special adaptation to something that did not occur in BRITAIN, *e.g.* such a metal as selenium, it would be stopped at the frontier, and would get no further unless it developed a form suited to growth without selenium; but if it were adapted to chalk, it would probably commence life upon chalkpasture very soon, and whether it remained there so as to form a member of the chalkpasture association, when that became filled up, would depend upon its degree of adaptation to chalk, as modified by its capacities in the way of adaptability.

It thus comes about that an area A gradually becomes occupied by a community *a*, and an area B by *b*, which will slowly take in new members till the association becomes " closed ", just as the human communities with which BRAZIL was first colonised, not a miscellaneous crowd, as in most British colonies, but made up of a definite proportion of agriculturists, mechanics, and so on, might be so described. Both, with changing conditions, are obviously liable to alter in their composition. One might, in western European spots, match the conditions very closely in which certain associations grow in BRITAIN, but as there would be more plants available in the flora, it is improbable that the association would be made up of just the same species. To reach this closed condition, it is clear that much time must be allowed (age and area), and as it is therefore the large genera (age and size) that have spread the furthest (size and space), it is they that will have been able to occupy the most places in the associations which they first joined. As time goes on, their adaptability will enable them to join other associations, and thus still further to extend their numbers and dispersal (" to him that hath shall be given "), whereas newcomers will be likely to be found entirely, or nearly so, in communities like the one in which they first arrived.

Monocots—Gramineae. Let us now take a large and well represented Monocot family, the *Gramineae.* It has in BRITAIN proper 45 genera with 131 species. Of these 18 species in 16 genera reach the maximum possible dispersal of 112, and another 5 genera, besides some species of the 16, show a dispersal of 111, so that nearly half the genera are very widely dispersed, an advance upon the *Ranunculaceae*, probably due to the rather cold and wet conditions that first prevailed after the disappearance of the ice. On the other hand, there are a number of late arrivals, like *Panicum*, the largest genus in the family, which reaches only 6 vice-counties in the south of ENGLAND, *Leersia* (4 only), *Mibora* (3), and one genus *Lagurus*, which only reaches the CHANNEL Is., and cannot strictly be considered British.

As in all large British families, a striking thing is the great proportion of the subgroups that are represented. This is a necessary consequence of the simple fact that, as we have shown in *Evol.* (Testcases III, IX, XIV, XX, &c),

the larger (older) genera tend to be divided by larger divergences than do the smaller (younger), and it is they therefore that give the characters to the subgroups; and as they tend to appear in any country more or less in order of size, many subgroups will appear in the flora. Adaptation has little or nothing to do with it, and it cannot be explained by the help of that supposition. The sooner that we get rid of the notion of an adaptational reason for every small individual step in the differentiation of families, genera, and species, the better.

There are in Britain no less than eight of the thirteen subgroups of the grasses, and it is worth while to look at a table of them :

Representation in Britain of the sub-groups of Gramineae

Group	World size about	Gen.spp. in Britain	Dispersal, in order of world size of the most widely dispersed sp. in each genus
Festuceae	120 gen.	15/67	112 112 112? 112 99 111 112 11 100 112 112 104 112 97 111. Average 102.
Agrostideae	60	10/27	71 112 112 111 7 93 65 19 25 3. Average 61.
Aveneae	40	7/14	98 98 112 111 112 112 6. Average 92.
Hordeae	30	6/14	112 46 80 112 53 108. Average 85.
Paniceae	70	1/1	6. Average 6.
Chlorideae	50	2/4	11 3. Average 7.
Phalarideae	7	3/3	111 112 3. Average 75.
Oryzeae	7	1/1	4. Average 4.
Andropogoneae	70	—	
Bambuseae	40	—	
Zoysieae	20	—	
Tristegineae	10	—	
Maydeae	6	—	

Such a table gives food for thought. The four top groups, which are essentially grasses of cool and even cold climates, are represented in Britain in order of their size, and they also show more species per genus in the larger (older) groups by reason mainly of the longer time that has been available for arrivals. It is fairly evident that the *Festuceae* is much the most important group, though the grasses, to judge by *Panicum* and the *Paniceae*, seem to have begun in warm climates. The leading genera of *Festuceae*, *Poa* (200+), *Eragrostis*, *Festuca*, and *Bromus*, are definitely grasses of the colder climates, though being old, they have had time also to reach the tropics, where however, they are not at home except in the hills. Much the same may be said about *Agrostideae*, though it seems to have been a good deal later in BRITAIN, and its leading genus, *Calamagrostis*, is probably younger than *Poa*. *Hordeae* is headed by *Danthonia*, which is largely southern (S. AFR. &c), and is headed in EUROPE by *Avena*, its second genus, which occurs in BRITAIN with five others. Except for the marked drop in dispersal in *Agrostideae*, which much needs explanation, each group shows smaller representation and dispersal than the one before it, so that if dispersal is to be explained by adaptation, some adaptational reason, which must be generic, is needed to explain the frequent small dispersal. Age is by far the simplest explanation of all the figures that we are bringing up.

Looking at the other nine subgroups, the first four of them in the list have a small representation in BRITAIN. *Paniceae* is a marked group of tropical and subtropical climates, only spreading much beyond in AMERICA. Its leading genus, the head of all the grasses, *Panicum* with over 500 species, has just been old enough to reach a few districts in the south of ENGLAND, and has not produced in the old world a genus more suited to the cold. *Chlorideae*, headed by *Chloris* with 60 species in warm climates, is represented in BRITAIN by *Spartina* (11 vice-counties) and *Cynodon* (3), both coast plants. *Oryzeae* is a very small group, headed by *Oryza* (rice) with 7 tropical species, but the genus that reaches BRITAIN, *Leersia* (4 vice-counties) was apparently born further north. Finally *Phalarideae* is represented by *Hierochloe* (20 spp., 1 in BRIT., 3 v. c.), *Anthoxanthum* (15 spp., 1 BRIT., 112 v. c.), and *Phalaris* (10,1 in BRIT., 111 v. c.). It is difficult to associate this group of northern genera with *Ehrharta* (30 mainly S. AFR.) as a parent, and it is by no means impossible that they arose from a separate but parallel mutation, for we have no evidence of any destruction of the transitional forms which would be needed under the Darwinian conceptions.

We may end with a comparison of Dicots and Monocots in Britain by genera :

Distribution of Dicots and Monocots in Britain compared

Vice-counties	Dicots		Monocots		Grasses only	
91-112	177 or	52%	49 or	40%	29 or	64%
61-90	71	20%	17	14%	3	7%
31-60	42	12%	16	13%	2	5%
1-30	53	15%	41	33%	11	24%

Thus 72% of the Dicots reach 61 or more, while only 54% of Monocots do so, or, if one omit the grasses, only 44% of the reduced total. On the whole, therefore, we may imagine some Monocots to have been late in arrival.

Of the 29 Monocots that reach 112, 18 are *Grasses*, 4 *Carices*, 3 *Juncus*, leaving only one each of *Iris*, *Potamogeton*, *Scilla*, and *Sparganium*, an assortment that perhaps suggests the type of country first available after the ice. Another fact that goes to show that the genera with the 112s are ancient is that among them the Dicots alone have 290 endemic or local species in Spain, and 512 in the Balkans. Of the whole 130 British species reaching 112, 18 are *Compositae*, 18 *Gramineae*, 9 *Scrophulariaceae*, 8 *Caryophyllaceae*, and 7 each *Labiatae*, *Leguminosae*, *Ranunculaceae*, large families, which we shall meet again in various other connections.

The difficulties that the study of distribution brings up for any explanation based upon adaptation are legion, and so long as that hypothesis holds the ground, there can be little but profitless speculation, as Hooker long ago pointed out. As a species appears to be born at one place and time by a single mutation, its adaptation must evidently be born with it, or it could not survive. Evolution is an independent process, and appears to go on without reference to natural selection, and distribution follows it, as we have seen and shall see, in a largely mechanical way, for which arithmetical rules may be found when one is dealing with large areas and with long periods. In individual cases, on the other hand, ecology comes in to settle, by natural selection, the exact spots where anything shall succeed and reproduce, while the adaptability with which it must also have been born settles whither and how far it shall travel in the time available.

This sketch must suffice for the present in regard to the British flora and its distribution. It affords ample material for a book, and we have tried to indicate some directions in which it is not impossible that useful work may be done. Geographical distribution ought not to remain in the Cinderella-like position that it has so long occupied. It is as open to inductive reasoning as any other branch of botany, offering a large field for possible labour, as yet little trodden.

CHAPTER II

Some continental and other floras

Leaving BRITAIN to east or south, one soon comes upon unfamiliar plants, at first almost always of British genera, and as most British species go beyond the boundaries of EUROPE, the genera become better and better represented as more new species appear. *Centaurea* is the most striking, with 12 species in BRITAIN, 22 in FRANCE, 87 in SPAIN, and 171 in the BALKANS. Of the Spanish species, 49 are local to SPAIN, or *endemic* there, and 112 are endemic in the BALKANS. This fact, which on a smaller scale and with a less steep rise is shown by all important British genera, offers an insoluble problem to the supporters of selection, or of distribution by adaptation only. As it is the large genera that show it, this adaptation must be generic. Why, too, are there over 1200 endemics in the BALKANS, and another 1200 in SPAIN, with practically none north of the ALPS? Endemics used to be regarded, and still are, as the relics of things that were once more widespread and are now dying out, defeated in the struggle for existence by plants better adapted to conditions. So numerous, however, are they in most large genera, like *Centaurea* above, that when they finally die out, the genera will become quite small, and one begins to wonder what is the proper criterion of " success " (*cf.* Testcase I, *Evol.*, p. 90), and also how small a dispersal is necessary that a species should be a relic.

Going on with our journey, we come upon genera new to BRITAIN, like the soapwort (*Saponaria*) or the chalk-plant (*Gypsophila*), both *Caryophyllaceae*, and familiar in British gardens, where they are quite at home. One usually meets one new species first, and others gradually, and every now and then one meets members of tribes, sub-families, or families that do not occur in BRITAIN. About 32 new subdivisions of families are met with in FRANCE, represented by such things as the paeony, the rosemary, or the lavender, while the rue of the south belongs to a new family, the *Rutaceae*. One meets about 25 new families before reaching GIBRALTAR, and it is of special interest to note that in 17 cases one first encounters the largest genus in the family in the world (cf. p. 27), while in two more it is the second, and only in *Acanthaceae* and in *Gesneraceae*, tropical families with little overlap into colder zones, is the genus a small one. In the far south, too, we come upon many genera that are localised or endemic.

The current theories, that evolution was by gradual structural adaptation. and that wide distribution was due to the possession of " superior adaptation ", are evidently helpless to explain such facts. But now that we know that distribution is largely governed by the laws of ASA, whereas previously we knew of few cases where it obeyed any law, it is clear that the explanation must be rather mechanical than vital. Most of the actual work of distribution of the individual plants *into their most suitable situations* is of course done by vital factors operating upon the plants in accordance with whatever may be the local conditions, which will differ from one place to another. But age, size, and area or space always influence things in the same direction, and working without reference to any vital consideration, they determine almost entirely what shall happen in large areas and in long time. The larger the area, and the longer the time, the more will their effects override the local and temporary results due to the vital factors. Only when we know what is due to the simple ASA factors, can we disentangle with any hope of success the effects of the vital factors upon ultimate dispersal, and the study of distribution will cease to be so much a matter of speculation as it is at present. It is for this reason that we have been so careful about laying down the rule about comparison only in groups, and with closely allied forms, so that all compared may be likely to resemble one another in habit, in mode of life, and in reaction to outside influences.

Barriers. The effects of age and of area are positive and cumulative, but they are always accompanied by the negative effects produced by barriers of different kinds, especially physical, climatic, and ecological. There is no need to repeat what we have already said in *Age and Area*, pp. 12, 20, 32-45. Two well marked barriers occur in going southwards from BRITAIN, the CHANNEL and the PYRENEES. Conditions do not appreciably change in crossing the channel, yet one finds a number of new species soon after landing in FRANCE; the presence of the sea has prevented them from crossing, though since its formation they have become frequent upon the French side. In the same way, there is a marked change in crossing the PYRENEES. Even the passes are so high that much functional adjustment would be required in order to cross, first in the direction of colder later in that of warmer, conditions, an adjustment that is apparently beyond the range of most lowland species in the time that has been available.

The things that are left behind at any barrier tend to be the smaller and more localised genera, and what corresponds to them in species—the more recently born, and therefore much localised species, which as we have seen are much more numerous in the larger genera. A comparison of the *Labiatae* in SPAIN, FRANCE, and BRITAIN shows :

	Genera	Species	Average per gen.	% of Span. gen.	of Sp. spp.
Spain	34	235	7	100%	100%
France	29	108	3.7	85%	46%
Britain	19	57	3	56%	26%

a marked decrease at each stage, especially, as we should expect, among the species. The Spanish genera left behind in crossing into FRANCE have 4, 1, 1, 1, and 1 species, and the same kind of thing shows at every stage, even including the change from the flora of BRITAIN to that of IRELAND, or other islands outlying, and again to the smaller islands outlying from these.

We may now compare the floras of BRITAIN, FRANCE, SPAIN and the BALKANS, dividing the plants into British and non-British, and we get the table on p. 47, in which the floras are taken just as they stand, with no attempt at equation, so that the British flora includes all the small *Rubi* and *Hieracia*, which fact goes to reduce the difference.

The figures given in this book are mostly too emphatic to suffer from lack of equation.

Proportions of British and non-British genera in the floras of Britain, France, Spain, and the Balkans

Total Genera and Species			% Dicots	British gen.		Spp. per gen.	Non-British gen.		Spp. per gen.
Britain (a)									
Dicot	347	1521	77%	347	1521	4.3	—		
Monocot	128	435		128	435	3.4	—		
Total	475	1956		475	1956				
France (b)									
Dicot	640	2494	79%	354	2019	5.7	286	475	1.6
Monocot	184	651		108	548	5.0	76	103	1.3
Total	824	3145		462	2567		362	578	
Spain (c)									
Dicot	748	4143	83%	343	3153	9.2	405	990	2.4
Monocot	179	806		101	666	6.6	78	140	1.8
Total	927	4949		444	3819		483	1130	
Balkans (d)									
Dicot	739	5449	84%	337	4184	12.4	402	1258	3.1
Monocot	209	1038		119	838	7.0	90	200	2.2
Total	948	6487		456	5022		492	1458	

(a) *London Catalogue*, 11th ed., including all *Rubi* and *Hieracia*.

(b) BONNIER, *Flore de France, Suisse et Belgique*, Paris (1911-35).

(c) WILLKOMM and LANGE, *Prodromus Florae Hispanicae*, Leipzig (1861-1880; and Suppl. 1893).

(d) TURRILL, *Plant Life of the Balkan Peninsula*, London (1929).

Slightly greater numbers for British genera abroad, and other irregularities, are due to different conceptions of genera by different authorities.

Alike in all, nearly all the British genera occur, but while in BRITAIN the Dicots have only 1521 species, the same genera have 2019 in FRANCE, 3153 in SPAIN, 4184 in the BALKANS, the average number per genus being nearly trebled there. The same happens in the Monocots, but the number of species per genus is lower throughout, perhaps indicating greater youth. Their increase in proportion westwards perhaps suggests that the climate in BRITAIN is more favourable at any rate to that portion of them which consists so largely of grasses, sedges, rushes, &c.

The increased size of the continental flora is largely shown by an increase in species of the British genera, which are much larger than the non-British, though the increase of the latter in similar proportion indicates that they are not inferior in adaptation, as was formerly supposed. The Dicots increase more than the Monocots, again suggesting greater age in EUROPE. Their non-British genera do not outnumber the British, and their proportion of small genera is greater, both confirmatory points. British species are supposed to be specially well suited to BRITAIN, but it is clear that they got their adaptation to it in BRITAIN, for they are just as well suited to the other countries, often with very different conditions.

It is clear that it is in general the larger genera rather than the smaller that pass the barriers, and each successive flora is a reduced copy of the one before. That of BRITAIN is in general a reduced French flora, and in the same way the Scottish or the Irish is a reduced English flora, that of the ORKNEYS or the SHETLANDS a reduced Scottish, and so on (*cf*. PALMGREN, and my work on STEWART, CHATHAMS, &c). In such islands as NEW ZEALAND itself, or the HAWAIIANS, however, it is not so easy to determine the origin or origins of the flora, for there must evidently have been different continental connections at different times. The help of geology becomes more and more necessary and important, as we shall see, the further back in time that one goes.

Land transport usual. GUPPY, who spent many years at this work, has shown (44, and *cf*. *Age and Area*, p. 17) that in the islands of the PACIFIC 90% of the plants have fruit that is not buoyant, and that could only be carried by sea under some accidental concurrence of circumstances. " DE CANDOLLE was quite right in minimising the effect of currents on the distribution of plants ". " One can scarcely controvert KERNER's opinion that the dispersal of plants as a whole is not appreciably affected by this process." The writer and Prof. STANLEY GARDINER's work upon the flora of the MALDIVES (162), a group of atolls about 400 miles from CEYLON, showed that the flora was simply a miscellaneous assortment of things that could be carried by water or otherwise, and as far as its composition went, might have come from any palaeotropical country.

Carriage by water could not but exert a selective action, for all seeds are not alike. But there is not the faintest evidence to show that this selection would on the whole pick out the genera with most species as those that ought to be carried, other than the fact that on the whole they are rather commoner. But the selection of the larger genera in any flora is somewhat too pronounced for this to be at all likely. And why is the change from FRANCE to BRITAIN, across water, like that from SPAIN to FRANCE, across mountains? Only land transport can explain such facts, and it is also not improbable that some mountains, like some straits, were at one time less of a barrier than they now are.

We have seen that the largest (oldest) genus of a family is the most likely to reach any given country, but there are many hazards that come in the track, and if conditions change rather rapidly, as in coming north, it probably puts a great strain on plants coming from the south, while genera born in the north will not have to encounter so much. Because a plant is not found (like *Hibiscus*, the largest Malvaceous genus), further north than the south of FRANCE, while *Malva* is common in BRITAIN, is no proof that *Hibiscus cannot* reach BRITAIN, given time enough for acclimatisation (*cf. Age and Area*, p. 29).

I have used as a working hypothesis for 40 years the supposition that such strains are probably the chief reason why new species and genera are developed, species with a moderate strain, genera with a greater.

Let us now look at the French *Ranunculaceae*, taking the facts from BONNIER (14). If, as we have suggested on p. 27, the oldest (largest) genera of a family are those most likely to be found near the outer edge of its distribution, we shall expect to find many of them in the British flora, while younger and smaller ones will gradually appear as we go southwards. In BRITAIN there are the first genus in the world (*Ranunculus*), second (*Clematis*), fourth (*Anemone*), fifth (*Aconitum*), sixth (*Thalictrum*), seventh (*Aquilegia*), eighth (*Caltha*), twelfth (*Helleborus*), fourteenth (*Actaea*), fifteenth (*Trollius*), and also the small genus *Myosurus*. Of the missing five, *Delphinium* (third) soon appears in FRANCE with one species, and has six more in the south of FRANCE, and a dozen in SPAIN; *Isopyrum* (ninth) has one species in FRANCE and SPAIN, *Viorna* (tenth, *Clematis* p. p.) occurs only in N. AMERICA, *Nigella* (eleventh) has three in FRANCE and five in SPAIN, and *Paeonia* (thirteenth), with three rather rare French species, is the first representative of the hitherto missing third subgroup *Paeonieae*, which, as has been pointed out in *Evol.*, pp. 80-87, is a group of lower rank than the other two, arising rather from a secondary than a primary shoot of the family. The original parent of the family, *Ranunculus*, belongs to subgroup III, *Anemoneae*, hitherto regarded as the highest representation of the family, although headed by such very old genera. It is just possible that *Clematis*, which is of slower growth and travel, and seems more southern in origin, may be an original parent; *cf. Evol.* pp. 70, 135. Under the theories that we are here bringing forward, there is no absolute necessity for it to belong to the same genetic line as the rest.

It is clear that the laws of ASA have had much more to do with the distribution of the *Ranunculaceae* than have questions of adaptation, selection, or relicdom, and the same may be said of most families. It will be shown later that there is evidence of a general kind to show that these latter factors have also had a hand in the matter, though not a very important one.

While the "British" genera found in FRANCE average there about seven species each, the new genera found only average three, and their average world size is only 47 against 88. The nearer one goes towards the centre of distribution of a family, the more do the smaller genera in world size—the relics upon the older views—come into the picture, so that the average size becomes less and less. We may therefore predict that in any family the genera that occur in BRITAIN will average more in size in the world than do those in FRANCE, including in the latter those that also reach BRITAIN. The same thing will be repeated at the PYRENEES. Taking the *Cruciferae* as an example we find : —

World size of genera of French Cruciferae, showing the differences between British and non-British genera

Brit.	260	240	120	110	90	80	60	50	50	35	30	25
Not	120	60	50	50	35	25	20	15	12	12	10	10

Brit.	20	20	20	20	12	10	8	8	4	4	2	2	2	
Not	7	6	5	5	5	5	4	2	2	2	1	1	1	1

British total	25/1282	Average 51 spp. in world size
Non-British	26/463	Average 18 spp. in world size

The prediction is completely borne out, every "British" genus being larger than its corresponding non-British one. We may go on to predict that the latter (the younger) will have fewer species in FRANCE, and arranging the genera as above, we get : —

Numbers of species in France of British and non-British genera of Cruciferae, added up in groups of five

Brit. 6 17 11 7 4; 9 4 4 3 5; 9 3 4 1 4; 1 2 2 4 3; 1 1 1 1 1
Not 10 2 2 3 4; 1 3 3 2 1; 1 1 1 2 1; 1 1 1 1 1; 1 1 1 1 1; 1

Totals of fives 45/21 25/10 21/6 12/5 5/5

The 25 British genera average 4.3, while the 26 non-British only average 1.8. Again the prediction is borne out, and it can be seen how on the whole the number of the species diminishes with the size of the genera (in the *world*). Individual variation is great, probably showing, among other things, the local effects of the vital factors, but disappears when they are taken in fives. The same kind of variation, cancelling out in grouping, is shown almost everywhere, and goes to show that the action of vital factors in dispersal is too local and too variable to overwhelm that of the mechanical factors like time.

The *Umbelliferae*, taken in another way, may form a further illustration :

British and non-British Umbelliferae in Europe

	Britain	France	Spain	Balkans
British Genera/Species	34/59	34/102	34/148	34/218
Average size of genus (local)	1.7	3.0	4.3	6.4
Non-British	—	32/43	40/69	48/116
Average size	—	1.3	1.7	2.4
Percentage of non-Brit. genera	—	48%	54%	58%
Percentage of non-Brit. spp.	—	30%	32%	34%

In this connection it is of interest to divide the Balkan flora into Dicots and Monocots, and these again into British and non-British : —

Balkan flora to show behaviour of genera of different sizes

Size of Genus	Dicots			Monocots		
(species)	Brit.	Non-Brit.	Proportion	Brit.	Non-Brit.	Prop^{n}
1	67	210	10 to 31	42	56	10 to 13
2	36	63	— 17	15	17	— 11
3-5	66	70	— 10	23	9	— 4
6-10	60	36	— 6	21	5	— 2
11-20	55	18	— 3	8	—	— —
21-30	20	2	— 1	8	—	— —
Over	33	3	— 0.9	4	—	— —

The proportion of non-British genera, high at first, especially in Dicots, rapidly shrinks, and most of the large genera are British. Most of the non-British genera are evidently recent arrivals in the Balkans as compared with those that reach Britain. The proportion of British Monocots is greater in the small genera.

As we have been pointing out for 40 years, all these statements are statistical, and must always be qualified by " on the whole ", and not applied to single cases if one expect reliable results. It is still needful to remember a comparison I made many years ago. Statistics show that on the average, or on the whole, the Scot is 1½ inches taller, and 10 lbs. heavier, than the Englishman, but many people imagine that fact disproved by the subordinate fact that the English John Matthews is taller and heavier than William Ferguson. This latter fact is cancelled out by the superiority of James Howie to Ernest Lowe, and as many more Scots in proportion to the total are superior, the statistics show the superiority of the Scot.

To return to the figures of French distribution (p. 47), as all the genera behave in much the same way, we may devote our attention to *Ranunculus* itself, which in species makes up about half the family in northern Europe. We shall see that the species found in Britain have a very wide dispersal indeed, as on the whole they were the oldest and the first to arrive. By the same law, those that only reach France will probably have less dispersal in the world. If we place the French species in the approximate order of their dispersal in France, we get:

Dispersal of French species of Ranunculus, in approximate order of dispersal in France

Species	France (14)	Britain	Aver.	World
+aquatilis	Very common	112	112	N. temp., Austr.
+repens	Very common	112		N. temp.
+bulbosus	Very common	112		Europe, W. Asia
+acris	Very common	112		N. palaeotemp.
+fluitans	Common	75	94	Most of Eur., W. As.
+divaricatus	Common	76		Eur., W. As.
+Flammula	Common	112		N. temp.
+Philonotis	Common	87		Eur., except far N.
+sceleratus	Common	104		N. palaeotemp.
+auricomus	Common	97		N. palaeotemp.
+Ficaria	Common	112		Eur., W. As., N. Afr.

Species	France (14)	Britain	Aver.	World
+Lingua	Rather common	93	93	N. palaeotemp.
arvensis	Rather common			C. Eur. and Medit.
nemorosus	Rather common			Europe, except far N.
+hederaceus	Here and there	112	50	Eur., W. and N.
+parviflorus	Here and there	62		Eur. W. and S., Medit.
+tripartitus	Here and there	3		W. Europe
nodiflorus	Here and there			SW. Eur.
macrophyllus	Here and there			Medit.
muricatus	Here and there			Medit.
falcatus	Here and there			C. Eur. and Medit.
+Lenormandi	W., SW., and Centr.	71	37	W. Europe
+ophioglossifolius	C. W. and S.	3		Medit.

Species found in Britain are marked +.

and also eighteen other species, none of which occur in Britain, described as Rather rare, Rare, Very rare, or in the case of the last twelve, mountain species, the actual locality given. None are endemic in, or confined to, France.

Roughly speaking, the dispersal of the French species, like that of the British, goes with their dispersal in the world, and all those above rather common, which show great dispersal in the world, occur in Britain, while only two below the middle of the list have done so. The last dozen or so are very local, and chiefly montane. But as there is often a large gap between the mountains, as between the Alps and the Pyrenees, they frequently show a dispersal that we call discontinuous, whereas we rarely apply this term to things far apart in Britain. There is so great a difference in climate between the high mountains and the plains in France that the things of high levels could not cross, except under special circumstances, like colder climate.

When the species are taken in groups, the average dispersal in Britain goes with the average dispersal in France, so that it is fairly evident that in large areas and in long time, the vital factors and the local conditions, so important in ecological and local dispersal, have but little to do with the general result which is the subject of geographical distribution, properly so called. It is clear that they treat alike no two individual cases.

Though the dispersal of the lower half of the species is small, none are actually confined to FRANCE itself, though in a few alpine species there is little overlap. Other members of the family, however, are very local; *Thalictrum macrocarpum* and *Adonis pyrenaica* are confined (*endemic*) to small areas in the PYRENEES, *Delphinium Requienii* to the little island of PORQUEROLLES, off HYÈRES, where it was probably formed by a recent mutation, and had not time for further dispersal before the island was cut off.

On the south side of the PYRENEES we find about 30 new *Ranunculi*, about half of which are endemic to SPAIN, while many others do not go very far beyond it. The term endemic is very loosely applied, and most people, being more or less politically minded, allow a Spanish species as an endemic, while refusing the title to one found in the smaller area of CEYLON and the southern end of INDIA, these being politically different. When one traces species about the world, as we have done for 40 years, and sees how they may be found on every size of area in the same genus, it is evident that a local endemic is, in the great majority of cases, a young beginner as a species. There is no evidence that these Spanish *Ranunculi* are relics of a previous vegetation, while it is possible that the widely dispersed species may be so in some cases, where some of the widely dispersed species may perhaps be able to survive a serious catastrophe, and go on again afterwards (cf. 57).

There is a regular progression in going northwards through EUROPE. In SPAIN there are species of enormous distribution like *acris* or *repens*, down to species of extremely local dispersal. In FRANCE there are less of these latter, so that the average dispersal there is greater, and in BRITAIN there are left practically only species of very wide dispersal indeed, which, by the law of age and area, are those that were also old enough to reach BRITAIN before the land connection was severed. The Spanish endemics, it may be noted, all occur in broken and especially in mountainous country.

Let us now follow the 15 largest genera of *Ranunculaceae* into many different parts of the world, to get an idea of their relative importance.

Occurrence of the 15 leading Ranunculaceae in 33 floras of different parts of the world

The object being merely to get an idea of the relative importance of the genera, any convenient and not too old flora has been used, the countries selected being Lapland, Russia, Britain, Spain, Balearics, Sardinia, Italy, Balkans, Crete, Asia Minor &c (Boissier), Egypt, Algeria, Azores, Canaries, India, Ceylon, Malay Peninsula, Indo-China, Hawaiian Is., North America, British West Indies, tropical Africa, Natal, South Africa, Mauritius, Australia, Tasmania, New Caledonia, New Zealand, Aucklands, Chathams, Chile, Juan Fernandez. The numbers of species of any one of the 15 genera in each of these floras are added together into total occurrences for each genus : —

Genus	Floras in which it occurs	Total occurrences	Genus	Floras	Occurrences
1. Ranunculus	28	743	9. Isopyrum	7	13
2. Clematis	26	181	10. Viorna	1 (large)	14
3. Delphinium	13	186	11. Nigella	10	50
4. Anemone	21	148	12. Helleborus	9	42
5. Aconitum	10	81	13. Paeonia	9	31
6. Thalictrum	15	133	14. Actaea	9	11
7. Aquilegia	12	47	15. Trollius	8	20
8. Caltha	13	29			

The floras for *Anemoneae* (genera 1, 2, 4, 6, 10) add to 91, the occurrences to 1219; for *Helleboreae* (3, 5, 7, 8, 9, 11, 12, 14, 15) the floras are the same in number, but for nine genera instead of five, the occurrences only 479; for *Paeonieae* 9 with 31 only. *Ranunculus* has an overwhelming preponderance, with 743 out of 1729 occurrences in 28 out of 33 floras, missing only the Malay Peninsula, New Caledonia, the West Indies, Mauritius, and Juan Fernandez, in all of which but the last, where *Anemone* alone appears, its place is taken by *Clematis*.

While the leading *Anemoneae* are more or less cosmopolitan, though their greatest concentration is in the northern temperate regions, the *Helleboreae* are almost confined to these, and the *Paeonieae* completely so. *Ranunculus* and *Clematis*, more particularly, are very widely spread, and it is clear that the genetic relationship between them needs further investigation, for *Clematis* (supposing that it is really a member of the same genetic series) is a more southern genus which looks as if it had been overtaken and passed by the herbaceous buttercups, and may really be the original parent of the family. *Ranunculus* is the only representative in the HAWAIIANS and some other outlying islands, and is well over 60% in NEW ZEALAND, the CANARIES, LAPLAND, and CHILE, over 50% in BRITAIN, TASMANIA, SPAIN, and SARDINIA. The greater the isolation of the region, the greater the share that *Ranunculus* takes in the flora.

The *Helleboreae* centre in the eastern Mediterranean region, and *Delphinium*, their leader, though next in size after the two just mentioned, has only a small area of distribution in comparison with them, though it may have had more at some time. If there were an early catastrophe, as some people think, that only left *Ranunculus* and *Clematis* at a few widely separated places, from which they have since filled in the blank spaces, it may have reduced *Delphinium* —which as younger would probably cover less area—to its central part. It is quite possible that many fossils are really relics of such catastrophes that killed out the local things altogether, but left the old genera, which covered large areas, unharmed in some of their stations. It is to such occurrences that we owe the present wide, but discontinuous, distribution of so many of the large genera that are found in both worlds, with a vast expanse of sea dividing them.

We may take the *Umbelliferae* as another example. While BRITAIN has 34 genera with only 59 species, the proportion per genus increases as one crosses the continent, and BOISSIER's great *Flora Orientalis*, which covers the region of the eastern Mediterranean where the *Umbelliferae* are most common, shows 123/629, or over five per genus. The 34 British genera, just over a quarter of the genera in BOISSIER, have there 305 species, or nearly half the total, five times as many as in BRITAIN. Eight of the eleven genera in BOISSIER with more than 15 species are British. Even in NATAL, ten out of the 14 genera are British, and all seven of the CEYLON genera, and all the genera upon the HAWAIIAN Is. (4), JUAN FERNANDEZ (4), GALAPAGOS (2); and *Hydrocotyle* is the only genus in MAURITIUS and the SEYCHELLES. Six British genera in NEW ZEALAND have 35 species, while the other five have only 26. The British genera, evidently old, are well represented all over the world. The large Monocot families give similar figures, and we need not labour the point in this book, which is only a sketch.

Contour lines. What is evidently happening in thus traversing EUROPE is that we are crossing contour lines in the way familiar to all who know how to read and use a good map of hilly country, the contour lines being the outer boundaries of the areas occupied by the various species (*cf.* the map of *Beta* in *Nat. Pfl.* 16 c, p. 461, 1934). If there be not some boundary like sea or high mountains, which may stop at the same place various species arriving there at different times, one generally meets a genus one species at a time, and as one approaches the other side of its area, the species fall off again in the same way, as one may see the species of a genus diminish in going northwards through EUROPE. On the whole, the genera found in northern BRITAIN go as far as any European genera, and some of them, like *Senecio*, *Ranunculus*, *Juncus*, or *Carex*, are cosmopolitan or nearly so, and usually have a great many species, though this varies with the affinities and the habit, water plants, for example, usually going much further with fewer species, and herbs of open ground than trees. The 39 British genera marked in my *Dictionary* as cosmopolitan average 312 species each. Why, incidentally, should a cosmopolitan genus, which must, upon the Darwinian theory, have a good adaptation, need so many species, and why should related genera, but with fewer species, have smaller distributions?

When a species or genus is small, like the monospecific genera of *Umbelliferae* of the PYRENEES (*Dethawia*, *Endressia*, and *Xatardia*) or like the local species of other and larger genera found there, its area is clearly enough marked out by a line drawn though its outer localities. But as it slowly increases its area, it may go across, or more likely around, areas with unfavourable conditions, such as those with communities in which it cannot find a place. Deserts, seas, lakes, mountain chains, obstacles of all kinds, interfere with direct expansion from the original birthplace, so that the area ultimately reached may be very irregular, as is so often the case in the broken and hilly country of western EUROPE. A plant already established may be killed out somewhere by some change of conditions or other happening, unless this be slow enough to allow of functional adjustment. Or when a plant travels a long way it may come to some place whose conditions suit it admirably, and may there extend and multiply, perhaps giving rise to an unusual number of new forms. *Compositae* are especially common, not only around the Mediterranean, but also in places like CALIFORNIA or CHILE.

For most of its plants, BRITAIN is at the edge of the contour maps. But this is far from saying that the edges of all the contours reach the outer edge of the BRITISH IS.; comparatively few actually do so. Roughly half of its genera, and half of those of NEW ZEALAND, which occupies a somewhat similar place in the south, have only one species, the numbers of species increasing as one goes more inland and towards the equator. This of course means that the oldest, and therefore largest, genera in any circle of affinity will be near the edge of its distribution, as we have already seen. Yet the conditions in BRITAIN are at least as varied as in other European countries, so that it is evidently a very weak contention that is sometimes brought forward, that the great numbers of species at the centres of generic contour maps are due to the great variety of conditions there. This is especially emphasised when one finds that these centres are scattered all over the world, though they are rare in the colder parts, and tend to aggregate in such regions as the MEDITERRANEAN, (BOISSIER's *Flora Orientalis* has 54/1 in 123 genera of *Umbelliferae*), or CHILE. In any such centre of genera (centre of creation in the pre-Darwinian expression), genera of one species (only) tend to be very numerous, which is a very remarkable fact if we accept the Darwinian view that such genera are relics; why should they be common at the very centre of prosperity? Some NEW ZEALAND contour maps are given in *Age and Area*, pp. 154-6-8, and one in *Evol.*, Testcase XXVII, p. 151, and on p. 65 below.

Effect of climate. As the climate alters more rapidly to the south than to the east of BRITAIN, at any rate in warmth, it has long been, and still is, customary to put down the greater alteration of the flora in that direction to the greater alteration of the climate. But there are several factors concerned in these results, and they must be disentangled before we can feel safe in any assertion. Darwinism considers the structural alterations to be adaptational, but they are not so gradual as the changes of conditions, being rather mutational, with definite steps, small or even large, appearing at long intervals of time and of space. There is little or no evidence to show that they are in any way adaptational, except in a very few possible cases. But the alteration in the flora from one country to another is at bottom structural. Were it not for the structural differences, we should not see any change in the vegetation at all, except for such things as density upon the ground. One flora usually changes gradually to another by the disappearance of some species and the appearance of others, thus altering the ecological make-up of the flora, but there are few characters in the plants of a family that show any adaptation to the conditions. The small proportional difference as compared with the general mechanical progression shows how small a part is played by adaptation as compared with that of mere time.

There are a number of things that go together in this connection, and the difficulty is to make out which is cause and which effect, or whether any one of them is really cause, and there is not some as yet unknown factor behind it. Structural alterations are the only thing to show that evolution has gone on at all, and as Darwinism set out to explain evolution upon an adaptational basis, adaptational value was necessarily given to these changes of structure—a value which has very rarely indeed been shown to exist, in spite of all the desperate efforts made to prove it. A leaf probably assimilates equally well whether ovate or cordate, palmate or pinnate, and so on, to say nothing of the fact, brought out in Testcase X, *Evol.*, p. 114, that the urge to improvement would fall off more and more the nearer the improvement came to perfection. Yet in actual fact, characters are usually shown in a perfect stage.

Adaptation under selection must be acquired gradually, but a great proportion of the structural changes are so distinct and widely separated from one another that they could only be acquired suddenly, and it is upon such prominent facts as these, and facts so universal, that we have based our theory that evolution was by sudden mutations, giving rise to new species, genera, or families at one operation.

Structural differences thus acquired can hardly be looked upon as adaptational, but rather as incidents due to the mutation, for unless the new form is at once, upon birth, sufficiently adapted to its place to be able to survive there, it will at once be killed out by the action of natural selection. All survivors (with rare accidental exceptions) *must* be adapted and the adaptation is presumably functional rather than structural.

What chiefly changes the look of a flora in travelling through a country is the ecological alterations of local distribution that are to be seen, and which of course are mainly dependent upon changes of climate, soil, and other conditions. Compared to these, the actual changes in the composition of the flora are of much less importance, and we have seen how far one must go in order to find a great difference in taxonomic composition. Even in SPAIN or in the BALKANS about 80% of the flora still belongs to genera native in BRITAIN, and even in NEW ZEALAND about 46%. One might have to travel a long way to find a greater change in the botanical landscape than one may see in the short journey from the DERBYSHIRE moors to the LINCOLNSHIRE fens.

There is, however, a fairly sudden structural change between one species and the next, and only rarely does one find any kind of zone of hybridisation between them. It is probable, as we have tried to show in *Evol.*, that the structural differences that distinguish one species from another have nothing directly to do with the climate or other conditions, and may be susceptible of a completely different explanation. Upon what interpretation of climatic effects can one explain the contour maps given by genera, with their centres scattered in all parts of the world, though principally in the warmer ones?

It is clear that to put down the increasing number and variety of species, in crossing EUROPE, and that especially in the British genera, to increasing differences in the conditions and climate, is to confuse the issue, for it is not to be supposed that the conditions in SPAIN should be two or three times as complex as in BRITAIN, nor those in the BALKANS still more so. Why should SPAIN need 499 *Leguminosae*, when BRITAIN is content with 90, and FRANCE with 287? Why should the BALKANS need 548? And why, incidentally, should *Leguminosae*, an obviously "successful" family, fall oft so quickly in numbers towards the north, as compared with some other families? The total number of them in BRITAIN is smaller than that of their endemics in SPAIN. It is worth notice that there are, in Mrs REID's list on p. 36, no *Leguminosae*, *Cruciferae*, *Ericaceae*, *Chenopodiaceae*, *Polygonaceae*, *Liliaceae*, &c. On the theories that we are bringing forward, a greater number of species at any one point is mainly due to the genus having been there for a longer time.

The conditional differences between area A and area B cause differences in the ecological make up of their floras, but flora A and flora B are both made up, by the work of natural selection, from the total flora that is available in that neighbourhood, and one can hardly doubt that if the total flora were larger, or if the dates of arrival of the species in the existing total flora had been different, the composition of the floras A or B might have been somewhat different. Ecology studies the flora A and its local dispersal, but distribution proper studies the whole flora X, of which A forms a part, and the movements of X and its members about the world in secular periods, and it is thus necessary to know how and when these members came into existence, or in other words to study their evolution in connection with their distribution.

To attempt to explain things that occur in large areas and in long time upon an adaptational basis, for which after all there is little evidence but wishful thinking, is to overstrain the capacity of any adaptational hypothesis, suitable as it is to local occurrences. The facts that we have described are quite inconsistent with any theory of gradual adaptation other than simply functional, but are easily explained by the laws of ASA, especially when supplemented by the theory of divergent mutation.

CHAPTER III

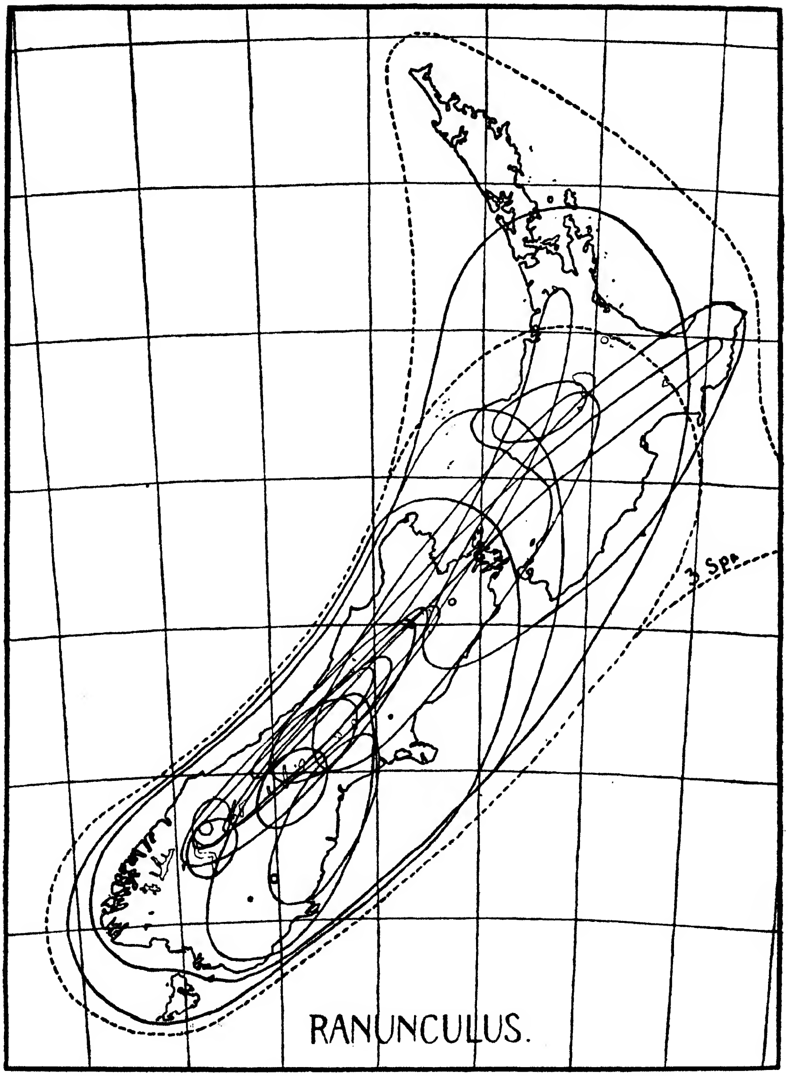
Endemism in Southern Europe

Endemics, both species and genera, as we have seen, appear in crossing EUROPE, and become abundant around the MEDITERRANEAN, which in pre-Darwinian days was termed a " centre of creation ", and might now be called a centre of evolution, as there are a great number of genera of from one to twenty species found only in that region. In the north endemics are but few, and in the far north are mainly circumpolar. The question of what they really are, and why and how, and where and when, they were formed, has caused endless discussion and controversy, for no explanation of distribution that does not explain them is of much value. Under selection one expects to find in many places the relics of species defeated in the struggle for existence; its supporters, therefore, found the harmless endemics a perfect godsend, as apparently fulfilling these conditions. They being especially common upon islands and upon chains of mountains, these places gradually became recognised as refuges for the defeated, though how these reached them was left unexplained. They would have to undergo some adaptation in doing so, and if so, why could they not become adapted to meet the competition in their old homes? It became customary to say that the competition was less severe on islands or on mountains; but the average number of competitors in any one place (six) is the same in both, and the widespread (" successful ") species are if anything commoner on the islands or the mountains (lower parts).

Another popular view, also almost purely speculative, was that endemics were not relics, but were things that had become adapted to some peculiar local conditions, in which they flourished as successes. As no evidence could be found to support either of these contradictory explanations, it is clear that real knowledge was still to seek. Both were continually met by insoluble difficulties, but such was the glamour of selection that these were pushed to one side, or ignored, a proceeding bound sooner or later to lead to trouble.

The writer has devoted much time to the study of endemism, and it may be said at once that while there are many genuine relics, within range, for example, of the coming of the ice, and while it is clear that any species, surviving and reproducing in any place, must be suited, or adapted, to that place in order to survive, there is no doubt that the dispersal of endemics by area follows in general the same kind of curves as other distributions. There is nowhere that one can draw any line to distinguish between endemics and non-endemics, any line that is actually drawn depending entirely upon the personal preference of him who draws it, for some would keep endemics to the very bottom of the curve, others would go higher up.

As this type of arrangement was universal, the writer proposed (in earlier papers, and in *Age and Area*, 1922) to regard endemics in general, whether species or genera, as young beginners that had not yet had the time, and sometimes of course the opportunity, needful to enable them to spread to great distances. The area actually covered was simply a rough indication of their age as compared with allied forms, for barriers, or differences in adaptation to conditions would affect some more than others. The first deductions made are given in *Age and Area*, p. 65. The facts go in so mechanical a way that some mechanical explanation is needed, and age is far more reasonable as such than is youth, under which the things of small area would be relics. The objections to the latter are dealt with in some detail (*l.c.* pp. 88-100), and no answer has been given, so far as I am aware. Positive proof has also been given by the success of all predictions based upon these mechanical laws, already considered in Chap. I. The real objection to them is that they are contradictory of the Darwinian hypothesis which founded evolution upon the natural selection of structural adaptational improvement, thus seeking to explain as



Ranunculus in New Zealand (by courtesy of the Editor, Annals of Botany). Wides... Endemics —.

adaptational the structural changes that mark evolution. It is hardly fully realised that adaptation to local conditions involves living in those conditions, and that distribution to great distances from them involves having plenty of time to get there by easy stages, acquiring local adaptation to each set of conditions in turn. Time thus becomes the all-important factor in dispersal, and its effects completely override those of the vital factors that are so important at any one place or time.

Endemism begins in the OLD WORLD chiefly at the great mountain barrier that runs from east to west, while in AMERICA, where the mountains run north and south, and in the southern hemisphere, with its more broken area, there is not so close an approximation to a limit of endemism. In and south of the barrier, endemism is well marked, probably primarily because the genera have been longer upon the ground (and the ground is more varied and broken) than in the colder north. In the mountains one finds representatives of genera that came from the north, or down the mountains, in the cold periods, and then, as the warmth grew, were driven upwards and northwards, till they acquired a discontinuous distribution, as shown by such a plant as *Diapensia*, with species in the HIMALAYA and in the arctic regions. Many endemics in NEW ZEALAND or in SOUTH AMERICA are as near the pole as north-central EUROPE.

This probable fact, that *Diapensia* and other things were caught in the south by the returning warmth, and *killed out there*, only having at the present time survivors at high levels in the mountains, or in the arctic regions, goes to show that a change of conditions may actually kill out the organisms that become subject to it, whether this was done directly (as by increasing warmth) or indirectly (as by the encouragement by that warmth of the growth of plants that too much overshadowed the first, or in some other way). We do not of course know exactly what happened, nor how far north the *Diapensia* had actually gone, but the fact of its present discontinuous distribution is due to the fact that it was near enough to them to reach two different refuges, while it is quite possible that had it been just a local thing on the TIBETAN plateau, the change of conditions might have been too quick for it to escape, and it might have been killed out altogether. Such a fate may have been the origin of many of the very local fossils that are known.

Upon our theory of the origin of endemics, they must, as young beginners, have had parents in the same place as themselves, living under the same conditions, and these parents are not necessarily, or even probably, killed out. It is therefore unlikely that there should be any country showing 100% endemism, even when we remember that there are many genera, all of whose species in some single country are there endemic (this will be dealt with later). Between 80 and 85% is the highest proportion of endemics anywhere found, and only in such long isolated places as W. AUSTRALIA, the HAWAIIAN IS., &c, as have given time for many endemics to form without being able to get beyond the country.

The areas occupied by individual endemic species or genera vary greatly, from those of *Coleus elongatus* with a dozen or more plants on RITIGALA summit in CEYLON, *Ranunculus paucifolius* with only 44 individuals upon four acres in NEW ZEALAND (as Prof. F. T. BROOKS kindly informs me), or the whole genus *Sphagneticola* in the little LARANJEIRAS valley now forming part of RIO DE JANEIRO, upwards to whatever area one may select as the largest possible for an endemic (*cf. Age and Area*, pp. 151-161).

It was this great variety of areas occupied, with no break between larger and smaller, that first attracted the writer's attention, making him realise that an endemic was usually simply a young beginner. Their numbers were largest upon the smallest areas, and decreased upwards, forming curves with the maximum at the base. These curves show not only with the whole flora of a country, but with individual families, and even with individual genera that have more than about a dozen species (*AA*, p. 161). " It is clear that the distribution of endemics is only a special case of a wide general phenomenon—that there are, in any family or genus of reasonable size, a few species of wide dispersal, and others of less and less dispersal in increasing numbers, the increase being more rapid as one descends the scale, so that the curve produced is hollow ". When, as in NEW ZEALAND, where there are many endemics, with their localities well worked out, so that one can draw a map (p. 65), one can see quite well how the smaller areas greatly outnumber the large, and how they tend to centre at some region of NEW ZEALAND where the genus probably entered.

There are many endemics in southern EUROPE, especially, as usual, species, and those mainly in the larger genera. At first glance they seem to be a completely casual assortment, but studying them in detail, one finds their appearance to be just as much, and as regularly, governed by definite laws and principles as any other features of a scientific discipline. We shall see that the endemism of any one MEDITERRANEAN country bears a very definite relationship to that of any other, and at the same time shows a clear relation to the composition of the flora of BRITAIN or of other countries in northern EUROPE. There is little or no doubt that most of the flora of such a country as BRITAIN is due to migration from the south after the retreat of the cold. The first plants to follow the increasing warmth and the newly available land would be determined by various causes, such as (1) how old they were in the south, and (2) how far north they were already found, these two of course going very much together, and being modified by (3) suitability or adaptability to somewhat wet and cold conditions, (4) capacity for quick enough travel to arrive before the cutting of communications, though it is not unlikely that the retreat of the ice would be slow enough for perhaps most plants to follow, subject to the third condition, and (5) general presence or absence of great barriers like the sea or high mountain ranges.

BRITAIN has long been cut off by the sea, so that only those plants which arrived in good time would reach it, *i.e.* those on the whole that were oldest in the south. But upon my theory of divergent mutation (*Evol.*) these older forms would probably have had time enough in the south to give rise to new ones, which of course would be endemic there, not having had time enough to spread further. The same thing would be true of the MEDITERRANEAN islands. The great majority of Mediterranean endemics, thus, would belong to the largest and oldest families and genera there, and these would be the same on the whole as the largest and oldest in BRITAIN. The arctic element in the British flora is not large enough to disturb this seriously. Here is where the stipulation as to allied species comes in. A monospecific genus of water plants, for example, meeting much more uniform conditions everywhere than is the case with land plants, might easily reach BRITAIN more quickly than a species of a large but woody genus of say *Leguminosae*, and the stipulation eliminates such difficulties. If on the other hand, all these endemics were relics, there would hardly be any *necessary* resemblance between those of one country and of another. One would be rather inclined to expect to find them in the smaller and less important local families and genera, which under Darwinism are supposed to be old and dying out, but upon my theories are simply locally younger.

Since families and genera with endemics in the south are probably older on the whole than those without, they should therefore, by the rules of ASA, be the largest and most widely dispersed southern families and genera, as well as the oldest. Let us take the recently worked up Balkan flora (**126**) as an example. Taking the Dicots, 55 of its families contain no endemics, but they are by no means the large or " successful " families, whose relics might have been killed out. They are the small and rare ones, only containing among them 114 genera and 287 species, while the 49 families with endemics have 625 genera and 5169 species, the *Compositae* alone containing 100 genera with 915 species, of which 323 are endemic, or more than all the species in all the small families. *Caryophyllaceae* have 175 endemics, *Labiatae* 153, *Scrophulariaceae* 128, *Umbelliferae* 106, *Leguminosae* 105, and so on. These six large families alone contain 990 out of the 1576 Dicot endemics of the BALKANS, or 63%, and incidentally contain 58% of the endemics in SPAIN, and 47% of those in the AZORES. For over 35 years the writer has been trying to bring home the fact that endemics chiefly occur in the large and " successful " families and genera, which would shrink to small dimensions if their endemics died out as relics. This fact clashes hopelessly with the Darwinian explanation of things, and little notice has been taken of it.

Endemism in the BALKANS shows a wonderful resemblance to that of SPAIN, as will be seen by looking at the table (Dicots only) that follows : —

Families in Spain and in the Balkans that show endemism

DICOTS

Spain

Family	No. in other list	Species	Endemics	Percentage of Endemism
1. Compositae	1.	646	217	33%
2. Leguminosae	6.	477	137	27%
3. Cruciferae	7.	300	112	37%
4. Caryophyllaceae	2.	251	78	31%
5. Scrophulariaceae	4.	200	78	39%
6. Labiatae	3.	236	75	31%
7. Umbelliferae	5.	217	61	28%
8. Ranunculaceae	11.	143	31	21%
9. Saxifragaceae	21.	60	31	51%
10. Rubiaceae	9.	77	25	32%
11. Borraginaceae	10.	85	24	28%
12. Plumbaginaceae	19.	55	24	43%
13. Cistaceae	38.	70	19	27%
14. Campanulaceae	8.	53	16	30%
15. Resedaceae	48.	23	15	65%
16. Rosaceae	14.	23	15	12%
17. Geraniaceae	27.	46	14	30%
18. Dipsacaceae	12.	42	12	28%
19. Euphorbiaceae	16.	58	12	20%
20. Papaveraceae	23.	38	9	23%
21. Valerianaceae	22.	31	9	29%
22. Chenopodiaceae	44.	53	8	15%
23. Crassulaceae	17.	43	8	18%
24. Thymelaeaceae	49.	22	7	31%
25. Malvaceae	39.	35	6	17%
26. Primulaceae	20.	36	6	17%
27. Fagaceae	—	22	5	21%
28. Orobanchaceae	31.	33	5	15%
29. Plantaginaceae	40.	31	5	16%
30. Violaceae	13.	16	5	31%
31. Gentianaceae	30.	33	4	12%
32. Hypericaceae	15.	21	4	19%
33. Polygalaceae	32.	15	4	26%
34. Solanaceae	—	28	4	14%
35. Caprifoliaceae	37.	11	3	27%
36. Frankeniaceae	—	5	3	60%
37. Lythraceae	—	8	3	37%
38. Onagraceae	—	24	3	11%
39. Polygonaceae	34.	42	3	7%
40. Salicaceae	—	31	3	9%
41-3. Convolv. (33), Eric. (—), Rhamn. (24), at 2 each		58	6	10%
44-53 Berb., Cappar., Celastr., Dros., Gesn., Glob., Lentib., Lin., Santal., Urtic., at one each		61	10	17%
		3859	1119	29%

Dicots

Balkans

Family	No. in other list	Species	Endemics	Percentage of Endemism
1. Compositae	1.	915	323	35%
2. Caryophyllaceae	4.	421	175	41%
3. Labiatae	6.	375	153	41%
4. Scrophulariaceae	5.	311	128	41%
5. Umbelliferae	7.	334	106	31%
6. Leguminosae	2.	548	105	19%
7. Cruciferae	3.	341	96	28%
8. Campanulaceae	14.	142	76	53%
9. Rubiaceae	10.	131	53	40%
10. Borraginaceae	11.	155	47	30%
11. Ranunculaceae	8.	196	37	19%
12. Dipsacaceae	18.	83	32	38%
13. Violaceae	30.	58	32	55%
14. Rosaceae	16.	187	23	13%
15. Hypericaceae	32.	52	22	42%
16. Euphorbiaceae	19.	77	20	26%
17. Crassulaceae	23.	59	16	27%
18. Linaceae	51.	39	14	35%
19. Plumbaginaceae	12.	39	13	33%
20. Primulaceae	26.	52	12	23%
21. Saxifragaceae	9.	45	9	20%
22. Valerianaceae	21.	38	7	18%
23. Papaveraceae	20.	50	6	12%
24. Rhamnaceae	43.	20	6	30%
25. Aristolochiaceae	—	13	5	38%
26. Asclepiadaceae	—	13	5	38%
27. Geraniaceae	17.	44	5	11%
28. Gesneraceae	48.	5	5	100%
29. Rutaceae	—	14	5	35%
30. Gentianaceae	31.	41	4	9%
31. Orobanchaceae	28.	41	4	9%
32. Polygalaceae	33.	16	4	25%
33. Convolvulaceae	41.	35	3	8%
34. Polygonaceae	39.	24	3	12%
35. Santalaceae	52.	17	3	17%
36. Aceraceae	—	10	2	20%
37. Caprifoliaceae	35.	17	2	11%
38. Cistaceae	13.	29	2	6%
39. Malvaceae	25.	30	2	6%
40. Plantaginaceae	29.	27	2	7%
41-9. Apoc. (—), Cappar. (45), Celastr. (46), Cheno. (22), Glob. (49), Lentib. (50), Resed. (15), Tamar. (—), Thym. (24) at 1 each		127	9	7%
		5171	1576	30.4%

Monocots

Spain

Family	No. in other list	Species	Endemics	Percentage of Endemism
1. Gramineae	2.	352	61	17%
2. Amaryllidaceae	6.	43	18	41%
3. Liliaceae	1.	121	15	12%
4. Cyperaceae	7.	108	8	7%
5. Iridaceae	4.	28	8	27%
6. Juncaceae	9.	39	2	5%
7. Potamogetonaceae	8.	21	2	9%
8. Araceae	5.	7	2	28%
9. Orchidaceae	3.	59	1	1%
10. Alismaceae	10.	7	1	14%
11. Hydrocharidaceae	15.	3	—	—
12. Scheuchzeriaceae	14.	3	—	—
13. Sparganiaceae	13.	3	—	—
14. Lemnaceae	12.	3	—	—
15. Typhaceae	11.	2	—	—
16. Butomaceae	18.	1	—	—
17. Dioscoreaceae	16.	1	—	—
18. Naiadaceae	17.	1	—	—
19. Palmaceae	+	1	—	—

+ not in the other list.

This is a very striking list, after studying which it is difficult any longer to believe that endemism is just a case of casual relicdom. It shows several interesting features, *e.g.* (1) the larger the family on the whole, the more endemics does it produce; (2) there is wonderfully close agreement between Spain and the Balkans, though they are 1000 miles apart; (3) the agreement goes into the proportion of endemism, which decreases with the size of the family, as shown in the table at foot of following page; (4) families with many endemics in one country also show them in the other, as is shown by the figures of position in the other list given after each (e. g. *Compositae* is first in both lists, *Leguminosae*, second in the Spanish list, is sixth in the Balkans, and so on; most of the earlier families occur in both lists; (5) the first seven families are the same in both countries, and are the largest in Europe; (6) their proportion of endemics is 67% of the Spanish, 68% of the Balkan, a result one would not expect upon any theory of selection; (7) only 26 Spanish and 19 Balkan Dicot. endemics, out of the very large totals, are in families that have endemics in one of the countries only.

It is difficult to find any argument based upon selection for such close agreement of the two lists of Dicots and also

MONOCOTS Balkans

Family	No. in other list	Species	Endemics	Percentage of Endemism	With endemics in Spain
1. Liliaceae	3.	252	93	36%	Sp.
2. Gramineae	1.	353	32	9%	Sp.
3. Orchidaceae	9.	99	14	14%	Sp.
4. Iridaceae	5.	62	14	22%	Sp.
5. Araceae	8.	12	4	33%	Sp.
6. Amaryllidaceae	2.	22	3	13%	Sp.
7. Cyperaceae	4.	140	2	1%	Sp.
8. Potamogetonaceae	7.	25	—	—	Sp.
9. Juncaceae	6.	39	—	—	Sp.
10. Alismaceae	10.	6	—	—	Sp.
11. Typhaceae	15.	6	—	—	
12. Lemnaceae	14.	5	—	—	
13. Sparganiaceae	13.	5	—	—	
14. Scheuchzeriaceae	12.	4	—	—	
15. Hydrocharidaceae	11.	4	—	—	
16. Dioscoreaceae	17.	2	—	—	
17. Naiadaceae	18.	2	—	—	
18. Butomaceae	16.	1	—	—	

All the families except the palms appear in both lists. The grouping of the families is very similar to that in the Spanish list. But the total of the seven large families with endemics is 940 species, 162 endemic, or only 17.2%.

the two lists of Monocots, with such different percentages. It has been suggested that it is due to a different rate of mutation, but we shall see in the SEYCHELLES that the figures go the other way there.

Figures of endemism (Dicots) in Spain and in the Balkans

Dicots	Spain			Balkans		
	Total	species Endemic	% endem.	Total	species Endemic	% endem.
First 7 families [1]	2327	758	32%	3245	1086	33%
Second [2]	543	170	31%	952	300	31%
Third [3]	361	86	24%	363	106	29%
Fourth	244	45	18%	183	39	21%
Fifth	155	29	18%	188	26	13%
Sixth	156	19	12%	123	12	9%

[1] The same in both.

[2] Four in common.

[3] One in common.

The smaller the family on the whole, the smaller its proportion of endemism. In other words, local size of a family depends upon local age to a large extent (laws of ASA), and the older that it is there, the more likely is it to have many endemics, which are usually simply the species of younger development.

In case it is asked why Italy is not included, its flora is constructed upon so different a standard of specificity that it would have required too much labour to equate them. But the proportions of endemism are much the same, and the genera with endemics also.

A still more striking feature in the table is that only 26 Spanish and 19 Balkan endemics, out of the large total of Dicots, belong to families that do not show endemism in both countries, though they are 1000 miles apart. Each list comprises about half the 100-odd Dicot families in the country, yet the two agree in all families with more than five endemics. Those that have them only in one list are marked (—) instead of with the number of the family in the other list, and these marks only begin at line 25. They comprise only 45 out of 2695 endemics, while the 43 families with endemics in both countries contain 2650, or 97% of the Spanish and 98% of the Balkan endemics.

A similar connection in endemism, but even more striking, as one would expect, is shown by Ceylon and the nearer parts of India, the Madras Presidency, Travancore, and Cochin. For a complete list of the species there endemic, a list which would have cost great labour to prepare, I am most deeply indebted to Mr C. E. C. Fischer, joint author of the *Madras Flora* (41), and with the aid of this I have worked out the following statistics :

	Dicot Genera with endemics	Endemic spp. in			
		S. India	Aver.	Ceylon	Aver.
129	in both countries	678	5.2	442	3.4
188	in Madras only	333	1.77		
99	in Ceylon only			157	1.58
416		1011		599	

Taking them on the whole, therefore, before any analysis is made, it is evident that the MADRAS genera are the older for those with endemics in both countries, as shown by their greater average, and even to a small extent, perhaps, for those with endemics in one only. Even though there are 188 MADRAS genera with no endemics in CEYLON, no fewer than 119 of them are represented there by wides, in decreasing order with size, 58 showing only one, 26 two, and so on. There are 69 left, of which 31 are confined to the INDO-MALAYAN region, and had not reached CEYLON in time. As in the MEDITERRANEAN region, they are small genera, none exceeding 25 species—any larger (older) than that have usually reached to greater dispersal. Five are endemic to the MADRAS region, all monospecific. Some are large tropical genera like *Mimosa* with 400 species, or *Jatropha* with 200, which had not yet reached CEYLON when it was cut off, and the rest mostly are palaeotropical, probably in the same conditions. It is not possible here to go into the details of the peopling of CEYLON with plants, though it is worthy of special notice that in the MADRAS endemics and in other features of the flora there is some definitive evidence that MADRAS was independently connected to FURTHER INDIA as well as round by CALCUTTA, for there are a number of genera of that region that do not occur in CEYLON, and other things.

The families with endemics only in SPAIN or only in the BALKANS are usually represented in the other country by a few non-endemics, which have evidently not been there long enough to give rise to local species. Indications like this, tending to show that some family or genus has reached A sooner than B, may prove useful in tracing migrations, and perhaps even in tracing regions of origin. *Resedaceae*, again, has 15 out of 23 endemic in SPAIN, and only one of eight in the BALKANS, so that it looks as if they had actually commenced in or near SPAIN, and spread eastwards. *Cistaceae* show somewhat similar phenomena.

All over the world, the large families show the largest numbers and proportions of endemics. Even in the HAWAIIAN ISLANDS, with perhaps the most remarkable endemic flora in the world, the bulk of it is found in *Campanulaceae*, *Caryophyllaceae*, *Compositae*, *Gesneraceae*, *Labiatae*, *Rubiaceae*, and *Rutaceae*. In the GALAPAGOS, it is chiefly *Amarantaceae*, *Boraginaceae*, *Compositae*, *Euphorbiaceae*, and *Rubiaceae*, again large families, but indicating a somewhat different source or sources of origin. Similar facts are true of the genera. It is abundantly clear that endemism is not a casual phenomenon of relicdom, but is obeying definite laws, and is open to inductive study, which may lead to many useful results, even though it does contradict the theory usually known as Darwinism.

Another interesting fact is that the representation of the families in SPAIN and in the BALKANS is not altogether unlike. After each family in the tables on pp. 70-3 is given its place in the other list. Adding these numbers up in eights, the first eight adds to 39 in the Spanish list, 42 in the Balkans, seven out of the eight families being the same in both. The following eights give 167/144, 210/206, 220/291, and 286/333. The number of endemics in other words, shrinks fairly well with the size of the family. The top seven families, which are the largest families in EUROPE, have 57% of the BALKAN species and 62% of the SPANISH, and contain respectively 67% and 68% of the endemics, a close agreement. They contain a good half of the whole flora of most, or all, European countries. Their percentage of endemics is markedly higher than that of their species, which bears out what we have said about the greater proportion of endemics in the larger families.

If one look into the sizes of the genera in any MEDITERRANEAN (or other) flora, one finds a striking difference between those that do, and those that do not, contain endemics. On the principles here employed, it is clear that the endemics should be in the larger (older) genera. Probably, of course, there will be exceptions, with various reasons behind them. One will not expect biological phenomena to occur with deadly exactness. But one will expect that even though the two sets of numbers overlap, those with endemics will be mainly towards one end of the scale, those without towards the other. Supposing that we examine the *Compositae* in the BALKANS and in SPAIN, we find

Proportions of endemics in Spain and in the Balkans in genera of the Compositae of different sizes

SPAIN

Size of genus	Number of gen.	With endemics	Without	% with	Total endemics	% of endemics
1 species	49	7	42	14.2%	7 spp.	3.2%
2-3	42	13	29	23.8%	14	6.4%
4-6	22	18	4	81.8%	30	13.7%
7-12	12	11	1	91.6%	31	14.2%
Over	8	8	0	100.0%	135	62.2%
	133	53	80	40.0%	217	

Average per genus 1.6

BALKANS

Size of genus	Number of gen.	With endemics	Without	% with	Total endemics	% of endemics
1 species	32	2	30	6.6%	2 spp.	0.6%
2-3	25	8	17	32.0%	11	3.4%
4-6	16	10	6	62.5%	20	6.1%
7-12	9	8	1	88.0%	23	7.0%
Over	18	18	0	100.0%	268	82.4%
	100	46	54	46.0%	324	

Average per genus 3.24

The greater the size of the genus, the more endemic species has it, in proportion, and upon the whole. The Balkan genera show a higher percentage of endemism, in the large genera especially, which goes perhaps to show that the *Compositae* are older in the BALKANS than in SPAIN. But full taxonomic investigation is absolutely needed, especially as the Spanish flora recognises more genera than does the Balkan.

An approximate count of the whole Balkan flora goes to show that the number of " ones " with endemics is 14, against 259 without, of twos 17 against 79, of tens 9 against 5 (note order reversed), while above 20 species there are 58 genera, ranging up to 171 species, and of these only two, *Salix* with 24 and *Medicago* with 29, are without endemics.

If now we take the Spanish and Balkan genera that contain the largest numbers of endemics, we get :

Spanish and Balkan genera with largest numbers of endemic species

DICOTS				Spain
	Position in other column		Endemic species	Spp. in world
1. Centaurea	(1)	Comp.	49	600
2. Hieracium		Comp.	37	750
3. Saxifraga		Saxi.	31	325
4. Genista		Legum.	29	90
5. Linaria		Scroph.	28	100
6. Ononis		Legum.	22	75
7. Ranunculus		Ranun.	21	325
8. Galium	(11)	Rubi.	19	250
9. Armeria		Plumb.	17	60
10. Senecio		Comp.	16	2000
11. Teucrium		Labi.	16	180
12. Thymus	(4)	Labi.	16	100
13. Ulex		Legum.	15	20
14. Arenaria		Caryo.	15	100
15. Dianthus	(2)	Caryo.	15	250
16. Iberis		Cruc.	14	30
			360	
		Average (world)		327

DICOTS				Balkans
1. Centaurea	(1)	Comp.	112	600
2. Dianthus	(15)	Caryo.	63	250
3. Verbascum		Scroph.	57	210
4. Thymus	(12)	Labi.	56	100
5. Campanula		Camp.	50	300
6. Silene		Caryo.	46	400
7. Viola		Viol.	32	400
8. Astragalus		Legum.	30	1600
9. Stachys		Labi.	30	200
10. Asperula		Rubi.	29	80
11. Galium	(8)	Rubi.	25	250
12. Trifolium		Legum.	23	290
13. Hypericum		Gutt.	22	300
14. Crepis		Comp.	21	240
15. Euphorbia		Euph.	20	750
16. Achillea		Comp.	19	115
			635	
		Average (world)		380

Families with genera/endemic species

1.	Compositae (1)	3/102	Compositae (1)	3/152
2.	Leguminosae (2)	3/66	Leguminosae (2)	2/53
3.	Caryophyllaceae (3)	2/30	Caryophyllaceae (3)	2/109
4.	Labiatae (4)	2/32	Labiatae (4)	2/86
5.	Scrophulariaceae (5)	1/28	Scrophulariaceae (5)	1/57
6.	Rubiaceae (6)	1/19	Rubiaceae (6)	2/54
7.	Saxifragaceae	1/31	Campanulaceae	1/50
8.	Ranunculaceae	1/21	Violaceae	1/32
9.	Plumbaginaceae	1/17	Guttiferae	1/22
10.	Cruciferae	1/14	Euphorbiaceae	1/20
	Total spp. Spain	360	Balkans	635

Numbers in brackets give position in other column. The first six are the same in each.

All these 28 top genera are British, as would be expected by the laws of ASA. They are all near the top of their families, nine being actual leaders. They contain 995 out of a total of 2695 endemics of Spain and the Balkans, or 37%. In each case they belong to ten large families, the top six of which are the same in both, with 24/788 gen./spp. against 8/207 in the other four. The average world size of these genera is very large indeed. These facts are repeated all over the world, and there seems to be no possibility of maintaining the thesis that endemics are relics, except in special cases. *Alyssum*, with 21 endemics in all, is the largest non-British genus, but there are many British genera that surpass this figure, up to *Centaurea* with 112 in the Balkans alone.

Roughly speaking, the great majority of those genera that have many endemics have some in both countries, and what reason should there be for this if these genera were relics. Much more probably, it is they that are the oldest in the Mediterranean region, and have therefore spread to the widest dispersal there, and therefore are most likely to be found also in the British flora. On the other hand, genera with very small numbers of endemics are usually found to show them only in SPAIN, or in the BALKANS, not in both, and to be rare, if found at all, in BRITAIN.

These tables provide many queries for the selectionist. Why should Centaurea have so many "relics" in the MEDITERRANEAN region, and none in BRITAIN, where there would seem to be less competition? Why is BRITAIN not a refuge? Why should Verbascum have 57 relics in the BALKANS with 25 widely dispersed species, and only 5 with 12 in SPAIN —the proportions reversed? Were some of the wides killed out in the fight with the endemics? Why has it only one relic in CRETE, close to the BALKANS, and an island, usually supposed to be a good refuge? Why should *Asperula* and *Galium* have 28 and 25 relics in the BALKANS, and only 5 and 19 in SPAIN, while *Senecio* has 17 in one and 16 in the other? There is no end to the awkward questions that may be brought up, and that are quite insoluble by the aid of the theory of adaptational structural selection, but which show that endemism is a subject that follows definite rules, and that will repay inductive study. There is still ample opening left for those who, in HOOKER's words, "find it far easier to speculate than to employ the inductive process".

The flora of Sardinia. Let us now consider one of the MEDITERRANEAN islands, further from the mainland than BRITAIN, and with deeper water between, probably sooner isolated. One may predict that the bulk of the flora will belong to the same families as in BRITAIN, the older, as usual, being the better represented. Taking the 14 families with more than ten genera, we find them, with one exception, the same as the largest families in BRITAIN; *Ericaceae* there replaces *Borraginaceae.* They have 379 genera out of 571, or 66%, while in BRITAIN they have 287 out of 475, or only 60%. The only families in SARDINIA that are not found in BRITAIN are 14 small ones with 20 genera among them. The proportion of endemism is not so high as one might expect, for what reason is not evident, but that of the Dicots is double that of the Monocots; there is a greater proportion in the larger genera, and the average world-size is greater :

Flora of Sardinia to show local and world sizes of genera, and British relationships

	Dicots			Monocots		
Size in Sardinia	Genera	Proportion British	World Size	Genera	Proportion British	World Size
8 or more species	31	100%	318	8	100%	243
4, 5, 6, or 7 species	71	84%	129	28	85%	84
2 or 3 species	122	58%	57	35	77%	41
One only	218	39%	42	58	48%	34
Total	442			129		

Arranging the families with and without endemics in parallel rows by their numbers of species in SARDINIA, we get :

Sardinian families with and without endemics

With endemics	183, 179, 77, 66, 58, 57, 52, 40, 35, 34, 26, 25, 21, 19, 18, 16, 16, 16, 13, 10, 9, 6, 4, 2/3.
Without	29, 21, 16, 12, 12, 11, 10, 9, 8, 8, 8, 8, 7, 7, 6, 6, 6, 6, 5, 5, 5, 5, 4, 4, 4, and 12/2, 19/1.

This very striking feature about endemism shows everywhere except in a few places where there are a few endemics and those undoubted relics, mainly places where they came under the influence of the cold in the glacial period.

The larger genera in SARDINIA are all British, but the proportion decreases down to the ones, where it is below 50%. This arithmetical phenomenon, of which the writer has published numerous examples, is inexplicable by aid of selection or of adaptation. There is here the effect of a definite factor, which has already been sufficiently shown to be mere age, that allows time for the resultant of all the active factors to work, and we must fully understand these mechanical effects before we can properly study those of the vital factors.

The figures show that the larger a genus or family is in SARDINIA, the better is its chance of appearing in BRITAIN. *Compositae* head the list by a large margin, followed by *Cruciferae*, *Labiatae*, *Leguminosae*, *Scrophulariaceae*, *Umbelliferae*, *Borraginaceae*, and *Euphorbiaceae*, all families that have already figured high in our lists. Just as in going northwards, and especially at great barriers like mountains or sea, the smaller families and genera are those chiefly dropped out, so are they dropped out in the formation of endemics, which is more and more rapid the larger the family (hollow curve). The older or larger families and genera are those that have had the most time, whether to travel northwards, to evolve many species, or to form others (which begin as endemics) from those already present (" to him that hath shall be given ").

The other MEDITERRANEAN islands may be passed over in a few words, as all show the same phenomena as SARDINIA. CRETE presents a point of interest. The average local size of a Dicot genus in the BALKANS (including CRETE) is 7 species, but of the 400 out of the total of 739 that actually reach CRETE, it is 11, while of the 191 Cretan genera that also reach BRITAIN, it is 18. The laws of ASA are very important in distribution, and practically dispense with any need to call in adaptation.

If we compare the endemism of SARDINIA and the BALEARICS with that of SPAIN or the BALKANS, we find that a great part of the genera that show endemism in the islands also show it on the mainland. They belong mainly to the genera that on the whole are the oldest, and therefore the most widely dispersed in the MEDITERRANEAN region.

The seniority of the Dicots in the MEDITERRANEAN area is so marked that one may with some confidence make the further prediction (**150** p. 87) that in the CANARIES, which are very old as islands, and are upon the extreme edge of the MEDITERRANEAN region, one will find the position of the Monocots, as regards endemism, to be even lower than in SARDINIA. This is strikingly borne out by the facts, for while the CANARIES have 418 species of Dicot endemics, which would lead one to expect about 105 Monocot endemics (four to one, *cf. AA.* p. 22), they have in reality only 27.

Relationships between southern endemism and the composition of the British flora. If, as we have seen good reason to believe, dispersal is chiefly regulated by the three laws of ASA, the large and old families, with many endemics in the south, will be the largest and oldest in BRITAIN. A glance at the table on p. 70 shows that all Spanish families with endemics are British, excepting three with one endemic each—*Capparidaceae*, *Gesneraceae*, and *Globulariaceae*. In the Balkan list six families, all small, do not occur in BRITAIN

—*Asclepiadaceae, Gesneraceae, Rutaceae* with five endemics each, *Capparidaceae, Globulariaceae,* and *Tamaricaceae* with one each. Even here, three of them also occur in SPAIN.

As the endemics are mainly in the larger genera, one may make about as good a prediction by picking these out as most likely to be found in BRITAIN. There are 96 with at least 15 species, and all but nine occur in the British flora. One may even make more predictions, for example that the British single genera (one only in the family) that have endemics in both SPAIN and the BALKANS will be larger in BRITAIN than those with endemics only in one of these countries. They actually show (in British species) 37, 26, 21, 16, 8, 8, 8, 2 against 5, 3, 2, 1, 1, 1, 1. Or again, one may predict that the larger genera of BRITAIN will usually have endemics in south EUROPE; this is the case for 93% of the Dicots, but for only 79% of the Monocots, again a difference in favour of the former. We may even expect that the most widely dispersed in BRITAIN will show the most southern endemics, and we find that those with one species only and with a dispersal in BRITAIN not more than 56 have southern endemics of 43% of their number, 56-112 of 61%, while the twos have 118%, threes 170%, fours and fives 188%, sixes to tens 196%, and larger 226%. These are again simple arithmetical relations, which help to make the support of the idea of relicdom rather precarious.

Range of dispersal in Britain. There are 101 Dicot species, in 71 genera, which range over all the 112 vice-counties of BRITAIN. Placing the families by the numbers that they contain, we get the table that follows. The first eight families contain the first seven of the lists of Spanish and Balkan families on pp. 70-3. *Rosaceae* displaces *Ranunculaceae* from the top eight of the Spanish list and *Campanulaceae* from the Balkan list. Of the 71 genera these families contain 46, and of the 101 species 62. They also receive more additions at 111, 110, &c. Smaller and smaller families come in as one goes down the list. These eight top families also contain 179 of the 347 British Dicot genera, or more than half, and 69% of the endemics of SPAIN and the BALKANS. There are 20 families with endemics that have no species reaching 112 in BRITAIN, but they only contain among them 202 endemics in the BALKANS, and the last five families, that have no species in BRITAIN at all, have only 17 endemics

Dicot families, any of whose members reach a dispersal of 112 vice-counties in Britain, in order of the number of genera that do so

Family	Place in Spain and Balkans	British Genera	No. with at least one species 112	Extra spp. 112	Total 112-105	Endemics in Spain	Endemics in Balkans	Total Endemics
Comp.	(1, 1)	43	14	4	30	217	323	540
Caryo.	(4, 2)	12	6	2	12	78	175	253
Labi.	(6, 3)	18	6	1	11	75	153	228
Legum.	(2, 6)	17	5	2	14	137	105	242
Crucif.	(3, 7)	24	4	1	9	112	96	208
Rosac.	(16, 14)	15	4	1	14	15	23	38
Scroph.	(5, 4)	13	4	5	16	78	128	206
Umbell.	(7, 5)	34	3	—	9	61	106	167
Ranunc.	(8, 11)	11	2	5	8	31	37	68
Rubi.	(10, 9)	4	2	2	6	25	53	78
Polygon.	(39, 34)	3	2	3	10	3	3	6
Eric.	(42, —)	11	2	—	3	2	—	2
Betul.	(—, —)	4	2	—	3	—	—	—
		209	56	26	145	834	1202	2036
15 fams. with one gen. 112[1]		48	15	4	32	103	174	277
		257	71	30	177	937	1376	2313
Percentage of Brit. Dicots		74 %						

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[1] Aral., Borag., Caprif., Chenop., Dips., Euphorb., Geran., Lin., Onagr., Oxal., Plantag., Primul., Urt., Valer., Viol.

among them. Of the genera with a dispersal in BRITAIN of 112-109, 76.9% have endemics, dispersal 108-101 63.6%, and 100 or less only 48% have endemics.

A good illustration of the way in which the endemics in the different MEDITERRANEAN countries agree in belonging only to the larger genera or families, and very commonly to the same ones in countries far apart, was given as Table XXVII on p. 89 in **(150)**.

So closely are the arithmetical laws of ASA that we have been illustrating followed, that we may even take single families or large genera to show them. Of the *Compositae* of SPAIN and the BALKANS, 74 genera show endemics there. Twenty-seven with endemics in each country show 442 endemics in all, and have an average world size of 215; while 47 show endemics in only one of the two countries, have 82 endemics in all, and an average world size of 30 only. Of the 27,85% are British, while of the 47 only 19% are.

If the British flora owed its dispersal and composition to adaptation, one could not do any prediction from the floras of southern EUROPE, whereas we have seen that most of the larger genera, and other features, can easily be predicted. Mere size or age of families and of genera has had an enormously greater influence than anything else in determining the composition of a flora, and the proportions of endemics contained in it in the countries where it is oldest.

Monocotyledons. So far we have dealt only with Dicots, not because they show better results, but to save space, and because the Monocots, while showing results that are essentially the same, yet show them in such different degree that there is evidently a hitherto unnoticed difference between the two groups. The table of numbers of species and of endemics, was given above.

This table offers points of interest. It shows clearly how the larger families have endemics in both countries, and that the smaller have endemics in one, or none in either. A noteworthy feature is the much smaller percentage of endemism than in the Dicots (14 and 15% against 32 and 33%). This at once suggests that the Monocots are later arrivals on the whole. It has been suggested that they are slower in mutation, but this does not explain cases where the figures go the other way. The differences between individual families are also very marked. Careful and detailed work upon such figures as are given here should ultimately teach us much about dispersal, but much more work is needed yet, and more mathematical skill than is usually possessed by the biologist, including the writer. It should also lead to results which will be useful in geological and other investigations.

Endemic genera. Most endemics are species in large genera, but there are also many genera that may be classed as endemic as they are very local. There are a number of these in south EUROPE, though often overlapping into AFRICA or ASIA. They behave like the species, *e.g.* in belonging to the larger families. *Umbelliferae* with 38 and *Cruciferae* with 34, both well-known Mediterranean families, head the list in Europe, *Compositae* and *Gramineae* with 24 each following, these four families thus having nearly half the total number of about 250 in that area. Not only so but they belong to existing sub-families, usually the most important. For example, more than half the *Umbelliferous* genera belong to the *Apioideae-Ammineae*, the largest division of the family. Only very rarely indeed, in any part of the world, does one find endemic genera as instances of very discontinuous distribution, or belonging to out-of-the-way groups.

If in conclusion we sum up the statistics, we get :

Proportions and distribution of Spanish and Balkan endemics

Dicots

British genera	Genera	Species (Spain)	No. per genus	Species (Bkns)	No. per genus	World size	No of 112s
Endemics in both	119	737	6.1	1098	9.1	172	83
Endemics Spain only	53	141	2.7	—	—	57	9
Endemics Bkns. only	34	—	—	88	2.6	69	8
Non-British genera							
Endemics in both	37	66	1.8	149	3.9	—	—
Endemics Spain only	100	176	1.7	—	—	—	—
Endemics Bkns. only	76	—	—	194	2.6	—	—

Monocots

British genera							
Endemics in both	15	72	4.8	73	4.8	154	6
Endemics Spain only	19	32	1.6	—	—	53	9
Endemics Bkns. only	11	—	—	63	5.7	32	1

Non-British genera	Genera	Species (Spain	Nº per genus	Species (Bkns)	Nº per genus		World size
Endemics in both	3	3	1.5	16	5.3	—	—
Endemics Spain only	10	12	1.3	—	—	—	—
Endemics Bkns. only	8	—	—	10	1.4	—	—
Total Dicots							
British	206	878	4.2	1186	5.7		126
Non-British	213	242	1.1	343	1.6		—
Total Monocots							
British	45	104	2.2	136	3.0		81
Non-British	21	16	0.8	26	1.3		—

The percentage of endemics in genera that appear in BRITAIN is fairly closely the same as the actual percentage of the whole number of species that belong to them. This fact shows in nearly all the larger families, and is an almost full denial of the supposition of relicdom. One can hardly imagine relics formed in proportion to the number of species. One or two families appear as if they might to some extent be polyphyletic, especially *Borraginaceae*.

The phenomena of endemism clearly show themselves in such a way that it is evident that they are determined by the action of law; it would be impossible that relics should behave in such a manner. This view might probably have been accepted long ago, had it not been that in this acceptance is involved the destruction of the Darwinian theory of the operation of evolution, that it proceeds by the selection of advantageous variations, and little by little. Endemism is clearly a normal accompaniment of the composition of any flora that has reached a certain age in the place where it is growing, especially, it would seem, if that locality be rather isolated, or mountainous, or otherwise broken, or when the plants there perhaps come under the influence of certain stimulants to a greater extent than usual, a fact which, upon the working hypothesis which I have used since 1907 (p. 96) would be likely to stimulate a rearrangement of the nucleus, most often only to such an extent as to produce a new species, but at times going far enough to produce a new genus.

CHAPTER IV

Discontinuous distribution
Destruction of transitions

The wide separation of plants with close structural relationships is very common, and has always presented difficulties. One may find in a monograph that a genus is placed for structural reasons in a position quite different from that to which its geographical relationships would point. Under any system of Evolution two structurally related things must usually have had some third, ancestral, thing in common, from which they perhaps derived their characters by selection of adaptational improvements. This ancestor would usually cover a fairly definite and continuous area, in all probability, and if it could be gradually changed into either of the other two, the matter would be simple enough. But for such change, in a definite direction, whether continuous or by small steps, there must be some force acting that will always pick out steps in that direction.

The only agency yet suggested that is likely to be able to do this is natural selection, ruthlessly acting upon the ever-present choice between (a) advantage and (b) non-advantage or disadvantage. Even then one must assume (*cf.* Testcase X, *Evol.*, p. 114) that the adaptational urge is so great that a character will be selected right through to the perfect state in which it usually appears. But for most structural differences, no one has ever been able to suggest any adaptational advantage, so that this argument has but little force. With it goes most of the value of the usual explanation of structural discontinuity, that the less valuable transitions have been killed out by better adapted things. Owing to the great production of offspring, there must always be much destruction going on, but it is of ill-suited *individuals*, one of species A being killed out in one place, one of B in another, rarely or never of all individuals of species A by those of B. Each is judged upon its own total merits; all A are not superior to all B, though there has in recent years been a great recrudescence of this fallacy. It depends upon the immediate local conditions which of them shall win in any given place. This being so, geographical continuity of the area that a species or genus may occupy becomes of greater importance than has hitherto been given to it, and any discontinuity in it needs explanation.

Real discontinuity. Discontinuity ranges over all possible distances and directions, and can be no better defined than endemism. In a fairly uniform country like BRITAIN, with no high mountains, it is usually disregarded, but a species found only in the ALPS and the PYRENEES, for example, is regarded as discontinuous. Here we have many different plants showing the same thing, in the same way, and in the same places, while the climate and other conditions differ in the intervening country, so that there is formed what we may call a real discontinuity in more than one feature. A case like this, where the species, or at any rate the genus, is the same on both sides of the gap, cannot be thrust aside. It is usually supposed that at one time a colder climate allowed these plants to flourish in the plains, while they retreated higher in the mountains when it became warmer. This is a sound explanation, supported by geological evidence, and by such further cases as the *Diapensias* of the arctic region and the central chain of mountains of EURASIA. Another widespread case of discontinuity like this is of course the separation by wide expanses of ocean, but here one must not forget that in such cases as the occurrence of a couple of species of a genus in MADAGASCAR and the same in CEYLON, the genus may have reached both by land, even if the INDIAN OCEAN were already unbridged. One may see something like this in the case of some of the *Berberidaceae*, of *Epigaea*, of *Shortia*, and of other things, which occur with a species or two in eastern ASIA and in eastern NORTH AMERICA. It is usually supposed that in a warmer period they grew in the far north, and that when the cold began to come, the roads of retreat open to them led one to E. ASIA, one to E. NORTH AMERICA.

Structural discontinuity. There is also a much more common discontinuity that we may call structural. Here a genus, or more rarely a small group, is found to exist in a region far removed from that in which its nearest structural allies are to be found, as judged by taxonomical work, which at present is founded almost entirely upon structural resemblance. A few examples may be taken in the usual way from books lying upon the table.

In *Phytolaccaceae (PR)*, tribe *Rivineae*, eight of the nine genera are tropical American, the ninth is in QUEENSLAND, NEW SOUTH WALES, and NEW CALEDONIA, a solitary species, separated from the rest of the *Rivineae* by the whole width of the PACIFIC. The subtribe *Barbeuinae* of *Phytolacceae* consists of a single genus *Barbeuia*, with one species on the east coast of MADAGASCAR, separated from the rest of the *Phytolacceae* on account of its two carpels (against 3 — ∞) and capsular (against fleshy) fruit, two obvious mutation characters. The only other *Phytolacceae* in MADAGASCAR are two *Phytolaccas* living in the hills near TANANARIVO, and it is probably a direct descendant of one of these.

In *Amarantaceae*, tribe *Amaranthinae (PR)*, which includes genera 6-17, 6 has one species in the CANARIES, one in CYPRUS, one in INDIA, 7 is AMERICAN, 8 INDO-MALAYAN, 9 HAWAIIAN Is., 10 the NILGIRIS (S. INDIA), 11 the ALDABRAS (north of MADAGASCAR), 12 is AFRO-MADAGASCARIAN, 13 (*Amarantus*) warm regions of the world, 14 N. AMERICAN, 15 western U. S., 16 INDO-MALAYAN and east AFRICAN, 17 SOMALILAND. The thinly spread *Amarantus* is the only one that could possibly be parental, and the structure and the geography do not harmonise over the twelve genera.

Or in *Santalaceae*, sub-family *Osyrideae (PR)* 3-7, forming a sub-tribe distinguished by mode of anther-dehiscence, are found in AUSTRALIA and INDO-MALAYA; 8 has one species only in S. BRAZIL, URUGUAY, ARGENTINA, 9 has four in PERU and ECUADOR, 10 has four in CHINA, JAPAN, and the southern U. S., 11 one in east AUSTRALIA, 12 one in the southern U. S., 13 the same, but also one in the HIMALAYA, 14 has seven MEDITERRANEAN to CHINA, 15 one U. S. to ALASKA; 16 has one on the DANUBE and five in N. AMERICA, while 17 has one in southern ARGENTINA and the FALKLANDS. If these had to be produced by selection, the destruction required is simply incredible, nor is there time, in the lifetime of this group, for such land changes to have come about. Simple mutation would make all the changes here necessary between genus and genus, once *Amarantus* or *Thesium* or some other big genus had travelled to the place required.

Or let us take a somewhat larger group, the *Phyllantheae* in *Euphorbiaceae* (*NP/2*, p. 44). Their thirty genera are thus divided : 20 in *Antidesminae*, with a curve of sizes 160 *(Antidesma)* 70, 70, 25, 20, 12, 10, 6, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1 ; 5 in *Glochidiinae*, with a curve of 280 *(Glochidion)*, 30, 4, 1, 1; 5 in *Phyllanthinae*, with a curve of 480 *(Phyllanthus)*, 20, 1, 1, 1, and so on giving a curve of 480, 280, 160, 70, 70, 30, 25, 20, 20, 12, 10, 6, 4, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, which is quite a good hollow curve, suiting well enough the dichotomous formation of new genera which we have seen to be the rule, and once more showing how the taxonomic (structural) breaking up of allied genera into smaller and smaller groups produces more and more confusion both in their geographical and in their systematic grouping, to say nothing of the way in which it spoils the " hollow-curve " arrangements. It seems impossible, if the basis of taxonomic work is genetic, that the hollow curve, demanded by the dichotomous division rule of formation of new genera, should thus appear only when one adds up a few of the smaller groups, in which it does not show itself. Upon whatever principle one makes the small groups, they are headed by comparatively important genera, by reason of the principle of divergence; but the followers are not in any way such as are proportional to the leader, as one may see in the groups just quoted, though the three together add up to form a good hollow curve.

Not only do the *Phyllantheae* thus form a good curve only when all taken together, but the same is true of their geographical relations. Though in the *Antidesminae* the two leaders are Malayan, the group includes 20, 12, 4/2, 3/1 in WEST AFRICA, and so on. This is a phenomenon of very great frequency, and goes to show that the characters that took these genera into the *Antidesminae* were derived from ancestors (or more likely from the genus of 20, which was probably the parent of this group, and was not itself the offspring of one of the Malayan genera) that did not belong to that group of the *Euphorbiaceae*. The more we enquire into the geographical distribution, the greater seems the probability of frequent polyphyletic origin of structurally similar characters. If we recognise this common origin of family characters, and that they are not due to later casual formation by selection of slight changes, it makes the whole position far simpler. One man thinks a genus most nearly allied to X, by reason of the characters A and B; another would ally it to Y because of C and D, and until we can find out what was its real parent, we shall get no further. One comes more and more nowadays upon such remarks as (apropos of the two families *Amarantaceae* and *Chenopodiaceae*) " Unterscheidung zwischen den beiden Familien fast unmöglich, die Trennung in zwei Familien überhaupt eine Convenienzsache." The more that taxonomic work improves, the more is it being realised that genera and families pass into one another; their characters are given to them by their ancestors by some system of permutations and combinations.

These examples might be much extended, for one can find similar cases everywhere. But to find remarkable geographical connections, one need not go outside of one genus. By kind permission of the Linnean Society, I extract the following quotation from (**151**). " In *Cardamine*, for example, species No 70 is in NEW ZEALAND and POLYNESIA, 71 in the AZORES, 72 in CHILE. In *Euphorbia* one finds allied species in VENEZUELA and in CAPE COLONY, in PERSIA and in AFRICA, in central ASIA and in N. AMERICA, and so on. If in the *Drabeae* of *Cruciferae*, one join up the allied and consecutive genera by a line, one crosses the ATLANTIC five times and the PACIFIC once, and usually goes well into the continent also (**151**). In the *Arabideae* the crossings are seven and six respectively, and in the *Lepideae* the whole map is covered with a web of lines. " To obtain discontinuous distribution such as this, upon the Darwinian supposition, there would have to have been land connections in almost every possible direction, and for long periods in many directions, and we have no evidence for such, nor for the truly fantastic contortions through which the land would have to go to bring them about. The destruction shows in some plants or in others, at all kinds of ages, in every direction, and to any distance. How all this destruction could be effected does not seem to have been properly thought out. Why did the stages between two genera of *Agrostideae* (Nos 143, 144 in *NP/1*) die out over so vast a space, between the MEDITERRANEAN on one side, and VICTORIA and TASMANIA on the other, a space which lies on both sides of the equator, involving so many and so great changes of climate. And what was gained (as one must always ask when selection is concerned) by leaving the completed genera so far apart? If there were a few other examples of this particular separation, some explanation might be required, but this is just what does not happen; it rarely occurs twice except by accident. The only connecting links (if any) that occur in most cases of structural discontinuity are the large and widespread genera that sometimes cover both places. Under mutation of specific rank, which we have been upholding for a very long time, though A, B, and C may be the closest possible genetic allies, they need not necessarily also be the closest possible structural allies, and it is here that genetics comes into the matter, with chromosome numbers and other phenomena which we have not yet fitted into the mosaic of taxonomy and dispersal, but which must evidently find a place there. It is becoming ever clearer that geographical and genetic relationships must be taken into consideration as much as structural.

If the two structurally allied forms are to be derived by selection from a common parent, that parent must have occupied positions upon both sides of what is now the gap. The differences between the genera under consideration are very commonly divergent to such an extent that they could not both be derived from a parent that only showed one of them. Either the common parent—and there must be one somewhere in the line of descent—carried both characters, or neither. Of this choice it is clear that the first is enormously more probable. If this conception be carried out to its logical conclusion, it follows, therefore, that the first genus of a simple family must have been carrying all the characters of the family, or more probably the potentiality of producing them under certain circumstances. This conclusion is strongly supported by the fact that the separation is often very wide, while the genera themselves are usually small (young) and there is no evidence to show that they were ever united, other than by some large genus of the family that overrides both localities, or some *two or more* that do this. The explanation which we suggest for this structural discontinuity, that the "neutrality" of the parents is simply due to the fact that they carry a Pandora's box from which any newcomer may take any of the characters that appear in that family (at least), is a far simpler one than the idea that they were derived by selection.

In some of these cases of structural discontinuity, which incidentally seem to become more marked in each successive monograph, there are genera like *Amarantus* above, found in or near most places where the structurally related small genera occur. They therefore may have been, as we have suggested, the direct and immediate parents of the small genera, though even then one can hardly bring in selection, for the separation is so often by such markedly mutational characters as could not be the subject of selection. It is much simpler to derive two genera that are closely related structurally, but A in one place and B in another a long way off, from a common generic, or even family, ancestor that happened to mutate in a similar way in both places.

The important point for the present is to remember the distinction between real and structural discontinuity. The former, if the separation is great, and by deep oceans, usually goes back to far off times (reflected in large size of the genus), when the aid of geology is required to ascertain what were likely to be the conditions of life. The barriers that now divide them were formed after they had spread to either side. The structural discontinuity, however, usually applies to small and local things, which could not have had a common and direct ancestor unless they were formed by separate, though similar, mutations, of some genus (or even two allied genera) that covered both their localities. The genus in common is a frequent enough phenomenon, but at times it belongs to some other taxonomic division.

This must suffice for our present purpose of explaining some of the circumstances and phenomena that frequently appear in a further consideration of endemism.

CHAPTER V

The characters of endemics I

The writer began to study endemism in CEYLON about 50 years ago. Over a quarter of the flora of about 2800 species is endemic, largely in the wet southwestern zone. Being then a believer in selection, he found, to his surprise, that the endemics, then usually supposed to be *local* adaptations produced by selection, were much rarer than the non-endemics (wides). They were found upon areas of all sizes, from a few acres up, the numbers decreasing quickly upwards. It was clearly impossible to find conditions to match, and opposition veered to the converse direction, endemics being regarded as the relics of a past vegetation, now dying out. Here the fact was ignored that the great bulk of them belonged to large and well-known genera.

Further study convinced the writer that both these positions were unsoundly based (*AA*, pp. 84, 166). The greatest obstacle to their acceptance was that the dispersal of the endemics, when graphically presented, was always in fairly smooth curves of the same form, so that one could not draw a line of separation between successes and failures. Nor could one conceive either of these hypotheses as working upon lines that would produce such curves. He therefore proposed a new one, that the dispersal of endemics in a country was simply a miniature of distribution as a whole, which showed similar curves. Endemics in general were simply young species or genera that had not yet had time to spread very far. Though simple and obvious, this was strongly opposed, probably at bottom because it gave a direct contradiction to the Darwinian hypothesis that new forms were produced by gradual structural adaptation, while the less " well-adapted " transitions were killed out.

Six years of tropical experience, and of detailed work upon the *Podostemaceae*, then supposed to be the last word in adaptational evolution, had already in 1902 destroyed for the writer the conception that such a process as natural selection could be responsible for the structural differences everywhere seen, and had also destroyed the notion that species competed as units. It was clear that competition was usually an individual affair. So, when 40 years ago he accepted the theory of mutation as put forward by de VRIES, he accepted it with what seemed to him the needful logical proviso that *a single mutation could cover any existing difference between parent and child*, inasmuch as mutation left no opening for gradual transition from one to the other. In a paper of 1907 (**132**) he suggested this kind of thing in the evolution of the *Dilleniaceae*, and it showed clearly in *Podostemaceae* (**136**), where there were no conditional differences other than depth of water, which was continually varying, even in the same stream. Many completely unlike species lived side by side, showing the greatest structural differences known among the flowering plants (cf. figures in **148**). Their evolution seemed to the writer to be due to the continual action of the maximum possible pressure of plagiotropism, which affected all alike, and from which there was no possible escape, owing to the fact that the roots could not go vertically down into the rock. This at once suggested what the writer has since used as a working hypothesis, that after being exerted for a certain time, any strain of changed conditions, such as that when the *Podostemaceae* began to live upon rocks under running water, may ultimately cause the plant to readjust its relations to its surroundings in such a way as to relieve it from this strain. This would be, perhaps, only after the lapse of a certain definite time, or perhaps more often when the strain was temporarily increased by some unusual cause, such for example as the action of cosmic rays, which has been suggested. This view was of course not unlike that put forward by my former chief, Sir FRANCIS DARWIN (**31**), where the effect was produced by the accumulation of engrams.

Any change of importance seems to be based upon the reactions of the cell nucleus, so that it seemed to me that such a nuclear readjustment took place as would put the hitherto strained adaptation, an adaptation which the ancestors must always have had, or they could not have survived, upon such a basis that it centred upon the new conditions. That of the parent had been centred upon other conditions, elsewhere. This readjustment, which we can now clearly see as probably some rearrangement of the genes, would necessarily produce a structural alteration of the new plant, and an alteration which might be of any rank, so far as one could imagine. The bulk of the characters of the parent would appear in the offspring, but some would be different, and in view of the work described in this book and in *Evol.* not only different, but usually divergently so. The rank of the newcomer would be settled by the number of such characters, and their commonness or rarity in the family—a combination which leaves plenty of room for dispute. It suggested itself to the writer nearly forty years ago that " a group of allied species represents so many more or less stable positions of equilibrium in cell division " (**131**, p. 15), and this idea seems to fit with what we have since learnt about the behaviour of chromosomes.

The actual steps in structural evolution in the *Podostemaceae*, as would be expected under such circumstances, took the form of a more or less continual increase in dorsiventrality, the most dorsiventral—the most highly adapted, upon the old selection ideas—being very local genera of very few species, the least so the widely dispersed and multispecific genera like *Podostemon*. The forms differ to an almost incredible degree in their morphological structure, yet most of them seem able to live together in the same places (**136**, p. 535). The conditions under which they live are uniform to a degree.

The writer has continued to study evolution and distribution together for forty years, with occasional publication, especially in *Age and Area* in 1922, and after unavoidable delay, in *The Course of Evolution* in 1940. No very valid objections to his theories seem to him to have been brought forward, and the fact that he has been able to go from prediction to prediction and to find them all confirmed by the facts, though he has now made several hundreds, has caused him fully to believe in their essential probability. The present book, which presents some novelties in its treatment of the subject, has been all but entirely written by the method of prediction, with subsequent verification. Another good confirmation has been the fact that there has been no need to search for illustrations, for these have always been found in any book that happened to be lying upon the table. There are indications in current publications of the gradual acceptance of some of the writer's views upon endemism at least, though their full acceptance involves some change in current outlook.

The idea of gradual transition is necessarily inherent in natural selection, if this is to be, as DARWIN conceived it, a guiding force in evolution, and not, as it is here conceived, simply an agency which will test all individuals at their birth, and pass for survival those that reach whatever standard is necessary at the moment. One must not forget that the standard will be different for every individual, low when the immediate local conditions are easy, high when they are hard. Selection must always be accompanied by the conception of great destruction of the intermediate or transitional forms, which would be killed out by the competition of their improved descendants, though one has always wondered how the two came necessarily to meet in competition. How did an improved *Senecio*, living at No. 44, find out that there was an unimproved one living at No. 397, and proceed to kill it out by competition? The destruction, if it went on "according to plan", would gradually tend to separate competitors both structurally and to a small extent geographically. But it is difficult to understand how or why, when the latter separation was once effected over a small distance, it should continue to increase until we get such enormous separations as are often found between genera or species that are structurally closely allied, such as we have seen in the preceding chapter.

One of the greatest difficulties of the selection theory has always been to account for generic and family differences. Being greater than specific, they suggest that the competition grows more severe the higher that one goes, which one knows from experience not to be the case, and which is also expressed in the proverb that "there is plenty of room at the top". There seems to be a tendency to explain genera otherwise than species, but if we suppose them directly derived from one another, which seems a simple way of explanation, why try to keep selection to explain species, and why not make the process the same for both, and give nature the credit for as good, as logical, and as inevitable results as she produces in physics or in chemistry?

Destruction of intermediate forms by selection is an easy way of avoiding the solution of many awkward structural problems, but only if the destruction can be proved, and if there is some adaptational advantage attaching to the winner. Fossils give no evidence to prove that progress must have taken place by structural adaptational changes, while age and area shows that most fossils of flowering plants are probably of side lines (p. 35), and not ancestral to anything now living. They can be just as easily interpreted upon our principles, here laid down, while under these distribution begins to take form, and one gets rid of the notion that nature advances mainly by trial and error.

Natural selection does not select species; as agricultural experience seems to show (*Evol.*, p. 177), it selects individuals, as in fact one sees in everyday life, killing out those that when born do not suit the conditions at their immediate birth-place well enough to survive and reproduce. It affects only slightly a species once established upon a small area, for though one individual may be killed out in one place, another will succeed somewhere else, and the species will go on, becoming gradually dispersed abroad, by virtue of the adaptability that it must possess in order to survive at all. But we may thus obtain a simplification of the problem, if it should prove to be, as we have suggested, that the structural evolution has little direct connection with natural selection, but proceeds in definite steps, which need not necessarily have anything to do with the improvement in adaptation, or at any rate with the increasing complexity, that seems to be continually going on.

The essential features of evolution by divergent mutation are that it seems to proceed by definite single mutations that can cover at one stroke the difference between one species, genus, or family, and the next, and is more or less completely independent of natural selection. The new form, when born, must have (and probably by simple inheritance will have) the adaptation needful to survive, together with some adaptability, but there seems no reason why there should be any necessary improvement. We have pointed out (**136**, p. 538) that "the whole family *Podostemaceae*, with its remarkable morphological constructions, is therefore adaptationally unnecessary. All its extraordinary features are *de luxe*, and cannot have arisen in response to any need for adaptation to different conditions, for there are no different conditions to which to be adapted ". Any individual not up to the standard of its birthplace would be killed out at or soon after its birth, while any showing a definite improvement would likely be preserved. Probably most mutations simply produce structurally divergent, but adaptationally indifferent, alterations, the local adaptation of the new species being a more or less functional and compulsory affair.

People say that it is not possible (which simply means that they have not seen it) to get a viable mutation showing great changes, and it is true enough that we have not yet got such a mutation in such a way that its actual occurrence, *and* its permanence in inheritance, cannot be denied. Such cases as *Aquilegia* (*Evol.*, p. 49) give reason to suppose that upon rare occasions such a mutation can occur, and that it cannot seems to be only an assumption. One viable mutation at any single spot upon the globe, and once in 15-30 years, is enough to account for all species that have ever existed, as Yule showed (**158**, p. 84). We are also without proof that a new species can arise by selection to such a stage that it crosses the sterility line, the rough and ready line of distinction between species, once and for all. But that such mutations *can* occur, even if not usually viable, is continually being shown by the facts of teratology, which are summed up in (**102**).

In these phenomena one may see for example, in *Ranunculaceae* :

1. Clematis : several ovules in place of one (the principal character of the other great sub-family *Helleboreae*).
2. cohesion of some, or all, sepals, the calyx thus forming a tube.
3. leaves in whorls of three, instead of opposite, even on the same shoot.
4. terminal leaflet replaced by a tendril (*cf. Evol*, pp. 57, 191).
5. Thalictrum : receptacle 3-partite, with three groups of stamens.

6. embryo with three cotyledons.
7. Anemone : stamens and carpels changed to honey-bearing pitchers, like those of some *Helleboreae*.
8. in *A. sylvestris* the peduncle branched, even as much as in *A. japonica*.
9. Hepatica : leaves of involucre more numerous, up to seven.
10. Myosurus : fertile stamens in place of honey-leaves.
11. Ranunculus : flower apetalous.
12. petals tubular, as in *Eranthis* or *Helleborus*.
13. K 3, C 3 as in *Alismaceae* (and *cf. Thalictrum* above).
14. Caltha : embryo with 3-4 cotyledons

and so on

Or we may take a few large *Compositae*, which among other changes show :

15. Senecio : forking of leaf.
16. union of two heads.
17. long tubular ray flowers, this case being described as a new genus *Eudorus* (Cassini in *Bull. Soc. Philom.*, 1818, p. 165).
18. disc flowers changed to ray flowers in *S. elegans* L.
19. no ray flowers in various species, some of which, like *S. Jacobaea* and others, produce a var. *discoidea* at times, and *at different places*, which helps incidentally to show how the discontinuous distribution mentioned above might come about.
20. in *S. vulgaris* L. heads in place of single flowers; rings of heads round a central one (hen and chickens variety); heads bell-shaped rather than cylindrical; flowers shortly stalked with much elongated corolla.
21. Hieracium : corolla 2-lipped in *H. alpinum*.
22. *amplexicaule* L. three cotyledons.
23. *brachiatum* Bertol. corolla tubular, not ligulate, in a fl.
24. *echioides* Lumn. reproductive adventitious buds on root.

25. *prenanthoides* &c. leaves in whorls.
26. *umbellatum* L. pappus hairs changed to leaves.
27. *Virga-aurea* Coss. fasciation with many-headed infl.
28. Centaurea : *collina* L. two stamens united fully to corolla, the rest free.
29. *decipiens* Thuill. no ray flowers.
30. *Jacea* L. single flowers in axils of leaves.
31. ray flowers often 6- or 4-merous.
32. *paniculata* L. ray and disc flowers often 6-merous.
33. *suaveolens* W. three cotyledons.

In *Rubiaceae* we find

34. Cephalanthus with fls. 4-5-6-merous, *Kadua* 5, *Pentas* 4-6, *Putoria* 3, *Mitchella* 3-5, *Asperula* 3, *Sherardia* 3-5-6.
35. Cinchona, *Houstonia*, *Coffea*, leaves in whorls of 3.
36. Coffea, *Galium*, *Sherardia*, 3 cotyledons
37. Mussaenda, 2-4 stamens petaloid.
38. Coffea, unisexual fls., polyembryony.
39. Rubia, lateral doubling of stipules.

In connected families we find for example

Cornus, leaves in whorls of 3, or spiral, one bract-pair scaly, involucre doubled, union of flowers and fruits, 1-3 stamens petaloid, flower with 8 stamens. *Aucuba* 3 cotyledons, *Abelia*, *Linnaea*, *Lonicera*, *Sambucus*, leaves in whorls of 3 or 4. *Diervilla* 3-merous flower.

Other examples of important changes are *Nasturtium* bracts present. *Silene*, gamopetalous corolla, 3-merous fl., 5 cpls. *Cerastium* 4-merous fl., two whorls of cpls. *Stellaria*, 4 cpls., apical fls., K4, C4, A4 + 4, G3. *Rubus*, transition from palmate to pinnate leaves, 3 cotyledons, increase of petals to 6-11, *Geum*, 6-merous fl., *Potentilla*, terminal leaflet pitcher-shaped.

Facts like these seemed to prove that any genus may be potentially carrying many, and therefore presumably all, of the characters found anywhere in the family, and perhaps in related families. If a given character in any genus was produced by selection, how did some other genus, not necessarily closely related to it, come to be able to produce it at one stroke, as a conjurer produces a rabbit out of a hat. We may take an illustration from breeding. If one want to produce a blue flower in any genus that does not show such a thing, it is usual to look at the family as a whole. If some other genus in it has a blue flower, there is quite a good chance that one will be able to produce such a flower in the place desired, but if no case is known in the family, then it will be found very difficult, if not impossible.

Teratological changes are often called exhibitions of atavism, or reversion to ancestral types, but there is no more reason for this than for calling them anticipations of future types. Ancestral types, upon the selection theory, must be simpler, but these sports are often more complex. But the parent *must* have been carrying either the character of the offspring or more probably the potentiality of producing it under certain circumstances. The character was there, but concealed or recessive in some way. And one at once wonders whether the changes that one sees going on are not some kind of expression of what one may call a super-Mendelism. We have tried in vain to find any feature that seems to give any numerical indication of such a thing, but it would almost of necessity be complex, and perhaps may reveal itself to someone of greater mathematical skill. If we consider the teratological character ancestral, the character shown in its place by the parent must have been derived from it, in the ancestral history, by selection, which is often an obvious impossibility. But why should the fully perfected, improved type of the parent be able to go back at one stroke to the form from which it was derived? If plants can make mutations like this, why waste time over selection, and why not do the whole operation at a single mutation? There seems no more reason for going backward than for going forward. Mutation produces a much more perfect result, while one cannot expect perfection with selection (*Evol. Testcase X*, p. 114). Mutation also removes the great difficulties presented by the divergences that are shown, often so wide that no selection could have produced them, as for example in the cases of Nos 1, 3, 4, 5, 6, 8, and 9 in the list above, and as will be seen below. Selection seems principally to fill the place of something like an "appointments board", selecting or rejecting candidates for any place that may be vacant at the moment, and of course considering the case of all new aspirants in the form of new genera, species, or varieties. Once passed, the new character will only be permanently altered by some new mutation.

Teratology suggests to the writer what may perhaps be called evidence of incomplete evolution. Certain characters of the family, or possibly and even probably in its previous ancestry, always lurking, so to speak, in any member of the family, appear under certain circumstances as yet not understood, but are not persistent in the heredity, unless for a generation or two, though there are exceptions like the cock's-comb. It looks like a first (or later) attempt to mutate, in which the change did not go far enough to enable the nucleus, in its rearrangement of genes, to reach a new position of stability. It may be that sufficient engrams have not yet been impressed upon it, and that after a much greater lapse of time the same change might remain permanent. The teratological changes seem to indicate things that *might* happen.

In teratology we have the proof that a character, though not visible at all in the parent, may yet be given, complete and perfect, to its immediate offspring. This strongly suggests once more what we have already seen suggested by other things, that a genus may, potentially, be carrying a set of characters, covering at least all those in the family, and probably many more, for use in a kind of kaleidoscopic manner. It even suggests vaguely that as a character, once adopted, grows old in the service of the family—like tetradynamous stamens in the *Cruciferae*—it may become less liable to sudden mutational change.

As an example of what we are describing, let us take the case of *Schizopetalon* (*Cruciferae*, 5 spp., CHILE), which shows the kind of occurrence that is common enough. As most *Cruciferae*, including all the large (old) ones, have no bracts, these were probably lost at the first mutation that gave rise to a crucifer. No use can be imagined for the rather futile little bracts that may at times appear in the family, and which in *Schizopetalon* and a few more are always shown. It is absurd to suppose that the local conditions were so peculiar as to demand the formation of bracts for adaptational reasons at the birth of *Schizopetalon*, but they were evidently different enough—not a difficult matter in such a mountainous country as CHILE—to involve a change of genus, when *Schizopetalon*, the new one, *incidentally* showed bracts as a necessary result of the particular changes that took place in the nucleus, but with no adaptational significance.

Many of the teratological changes above described are probably caused by changes of conditions, such for example as are brought about by cultivation, and are therefore quite compatible with my working hypothesis (p. 96). After the change has been effected by mutation, selection will then pick out, in reference to the conditions existing at that place at that time, those members of the species concerned which show the most efficient *combination* of all the characters that they possess, whether they are the same as those of the parent or divergent from them. It will not pick out all those that carry a new character, unless, under all circumstances, that character conveys some definite advantage which is not cancelled by something in some other character or characters—a thing that is probably only a rare occurrence. The structural alterations that make the new species will usually be a matter of indifference to selection, as offering nothing on which it can get a leverage.

In this connection we may call attention to HURST's statement (67) that " In maize eight specific characters, which had hitherto remained entirely constant, mutated under the influence of X-rays, thus providing valuable evidence that specific characters are also represented by genes (*cf.* p. 219). " This fits in well with what we have said above about the " recessive " concealment of one or the other specific character in parent or child.

Looking over the important characters used to separate species, genera, &c, there are many that could only have been formed by some sudden mutation, and that usually have no conceivable adaptational value, nor will allow of any transitional stages to the character that is contrasted with them, like alternate and opposite leaves, inflorescence terminal or lateral, racemose or cymose, flower 3-4-5-merous, and so on in great variety. Most genera show some of these mutational characters, and it is unusual to find two genera where all the differences could be gradually passed over.

Among other places where this divergence is well shown is usually the formation of the first endemic species from a wide that already exists in the country. In a recent paper, we gave 18 examples from CEYLON, where there are over 50 cases of one wide accompanied by one endemic (WE), while in MALAYA there are some 70, this being about the most frequent way in which endemism is shown. Practically all local genera of two species (and the great majority of the 1600-odd are localised) count as other examples. Only in very long isolated places is any other display of endemism, such as WEE, commoner than is WE. So marked is this that it is clear that endemism tends to appear first in the WE form, while later there may be added a second, and even more, endemics. Endemics must in the vast majority of cases have been formed at or near to the place where they are now growing, and the fact that there are such hundreds of cases of WE goes to show that one can hardly conceive of the endemic otherwise than as the descendant of the wide close by. If it were the other way round, the endemic would be the relic, the wide a younger species, but as the same wide is usually accompanied by different endemics in different countries (*cf. Rhamnus* below), one has then the difficult problem of explaining why there are so many endemics. We have gone into this question of age or youth in *AA*, pp. 89-93.

We may take it that the wide is the parent of the endemic in at any rate the vast majority of these cases of WE, so that any character that the endemic shows must have come from the wide, *whether the latter shows it or not.* The difference between the two is often so marked that it is recognised by the taxonomists as sub-generic. It is also most commonly of a kind only produced in perfection by a single mutation (*cf. Evol.*, p. 114), such as those instanced in last paragraph but one. If we are determined to avoid this conclusion, we must make the endemic older than the wide, and the latter a casual later arrival, a proceeding which will not agree with the regular progression and falling off in numbers of WE, WEE, &c; or we must in some way persuade the facts of genera that show only endemic species in a given country to furnish evidence in the direction desired.

As an endemic species, especially in a large genus, may have been produced at a time when the genus had already many species, it would seem not improbable that the formation of a new species regularly involves divergence, and that the phenomenon is not confined to the first dichotomy. Perhaps the cases like *Memecylon* and other genera with closely similar endemics in CEYLON are due to some phenomenon which is more of the nature of the formation of varieties, though it is quite clear from the observations upon *Hieracium* and *Rubus*, described on pp. 182-3 that their evolution and dispersal has proceeded in exactly the same way as that of larger groups like sub-families or sub-genera.

CEYLON has two *Rhamni*, sub-generically distinct, *Wightii* (high montane, and also in S. INDIA) with C 5, A 5, in the sub-genus *Frangula*, and *R. Arnottianus* (CEYLON endemic, high montane) with C 0, A 4, in *Eu-Rhamnus*. In S. INDIA *R. Wightii* is accompanied by another endemic, *R. virgatus*, also in *Eu-Rhamnus*. These two endemics are almost, if not quite, as divergent from one another as are the two CEYLON or the two MADRAS species, which are placed in different sub-genera. The MADRAS one has spiny bracts and fascicled flowers, the CEYLON one non-spiny bracts and solitary flowers. The most reasonable explanation is that *R. Wightii* gave rise in MADRAS to one endemic, in CEYLON to the other, by divergent mutation, the endemic crossing the taxonomic line between the two sub-genera upon each occasion. If, as we suppose in these cases of WE, the two are parent and child, the differences must have been produced at birth, and in all probability by a single mutation, for they are of the type that allows no transitions and has no adaptational value. Hundreds of similar cases occur in CEYLON and other places. The further subdivision of these sub-genera is also largely based upon mutational characters, like inflorescence cymose or racemose.

As nearly always occurs with taxonomic distinctions, there are exceptions in places, and though 4- or 5-mery is the chief point of distinction, one cannot safely use it alone, without consideration of other characters. This simple fact, that no character can be used alone with complete confidence, is almost enough to show that differences between species &c must be a matter of mutation, which is liable at times to be reversed, or to appear independently in different places, or where a change in one character may involve changes (often only small) in others. If plants had acquired their characters gradually, by selection or otherwise, it is practically certain that the same process would not be frequently gone through in different places, or even reversed. It is largely for this reason that destruction of intermediates has been called in upon such a scale. As the character shown in an exception is often one that occurs somewhere else in the family, it is evident that there must be some factor in the chromosomic make-up of the plant that will at one time produce 4-mery, at another 5-mery, and so on, and such factors can hardly be considered as working under the urge of local adaptation in any way at present known to us (cf. HURST, on p. 105).

The distribution of both sub-genera of *Rhamnus* is very discontinuous, but if we add them together, the ground is far more efficiently covered, in fact with hardly any gaps. This behaviour is frequent, and now that we know of what mutation is capable, and that a sub-generic difference may easily arise in a single mutation, it is asking altogether too much to ask one to believe that the discontinuity of the sub-genera of *Rhamnus* or of any other genera that show the same phenomena is due to the killing out of members of the same sub-genus that once filled up the gaps. It is a very striking fact that the more our taxonomists split up genera into sub-genera and smaller groupings, the more discontinuous geographically do they seem to become. But if we adopt this explanation, it means that for example the change from 4- to 5-mery, or from thorny to thornless, or the reverse, must be frequent, and as it may occur in either direction, must be mutational and without adaptational significance. If this position be accepted, it of course shows that there is necessarily a considerable element of artificiality in our classifications, for if offspring can go, as they seem frequently to go, across from one group to another, as in *Rhamnus* above, or in the reverse direction, genetic relationship thus crosses existing taxonomic lines of distinction, so that these cannot be genetic. We have seen that the earliest, and therefore the most closely related, members of a family tend to be the most divergent of all, so that even in a small and outlying flora like that of BRITAIN a large part of the chief divisions of a family appear, inasmuch as the subgroups tend to be headed by the largest genera, which are at the top of the family. We shall expand this discovery later, and show how it bears upon various questions.

It is clear that at present various assumptions are needed to explain the facts, these being chiefly (1) that closeness of relationship is shown by closeness of structural resemblance (2) that structure changes gradually in response to adaptation, and (3) that the geographical gaps between species and genera that structurally are very closely allied are due to the destruction of the transitions that once filled these gaps. This last is very hard-worked, being required to explain many hundreds of cases in every possible part of the world. But no serious evidence has yet been adduced to show that such destruction ever went on upon land upon the scale needed, nor that the submergences needed in many cases have ever taken place—to say nothing of the very formidable argument to the contrary brought up by the discovery of the law of size and space, for the discontinuity is so very often among very small and therefore in nearly all cases very young genera, while the submergences must date enormously far back in many cases. It is simpler, and corresponds much better with the facts to abandon these assumptions, and to imagine that evolution had no immediate adaptational structural basis, but that, as a form *had* to be adapted (or it could not have survived) to the locality in which it found itself, its adaptation was likely to be due primarily to its inheritance, and not very different from that of the parent, which must usually have been living near by.

We shall now give a table of the whole flora of CEYLON to show how largely it is constructed upon simple arithmetical lines :

The general composition of the flora of Ceylon

I. Genera with no species endemic

	1 sp.	2	3	4	5	Over	Total
Dicots	360	91	32	17	6	6/6 (6 of 6 spp.), 3/7, 2/8 2/9, 4/10, 1/11, 1/12, 1/15	526
Monocots	119	20	11	4	3	3/7, 1/9, 2/10, 1/13	164
						Total of I	690

II. Endemic Genera

Dicots	20		
Monocots	5	Total of II	25

III. Genera containing endemic species

A. Dicots.

Wides	Endemics 1	2	3	4	5	Over (spp. in genus)	Total
0	47	7	3	—	3	7 7 7 9 13	65
1	34	10	5	3	—	6 9	54
2	12	4	3	2	—	—	21
3	9	4	3	2	—	9 9 17 25	22
4	10	3	2	1	—	8 9	18
5	2	1	4	—	—	6	8

and also (wide/endemic) 6/2 6/2 6/3 6/15 6/21 7/3
8/1 8/2 9/8 11/4 11/9 12/8 14/18 16/27 17/3 18/2
21/1 24/1 18

206

B. Monocots.

Wides	Endemics 1	2	3	4	5	Over	Total
0	12	3	—	—	2		17
1	17	4	1	3	1	6 11	28
2	6	—	—	—	—	7	7
3	5	1	1	—	—	7	8
4	1	—	1	—	1	—	3
5	1	—	1	—	—	—	2

and also (wide/endemic) 6/2 6/2 6/3 7/1 7/5 8/1
9/1 9/8 11/2 11/7 13/1 16/5 26/3 36/1 39/1 15

80

Total of III (with endemics) 286
Grand total 1001

Whether in Dicots or in Monocots, there is an evident concentration towards the top left-hand corner. In the top lines of III, A and B, are given the genera with endemics *only*, other than the actual endemic genera. They will be considered in Ch. XIII. The second line gives the genera with one wide and one endemic each (WE), one wide and two endemics (WEE), and so on. As under our theories the endemic must have been formed near to the place where its parent was living, and cannot be regarded as a relic without special and individual proof, it must be the offspring of that wide, whether its characters agree or not. We shall see that some of its characters are usually markedly divergent. This is a great change from the former outlook, but is much simpler, and evidence in its favour is quickly accumulating.

It is clear from the gradual fading away of the numbers in the table, whether downwards or from left to right, that they have been formed as usual in a more or less mechanical way. The only reasonable explanation seems to be that WE is the first stage in the production of endemism, followed by WEE, and so on. In other words, the endemic must be the direct offspring of the wide near by, and must have crossed at one step, at least in nearly all cases, the separation of character that now shows itself between them. In any case, any species that we see must have been descended from something else, so that, if we find, as we do, completely divergent characters between them, there must be some place in the ancestry where these characters fuse with one another, or where both arise from an ancestor that only showed one of them. However far back, even beyond the genus, one may have to go, this must happen somewhere, while in a great number of cases the characters cannot fuse, unless one imagine them both to start from nothing. Even if the fusion were possible, there must be some urge or adaptational reason for gradual selection, and no one has ever been able to suggest such a thing except in a very few and rather doubtful cases. Direct mutation, with no adaptational significance, gets us out of this difficulty (which was DARWIN's difficulty also, cf. *Evol.*, p. 74), at a stroke.

The following table gives, for each pair of WE (wide/endemic) in CEYLON, the contrasting characters of the wide and the endemic, taken from **(125)**:

Ceylon genera of two species, one wide and one endemic

	Genus	Char. of wide	Char. of endemic
1.	Ranunculus	Leaf much divided	Leaf undivided
2.	Miliusa	L. 1-3", obtuse. Fr. cpl. smooth	L. 3-6", acute. Fr. cpl. granular
3.	Ionidium	Ls. few spreading	Ls. many imbricate
4.	Pittosporum	Simple sessile umbel	Stalked racemose corymb
5.	Salomonia	L. not ciliate	L. strongly ciliate
6.	Mesua	L. oblong-lanc., 3-4"	L. linear-obl., 8-12"
7.	Ternstroemia	L. sub-acute, fls. yellow	L. very obtuse, fls. wh.
8.	Hugonia	L. glabrous	Densely silky beneath
9.	Glycosmis	Ovary 5-locular	Ovary 2-loc.
10.	Aglaia	L. glabr. below; fr. 1"	Densely scaly below; fr. smaller

Genus	Char. of wide	Char. of endemic
11. Walsura	L. tri-foliolate	L. uni-foliolate
12. Gymnosporia	Lateral branchlets spinous; l. entire	Not spinous; l. crenate-serrate
13. Rhamnus	Petals and stamens 5	Pet. 0, sta. 4
14. Nephelium	Leaflet entire	Dentate-serrate
15. Connarus	Fr. stalked, not striate	Not stalked, striate
16. Pygeum	Sta. 20 or more; ov. and l. quite glabrous	Sta. 12; ov. hairy; l. hairy on veins below
17. Laurembergia	Fr. not ribbed or tubercled, pubescent	Strongly ribbed and tubercled, glabrous
18. Carallia	Fl. sessile; C 7-8	Fl. stalked; C 4
19. Momordica	♂ fl. solitary, with large hooded bract	Usually in racemes, without bracts
20. Alangium	Small erect tree; fr. 1"	Subscandent shrub; fr. 5/8"
21. Mastixia	Sta. and pet. 5	Sta. and pet. 4
22. Urophyllum	Stip. small, triangular	Stip. large, oblong
23. Anodendron	Seed-beak 1/4", stout	3/4-1", very slender
24. Caralluma	Fl. solitary, axillary	Umbellate, terminal
25. Tournefortia	C rotate, 5-lobed	Tubular, 4-lobed
26. Klugia	Post. angle of K-tube a large crest	All angles of K-tube equally narrowly winged
27. Cyathula	Fl. clusters solitary	In globose heads
28. Dicraea	Thallus broad algiform	Slender, cylindrical
29. Cryptocarya	L. coriaceous, pubescent below	L. thin, glabrous
30. Balanophora	♀ head globose; bracts of ♂ shorter than ped.	♀ head pear-shaped; br. of ♂ as long or longer
31. Putranjiva	♀ K 5-6; fr. globose	♀ K 4; fr. pointed
32. Trigonostemon	Pet. of ♂ = twice sep., not 2-lobed	As long as sep., very deeply 2-lobed
33. Claoxylon	Herb, leaf under 3"	Shrub, leaf over 4"
34. Artocarpus	♀ receptacle globose	Oblong
35. Arundina	L. 8-12". pets. orbicular, obov., apiculate	L. 2-5", pets. ovate-obl.
36. Calanthe	Mid-lobe of lip bipartite	obcordate
37. Hetaeria	Spike 3-5"	Spike 4-10"
38. Cheirostylis	Raceme short, glandular pubescent	Elongate, puberulous
39. Vanilla	L. imperfect or none	Leaf 5-7" long
40. Zingiber	Spike sub-capitate	Spike elongate
41. Phrynium	Spike lateral, high on petiole	Sessile on rootstock
42. Areca	Stem 40-80 feet	Stem 8-12 feet
43. Phoenix	Stem very short, stoloniferous	Stem 8-20 feet
44. Amorphophallus	Tuber leafing after flowering	Leafing and flowering simultaneously

Genus	Char. of wide	Char. of endemic
45. Hypolytrum	Glumes obtuse; nut 1/10" to 1/8"	Acute; nut 1/20"
46. Mapania	Scapes naked	Clothed with imbricate sheaths
47. Leptaspis	Utricle erect, orifice terminal	Decurved, orifice lateral
48. Eremochloa	Glume I 2-winged below the tip	Not, or obscurely, winged below tip
49. Zenkeria	Glume acute or acumin.	Obtuse or sub-acute
50. Coelachne	Spikelets in interrupted spiciform panicles	Spikelets in open panicles
51. Lophatherum	Glume I naked	Bearded

It is perhaps worth notice that most of these genera are large, some very large, and eight actually heads of families. A mere glance shows how marked the characters are, and how great are the possibilities open to the direct single mutations by which the endemics appear to have been formed, and it shows also in how many ways divergence may take place. The characters given in the table are not the only divergences found, but they are those most suited to making keys. If we cross over to MADRAS, we find a number of the same wides accompanied by different endemics, and it will suffice to quote a few examples :

Ranunculus	Achene compressed. Leaves deeply divided	Wide
	Achene not compressed. L. only coarsely crenate	E
Ionidium	Undershrub with red flowers	Wide
	Large shrub with pink flowers	E
Pittosporum	Stout simple or sessile umbels	Wide
	Slender simple racemes	E
Nephelium	Petals. Fruit with round tubercles	Wide
	No petals. Fruit with soft weak prickles	E

In (**131**) we called attention to the way in which so many large genera, like *Anemone* or *Clematis*, have one widely ranging species which at different parts of its range is accompanied by different endemics, and we returned more fully to the topic in Testcase XXX, *Evol.*, p. 158. For example *Anemone rivularis* ranges all over INDIA and CEYLON, with the endemics (*l. c.* p. 159) mainly in the northwestern HIMALAYA (the probable route of arrival of *Anemone*), but showing a few as far as the KHASIA or MISHMI hills in the far east. Other examples given in *Evol.* were *Clematis* and *Portulaca*, and a discussion of the question follows. CEYLON shows no endemics in these genera, though its mountainous nature lends itself to endemism, because these genera are not yet old enough in CEYLON to have any species as local offspring.

To what has been said about the WE cases in CEYLON, we may add a few notes about the many genera that contain more than one wide, but only a single endemic. It is of course a risky venture, unless one of these is very much commoner than the rest, to say which is the probable parent of the endemic among the wides, so that it is of interest to find that in most cases the endemic shows some characters that are not to be found in any of the wides. For example in *Uvaria* there are five wides, all shrubby climbers, while the endemic is a straggling shrub; in *Garcinia* the endemic has stamens in two or four spreading bundles, the wides in one or five; in *Sterculia* the endemic has winged seeds, the five wides not. Here ALSTON makes the endemic into a separate genus, largely on account of this well-marked difference (1). In *Triumfetta* the endemic is semi-shrubby, the four wides herbaceous, and so on in many more genera. It is rare for an endemic to show characters that could have been derived from those of any of the wides by selection.

Such tables as these make the explanation of relicdom for most endemics seem somewhat absurd. Why should so many more " relics " be accompanied by one wide than by two or more? Why should they almost always show such structural differences from that wide—differences which obviously are equally hard to explain, in whichever direction they go? None, either of wides or of endemics, has any visible character that would lead one to suppose it either superior or inferior to its opposite number. Why should they differ in so many characters? This simple fact is almost enough to discredit the action of selective structural adaptation. If we represent perfection, such as is usually shown, by 10, and imagine three competitors, with characters developed to the following degrees, but with the marks adding to the same total in each, the competition would probably be severe, but which one would win? Whichever were chosen, the effect upon gradual perfection of the characters would be important, for some would be improved, some deteriorated, while if the third were a loser, the character C, already perfected, would go decidedly back, and all its gains would be wasted.

First competitor	A 8,	B 4,	C 5,	D 9,	E 4	Total	30
Second	7	5	7	8	3		30
Third	9	3	10	6	2		30

Why, again, is the connection between the characters so small, if any? In *Lauraceae*, at random, what connection is there between alternate, éxstipulate leaves, oil-cavities in the tissues, regular trimerous flowers, homochlamydeous perianth, anthers opening by valves, unilocular ovary with one pendulous ovule, and absence of endosperm? Could this combination be produced in its present perfection by any selection? It might, perhaps easily enough, be produced by a series of disconnected casual mutations, as we have suggested that two such might produce *Myosurus* from *Ranunculus*. But the general evidence that we are bringing forward in this chapter and the next suggests rather that a new species, genus, or even family, may be formed at one stroke, though this of course does not exclude the possibility that at times they are due to accumulation of mutations.

Biologists have tried to make selective adaptation work too hard. Provided that a new form is born with enough adaptation to the local conditions to be able to survive and reproduce (for if not, it will be promptly killed out, and will count for nothing in the evolution), that seems to be all that is necessary, and we do not have to look for a vast destruction of intermediate forms that were defeated by better adapted ones. The best will survive, just the same, but without needing, or showing, structural change indicating improved adaptation. The two things are independent, and the structural change is usually marked and sudden.

It is clear from the table that the world size of the genus, whether large and widespread like *Ranunculus* (325 cosmop.), of medium size and dispersal like *Pittosporum* (160 warm OLD WORLD), small, or very small, makes little or no difference to the divergence that may be shown. One may find divergence of similar type elsewhere, in the same genus, as is shown in the tables. For example there are only two *Ranunculi* in the HAWAIIAN Is., both endemic there. One has the leaves trisect, the other twice trisect. One may compare this with the phenomena shown in CEYLON by *Ranunculus* (leaves not divided, or much divided), and *Walsura* (3-foliolate or 1-foliolate); or in MALAYA by *Walsura* (imparipinnate leaves of 5-9 leaflets, or paripinnate of 4), and so on. In the present state of our knowledge it is clearly impossible to say whether one mutation is or is not larger than another, especially perhaps when they are of the same type. We shall return to this later, when we have seen that what really seems to matter in the present connection is the relative age of the mutations.

However one may look at the origin of the endemics, some of their characters must have been received without being shown by some ancestor, whether immediate or further back. This, of course, while a necessary implication of the theory of endemism, is a direct contradiction of Darwinism, which makes one structural feature arise out of another, usually fairly closely similar, by stages; but it does away with the great difficulty, if not impossibility, of explaining the incidence of characters by selection, a difficulty which has been steadily becoming more acute with the improvement of taxonomic enquiry. The great discontinuity of the incidence of *characters*, which is a distinct phenomenon from the real discontinuity of genera or species, seems to become more marked as time goes on, as taxonomic methods improve, and as species become more and more split up. The greater the splitting, the greater the number of the "pieces" that seem to appear in any given country, however recent, or however isolated, its flora. For example, under *Hieracium* the *London Catalogue* remarks "ZAHN arranges his plants under capital or group-species, each of which has as a rule many sub-species attached. *Pilosella* L., for instance, has no less than 624... About 40 of these capital species are represented in BRITAIN."

When one looks at the characters of endemics all over the world, one is soon at a deadlock if one try to visualise them under the supposition that they are relics. The characters shown in a large genus are almost necessarily more than in a small one, but to get the larger total, one must include, not only those of the wide-ranging species, but those of the far more numerous species that are confined to small areas and are usually within the range that people allow to an endemic. The range of the wide-rangers is often so enormous as to be very impressive, *e. g.* in *Ranunculus*, but in actual fact there are few of this kind in any one genus. If one take from the *Index Kewensis* the actual range of all species of *Ranunculus* (disregarding equation except such as was done in earlier volumes), one finds that there are perhaps 25 species, out of 410 there given, and which would probably be reduced to about 325-350 by a monographer. Thus there is a percentage of less than 8% of these very widely distributed species, which have a range of say at least 6000 miles along the greater diameter of their area. A considerable number exceed this to a large extent, by reaching the whole length of EURASIA (7500 miles), or even going also across NORTH AMERICA. If as a contrast in some ways, we take *Symplocos*, which has 281 species in the monograph in *PR*, we find it a genus of warm countries, of woody habit, living largely in forest, and widely removed taxonomically from *Ranunculus*. Its size is not so very much less and may be looked upon as less than one species-generation below *Ranunculus*, but conditions have been very different. The greater number of its species (172 in all) are Asiatic, the rest American and all but one south of the UNITED STATES. This indicates that they are younger in AMERICA, and so will likely show less range there, as in fact is the case. The species of greatest range reaches from INDO-MALAYA to JAPAN, a distance of at most 4500 miles, while in AMERICA the maximum is about 1000 miles. A greater proportion of the species of *Symplocos* are within the range that everyone allows to an endemic, but it simply means that the genus is perhaps younger than *Ranunculus*, and at any rate has not had the time to cover larger areas. In ASIA, for example, there are 23 local species in CEYLON *(PR)*, 14 in SOUTH CHINA; there are 13 in NEW CALEDONIA, and so on. In the new world, where the genus is apparently younger, there are 11 in the small Brazilian state of RIO, 10 in MINAS, 11 in the very mountainous COLUMBIA, 9 in PERU, and so on, though the total is less than in the old world.

The range of the few wide-ranging species in a large genus (or a small one in water plants, where conditions are more uniform) is often so impressive that one is apt to forget the great crowd of followers upon smaller areas, a crowd which on the whole increases with the smallness of the area. And one is also apt to forget that the very large areas mainly occur in very old (large) genera. Detailed studies of areas over entire genera will probably lead to interesting and valuable results, but we can only give slight indications here.

We have thus seen from the facts of teratology that a plant carrying the character A may give rise by a sudden and divergent mutation to a plant that carries B, a more or less divergent character, often so divergent that no selection could accomplish the difference. And the difference may show in two or more characters that seem to have nothing whatsoever to do with one another. Various explanations have been made of teratological phenomena, which are not permanently inherited, except in rare instances like the cock's-comb. The most common one, that of their being illustrations of atavism, or reversion to ancestral type, is largely a " verbal anodyne ", for we do not know what the ancestral type was like. But the characters are often so unlike, and so divergent, that no fusion can be imagined, however far back one may go in the line of inheritance, unless one reach the *reductio ad absurdum* of making the transition go through a stage of nothing at all between the two extremes. For the teratological formation of many of the temporary characters that appear and which are often generic characters somewhere else in the family, one must invoke direct mutation, so that there is no reason against its being the explanation of the same characters when they are permanent in the inheritance. And we now have the evidence which has been given in this chapter in favour of this phenomenon, and which could be expanded if needful to hundreds or thousands of cases. There is therefore no need to call in the *geographical* destruction that has hitherto been invoked. The local destruction of less efficient individuals of any species will go on all the time, as demanded by Darwinism, but there will be no *necessary* destruction of *transitions*, a destruction which would ultimately make, if it went on according to plan, the structural gaps that show between species and genera. It has never been explained, however, why it should make such immense geographical gaps as are often found.

To end the chapter we give a further list of WE combinations in other countries, chosen to exhibit the variety of ways in which the divergence between the two may be shown : —

			Wide	Endemic
1.	Colubrina	Malaya	Seashore shrub	Jungle tree
2.	Waltheria	Malaya	Erect, twiggy	Prostrate
3.	Stipa	S. Afr.	Annual	Perennial
4.	Cocculus	Socot.	Much branched climber	Hardwood shrub
5.	Acacia	Baham.	Unarmed	Base spiny
6.	Ravenia	Jam.	L. 3-foliolate	L. simple
7.	Poranthera	N. Zd.	Leaf flat	Margin revolute
8.	Sapium	Jam.	Petiole with glands	Without
9.	Mimosa	Baham.	Herb; leaf sensitive	Shrub; not sensitive
10.	Acronychia	Malaya	Flowers in cymes	In racemes
11.	Sericocoma	S. Afr.	Flowers in heads	In spikes
12.	Diospyros	S. Afr.	♂ fls. cymose, A 10-16	Solitary, A about 30
13.	Securidaca	Malaya	Bracts caducous	Persistent
14.	Dinochloa	Malaya	Empty glumes 3	Empty glumes 4
15.	Pterocymbium	Malaya	K campanulate	K tubular
16.	Synaptolepis	S. Afr.	Disc of small scales	Cup-shaped, lobed
17.	Illicium	Malaya	Stamens 9-13	Sta. 30-50
18.	Portulaca	Haw. Is	Sta. 7-12	Sta. ∞
19.	Sericocoma	S. Afr.	Staminodes present	Absent
20.	Adelia	Jam.	Sta. on central prominence	On central column
21.	Rourea	Jam.	Cpls. subequal to sta	Much shorter than sta.
22.	Omphalea	Jam.	Ovary tomentose	Glabrous
23.	Heritiera	Malaya	Fruit ovoid, keeled	Obovoid, winged
24.	Entada	Malaya	Pod straight, woody, indehiscent	Spiral, coriaceous, dehisct. into joints
25.	Laportea	Malaya	Achene smooth, with longish beak	Achene pustular, edge keeled

Two or three have one wide and two endemics; in these cases both endemics show the character in second column.

From WE contrasts we can go on up to larger and larger genera, but we find no larger contrasts even in their first divisions into sub-genera, as we have already pointed out in *Evol.*, pp. 10, 70, 106, 138, 170, &c. and especially App. III, p. 199. Thus it is clear that our explanation—that these characters are due to direct mutation—is probably sound, and the fact that a genus, at its first production of a new species, so often divides into what will later be sub-genera, has in it an indication of the whole matter.

It is also clear that divergence, often strongly marked "may be shown in any mutation that appears" and when viable, "forms the beginning of a new species", genus, or even family, as one may see in the formation of endemics.

CHAPTER VI

Endemism contd. The characters of Endemics II

After the evidence that has been produced, here and elsewhere, there can be little doubt that endemics are the descendants of wides of the same place, or usually near by, and were born near the spots where they are found. Apart from genera with endemics only, which we shall presently consider, the commonest type of occurrence is WE, the next WEE, and so on. This does not mean that there are few species at the top, for the genera there may contain many endemics. The curves are too regular to allow of a dividing line being drawn to separate successes and failures or to cut off the relics. The ones and twos especially can only be young beginners. The acceptance of this view changes geographical botany from a confused mass of facts to an arithmetically based subject, and opens up possibilities hitherto unsuspected in economic and in other directions.

Let us now go forward to examine the WEE type of appearance, of which there are 14 examples in Ceylon. The first, *Xylopia* (**125**, I, p. 28) is there given as three endemics, but *X. parvifolia* has now been found in Madras, and may be regarded as the probable parent of the other two. Of these we have put first the endemic with the widest dispersal in Ceylon. Arranging the characters of the three, as given by Trimen, with the wide on the left, we get :

Wide	Endemics
a) Flowerbuds narrow acute	E1. *Broad*, *ovoid*, *obtuse* 2. Narrow acute
b) Pedicel straight	E1. *Curved* 2. Straight

Wide	Endemics
c) Cpls 5, sunk in receptacle	E1. *Solitary*
	2. Five, sunk in receptacle
d) Seeds not enveloped in pulp	E1. *Enveloped in pulp*
	2. Not enveloped
e) Sepals connate halfway up	E1. Connate
	2. *Slightly connate at base*
f) Ovules 4-6	E1. Ovules 4
	2. *Ovules about 10.*

We have already seen in the WE genera how markedly divergent the characters are, and how often the difference can only be due to mutation, and the same thing shows in these WEE genera.

The first character, a, is the one used by Trimen in his key as being the most easily noticed; the rest are taken from his descriptions. The keys always divide one from the other two. whether it be W/EE, or WE/E. It will be seen in *Xylopia* that in each of the six characters, *one of the endemics has the parental character, the other a divergent character* (in italics) *which does not show in the parent* (could not, in fact), but is handed on by it. This phenomenon is fairly universal, and examples from all the other Ceylon cases are given in the list that follows : —

Divergent characters shown in Ceylon groups of WEE endemics (Dicots). Number of endemic, first or second, in brackets

	Wide	Endemics
Orophea [1]	Pets. valvate	(1) outer imbricate (2) inner imbricate
	Sta. 6 in two rows	(1) 9 in three (2) 6 in two
	Cpls about 15	(1) 1 or 2 (2) 3
Alsodeia (I. 68)	Anthers distinct	(1) connate (2) distinct
	Disc annular	(1) of 5 scales (2) annular
	Leaves acute	(1) and (2) obtuse
Scolopia (I. 70)	Fruit green when ripe	(1) bright scarlet (2) green
Sophora (II. 94)	Leaflets 15-17	(1) 7-11 (2) 17-23
	Fl. yellow	(1) white (2) violet
Gynura (III. 43)	Leaf with large auricles at base	(1) without (2) with

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[1] *Orophea zeylanica* (Trimen, I. 35) is the wide; *Bocagea coriacea* and *B. obliqua* (I. 33), now placed in *Orophea*, the two endemics.

	Wide	Endemics
Adenosma (III. 231)	Fl. blueish-purple	(1) yellow (2) purple
	Stem erect cylindrical	(1) bluntly quadrangular (2) quadrang., decumbent
	Leaves whorled	(1) and (2) opposite
Didymocarpus (III. 273)	Rhizome erect, short	(1) erect, short (2) creeping
	Capsule pubescent	(1) pubescent (2) glabrous
	Corolla pubesc. outside	(1) and (2) glabrous
Hemicyclia (IV. 36)	Much branched shrub	(1) small tree (2) moderate sized do.
	Stamens 6-8	(1) about 24 (2) 10-16
Chaetocarpus (IV. 74)	Capsule with rigid prickles	(1) with tubercles (2) with rigid prickles

Some of the important characters of the wide species of each of these WEE genera are shown *in one or in the other* of the two endemics, so that, upon the structural basis which at present rules in taxonomy, they are all closely related. This one would hardly expect unless the endemics were the direct offspring of the wide, and not relics of some more ancient members of the genus. Only very rarely is there anything near by in some other country, that might have been carrying these divergent characters, and might have crossed with, or have itself been, the parent. However divergent one of the characters may be from the other, both must ultimately come from the head of the family, which could not *display* both, but must have been carrying one of them in some kind of recessive manner. Some degree of divergence seems to be shown even in births within the same species, though less perhaps in plants than in animals, where it is specially noticed in one of the earliest families upon record—Cain and Abel were both sons of Adam and Eve, and such differences are by no means infrequent, though not perhaps always solved in the same drastic way, where the solution, be it noted in regard to recent European affairs, was not based upon the real value of the characters in question, and in regard to the actual conditions, but upon other and quite different characters and conditions, which were called in, in the hope that they would be capable of settling the difference in favour of the caller-in. The whole proceeding was illogical and wasteful.

The division of the parental characters between the offspring, especially in plants, is a phenomenon which requires careful genetic investigation, as it seems to suggest some kind of super-Mendelism. In any case, it still further dissipates the idea that dispersal depends in the long run upon adaptation and selection. No one, presented with a list of the characters of the wide and of the two endemics, would be able to say which was the most likely to be successful or widespread, just as he would be in the same difficulty in placing a plant in the ecological association to which it belonged, save in one of the extremes of water-plants or xerophytes, unless he knew in advance where it was found. It may be worth while to refer to *AA*, ch. XX, especially to the quotation from HOOKER on p. 205.

It is becoming increasingly clear that the great Darwinian theory of evolution[1], probably the most important advance ever made in biology, has a foundation which is not largely chance, as its author supposed, but is based upon a predetermined mathematical formula of some kind, as was indicated in *Evol.*, and as was worked out by YULE in more detail in **(158)**. In **(159)**, YULE and the writer said "Inasmuch as all families, both of plants and animals, show the same type of curve, whether graphic or logarithmic, it would appear that in general the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan". WENT's paper **(161)** may also be referred to. As we have shown in **(146)**, special creation explained the differences of species as outside the region of man's comprehension, but did not explain the obvious close resemblances, which had always been familiar. DARWIN explained them as due to inheritance, but did not properly explain the divergences, often so great and so complete that as they can only come, as he showed, from common ancestors, there must at times have been in the descent some divergences, to produce them. Such a change

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[1] I insert the word Darwinian with deliberate intent. Since 1902 my work has been so largely devoted to overthrowing the theory of the natural selection of gradual and adaptational improvement in structure, which has always seemed to me so completely illogical, that many people seem to think that I am simply an anti-Darwinian. In actual fact, I only wish to free the immortal theory of evolution from what are now its great encumbrances of swaddling-clothes, which by reason of their popular appeal became so well established that the name of Darwinism was given to them, rather than to the theory of evolution, where it properly belongs.

might for example be from an introrse to an extrorse anther, or *vice versa*, berry/capsule or *vice versa*, and so on. The theory that we are putting forward, partly derived from de Vries, partly from Geoffroy St Hilaire, partly original, in a way combines the previous theories, for the new form is supposed to appear, without the aid of selection, by a sudden mutation, so that its production may be described as a creation, though apparently a compulsory one, under the conditions ruling at the spot.

In another set of cases, the character in the wide shows a change in both endemics. In *Scolopia*, for example, the lax racemose panicle becomes a simple lax raceme in one endemic, a dense axillary raceme in the other. In *Sophora* a yellow flower is replaced by a white in E1, a violet in E2, while pubescent leaves are replaced by glabrous in both endemics. The 5-angled stem in the wide *Gynura* disappears in both endemics, and so on. All these are Ceylon cases.

In Monocots the characters are more frequently of a numerical or dimensional kind. As an instance let us take *Coelogyne* (Ceylon, Trimen IV, 159) : —

	Wide		Endemics
a)	Bracts ½ inch to $^2/_3$ inch	E1	$^2/_3$ inch to 1½ inches
		2	$^1/_4$ inch
b)	Leaves 2½ inch. to 4 inch.	E1	3 to 5 inches
		2	4 to 6 inches
c)	Pseudobulbs about 1 inch	E1	1½ to 2½ inches
		2	½ inch
d)	Pseudobulbs subglobose	E1	Narrowly ovoid
		2	Obpyriform or ovoid
e)	Sheaths hyaline	E1	Broad, coriaceous, red-brown
		2	Bearded at base with red-brown fibres of old sheaths
f)	Racemes 2-4-flowered	E1	4-6-flowered
		2	2-flowered
g)	Pedicel from base of old pseudobulb	E1	From base of terminal pseudobulb
		2	From base of old pseudobulb

The other CEYLON WEE Monocots are

Wide	Endemics
Cleisostoma (TRIMEN IV, 200)	
Leaf oblong or linear-oblong 1-1 ½, stem long, scandent	L. lorate, unequally 2-lobed, 6-7", stem long
	L. lorate, uneq. 2-lobed, 5-10", stem short and stout
Podochilus (IV, 205)	
Leaf 1/3 to ½" long, petals linear	L. ¾ to 1" long, pets. orbicul.
	L 1/5 to 1/4 " long, pets. obovate-oblong, obtuse
Curcuma (IV, 240)	
Spike on long leafless ped., many-flowered	Do., few-flowered
	Spike terminating leafy stem
Sciaphila (IV, 368)	
Style much longer than ovary, Stamens 4	Much shorter. Sta. 6. Stigma capitellate
	Much shorter. Sta. 6. Stigma penicillate

Dimensions seem to come more into the characters of Monocots, though the differences are usually too large to be passed over by selection, which would hardly for example produce one *Cleisostoma* with a leaf of one inch and another with a leaf of 6 inches.

A very important point is the differences that exist between the two endemics themselves, which one may see in looking at any flora that contains them. At the same time, of course, both agree with the parent in characters numerous enough to put them all in the same genus, though it must be pointed out that we have no guarantee that this always happens and it is possible, or probable, that at times sufficient characters, or certain characters, may change in such a way that the result will be a species in a new genus. Or again, it might happen that the offspring took over from its parent a group of characters that placed it in some genus already known. This of course means, that as BOWER suggested with regard to ferns (16), a plant now in a comparatively large genus C may have come, not from a parental C, but from B, while B in turn may even have come from A. But there is little doubt that this is a comparatively rare occurrence, and that most species in C have probably descended from parents that were already in the genus C.

The whole behaviour of these characters of endemics, in their relation to the " wide " parent, is of considerable interest especially in its resemblance to the phenomena of Mendelian inheritance. It suggests studies in hybridisation between the wide and the endemic in WE combinations, especially where a similar combination, in the same genus, can be found in two or more places; now that the new technique of doubling is coming into use, it might lead to interesting results.

As a confirmation of what we have said, let us look at the flora of the MALAY PENINSULA (107). Taking only the first volume the wide *Tinospora* and one endemic have herbaceous leaves, truncate at base, while the other endemic has subcoriaceous leaves with round base. The wide *Zanthoxylum* is a shrub with trifoliate leaves; one endemic is a shrub, but the other is a thorny tree, and both have pinnate leaves. The wide *Strombosia* has pedicelled few-flowered cymes, while the two endemics have sessile many-flowered fascicles. In *Euonymus* the wide has fascicles, the endemics lax cymes. In *Pometia* the wide and one endemic have a pubescent calyx, the other endemic a glabrous one. In *Paranephelium* the fruit of the wide has long stiff acuminate spines, while one endemic has short thick spines, the other a scurfy fruit.

In the WE genera we have seen that the marks of separation are most often of a kind allowing of no transition stages between them; in fact they are frequently subgeneric. And the WEE genera again show much the same kind of thing. If the distinction between one species and the next were in one character only, the task of selection, to say nothing of classification, would be much more simple. Unless so correlated, as in climbing plants, that a change in one character must be accompanied by change in another, it must be more difficult to change two than one, and the difficulty grows with further increase, and if one plant-form were selected in preference to another, it would often be at the expense of one of the characters (p. 115). This is clearly evident if we suppose the evolution to be gradual; and if we substitute small mutations, as is so often done, what is to ensure, as they convey no advantage, that they shall run in the right direction (and *cf.* Testcase X in *Evol.*, p. 114)? In fact the only process that can easily change two or more apparently unconnected characters at once, and do it perfectly and completely, is a sudden mutation, where the surprise would rather be to see the change incomplete or imperfect.

The connections between characters that occur in any taxonomic difference do not allow of having been produced by selection once for all, for every kind of combination may be seen, and any one character may appear in almost any connection, so that if it were due to selection, it would have to be selected over and over again (*cf. Evol.* Testcases X, p. 114, and XXIV, p. 138, where I have shown how in three different, but allied families, the change from mono- to dithecous anthers, or *vice versa*, has occurred independently in each, though of no conceivable value). It was occurrences like this, which are very common, that among many other things led the writer to the conception of kaleidoscopic evolution (155), at which he has now worked for about 35 years.

For taxonomic purposes, a character is mainly valued upon how frequently it occurs among plants which seem to be closely related by having other characters in common. One cotyledon is characteristic of a very large group of plants which also *usually* show 3-merous flowers, parallel-veined leaves, or a peculiar anatomy. There are many more characters found in fewer Monocots, though one can give no reason for their presence or absence (when there is usually something divergent present). Some occur in groups of families, like perisperm in the *Marantaceae* group, or fleshy or oily endosperm in the *Liliaceae* group. Others are confined to one family in any connection, or even to one genus, and as one thus descends the scale, one finds exceptions to the appearance of any one character becoming more frequent, so that in giving the characters of a genus or family one constantly has to use the expressions " usually ", " often ", " rarely ", &c.

But all this is so familiar that only a reminder is needed. The essential point is that some characters go very far back in time, in their existing line of heredity, without, apparently, having undergone any serious change or difference since they first appeared. Others may appear again and again in different places, sometimes remaining unchanged long enough to mark a whole family, a part of a family, a genus, or only a part of a genus, or even showing change from one species to the next, or upon the same plant, like the alternate and opposite leaves frequently found upon one plant in *Compositae*. As a character may thus appear under any of these descriptions, it becomes impossible sharply to distinguish between family and generic characters, for example, though most characters appear most often in one or the other capacity. But one cannot say of any character what its value will be in any family, until one has examined the family in detail, and only then can one make a proper classification.

This complication of behaviour, hitherto looked upon as " pretty Fanny's way ", with no explanation, falls properly into place under mutation such as that for which the writer is contending, where it does not depend for its appearance upon selection. If at one place a character is very old, and also very constant in inheritance, it will be, *there*, of great value, while in another place it may be young, or inconstant, or both, and be of little value. And we must never forget that descent from two or more independent ancestors is always possible, even though not very probable, once we realise that any of the characters of a family or genus seem possible of production in it at any moment. In fact, the formation of new species and genera has a close analogy, which may be more, with human birth and evolution.

The close similarity of species in a large genus is most often, apparently, due, as in *Hieracium* or *Rubus*, to the further breaking up of its larger species into smaller or into varieties, but it must not be forgotten that mere increase in number, especially if combined with a decrease in " size " of the mutations, may have a considerable influence upon the overlapping of species.

The contrasting and incompatibly divergent characters that we have seen in the endemics, appear also, as we shall presently see, in almost all of the small genera. The number of these small genera is very great. We have seen (figures of 1922, in *AA*, p. 185) that out of a grand total of 12,571 genera of flowering plants, there are 4853 ones, 1632 twos, and 921 threes, these alone making up 58.9% of all the genera. If we go back to the now untenable theory that all these little genera are relics, there seems to be no reason whatever why they should all show marked divergences of character when they have more than one species. Yet this is just what occurs, with a very few exceptions, and the only reasonable explanation seems to the writer to lie in the general tendency to mark the evolution of new species or new genera by divergence of some kind, generally well marked, a fact which fits very well with Dr. Balfour Stewart's suggestion (*Evol.*, pp. 47, 182) of an electrical force controlling sexual cell division.

We have seen that endemism, though easily described, is very difficult to define, as to the area occupied. In actual fact, if we look at the genera of not more than three species, we shall find that a very large proportion are distributed over an area so small that the title of endemic can hardly be refused, even though it be not given to larger ones. Let us begin with a small family, whose monograph happens to be lying upon the table, the *Styracaceae*, in which Bentham and Hooker, with their greater caution, included the *Symplocaceae*. As now made up the family has six genera, five of them not exceeding three species :

Pamphilia (confined to province Minas in Brazil)	
Inflorescence spicate, fls. sessile or sub-sessile	
Petiole 1 to 1.5 cm.	1. styracifolia
Petiole 0.5 cm.	2. aurea
Inflorescence racemose, fls. pedicellate	3. pedicellata
Bruinsmea (Java, Celebes)	
Filament of sta. glabrous; anther 1 mm. long	1. styracoides Java
Filament of sta. stellate-pubescent, 2.5 mm.	2. celebica Celebes.
Alniphyllum (S. China, Formosa)	
Leaves broadly ovate, ovate, or obovate	1. Fortunei S. China
Leaves oblong-lanceolate	
L. papery, densely stellate-puberulate on both sides	2. pterospermum Formosa.
L. membranous, glabrous above, thinly stellate-hairy below	3. Faurei Form.

Halesia (SE. U. S. A.)	
Fruit 4-winged. Corolla lobed, 1-2cm. long. Filaments connate at base only	1. carolina
Fruit 2-winged. C divided almost to base, lobes 2-3 cm. Style tomentose. Fil. connate to middle or higher	2. diptera
Fruit 2-winged. C lobed, 8-12 mm. long	3. parviflora
Pterostyrax (Japan, China)	
Fruit 5-winged, thinly tomentose	1. corymbosus Japan
Fruit cylindrical, densely hispid	
Leaves densely hairy below	2. hispidus Jap., Chi.
L. thinly pilose on veins below	3. psilophyllus Chi.

This is so hopelessly incongruous an assortment of genera from the geographical point of view that without real and valid individual evidence that they are relics, we must look upon them as perhaps all descended directly from some overriding genus (151). The sixth genus is *Styrax* itself, which covers all the necessary regions, but a still better one is probably *Symplocos*, which is a very widespread and common genus, but was ejected from *Styracaceae*, in which it was placed by Bentham and Hooker, on account of its inferior ovary, completely divided into loculi, and its round, not narrow, anthers—both obvious mutation characters, which are continually shown in mutations that are really the probable result of some strain placed on the nucleus by some change of conditions. Their appearance thus became inevitable, but adaptation has nothing to do with it, for they have no adaptational significance. Their appearance was not a cause of evolution, but a by-product of it.

But these divergent characters of endemics that are thus shown are in no way characteristic of endemics as such. They occur in all small genera with a very few exceptions, such as those genera whose generic rank is still uncertain. Suppose that we now look at a number of the small genera found upon continental areas, which are not generally, though for no good reason, considered endemic, unless found in a part that is comparatively isolated, like South Africa or WEST AUSTRALIA. I have worked out, under various headings, the characters shown by these genera in over a thousand cases. Under the theories which we are here bringing forward, they are just as much beginners as are any genera that are admitted by everyone as endemic. We shall take a few examples from " Leaf— different forms and insertions " : —

Genus	Fam.	No and dispersal	Contrasting characters found
Helietta	Rut.	4 trop. Am.	L. opp. or alt.
Fresenia	Comp.	3 S. Afr.	L. opp. glabrous, or alt. villous
Stilpnophytum	Comp.	2 Karroo	L. alt. or opp.
Codonobea	Gesn.	3 Malay Pen.	L. opp. in two, alt. in one
Epipetrum	Diosc.	3 Chile	L. alt. or fascicled
Acidoton	Euph.	3 W. I.	L. large, distichous, or small, spiral
Bosistoa	Rut.	2 E. Austr.	L. pinnate or ternate
Koelreuteria	Sap.	3 China	L. pinnate or bi-pinnate
Eremia	Eric.	4 S. Afr.	L. 3-nate or 4-nate
Touroulia	Quiin.	3 Gui., Braz.	L. simple or pinnate
Thraulococcus	Sap.	2 India	L. simple or pinnate
Bernardinia	Connar.	4 S. Am.	L. trifoliolate (Peru), bijugate (Costarica), 5-jugate (Braz.), imparipinnate (S. Braz)

It may be noted that these are just a dozen examples under one character, but that in practically all of the 1047 genera examined, contrasts were to be found. Divergence in mutation is the outstanding feature of all young genera, and were it necessary, it would be quite simple to make subgenera in them. But for purposes of identification, for which classification is mainly designed, this is simply a waste of time. The important point is that the characters that would be used to mark these subgenera are essentially the same characters as are so much used in the large genera. For example, taking the first book that comes to hand, the first genus shown with subgenera is *Rumex* (fls. ☿ or ♂ ♀) a distinction which happens to be matched by the first genus in that heading in my list of small genera— *Galopina* (*Rubia-*

ceae) with two species in SOUTH AFRICA, one with ☿ flowers, one with ♂ ♀. Practically any characters of the subgenera of larger genera can be matched among the specific characters of smaller ones, as has long been vaguely known. In both cases *they are divergent characters that appeared early in the life of the genus.*

It is thus fairly evident that at least a great part, if not all, of the characters of a family, may appear anywhere in it, so that the probability is that any member of the family carries with it, dominant or recessive, all the characters of the family. And probably more, for it is a familiar experience that characters may appear in more than one family, like inferior ovary, or porous opening of pollen sacs. In fact, as we have already pointed out, any character may appear in one place in quite a minor role, in a genus or two, in another in the whole of a subtribe, a tribe, or a family; it simply depends upon the age of the character in that place.

We have now seen a good many cases where the characters of plants show such a behaviour that it is best explained by the conception that they were drawn from a kind of Pandora's box which each genus and species carries, and in which are contained all the possible characters (including their own various divergences, like leaf simple or compound, palmate or pinnate, hairy or not in various ways, and so on). If an individual draws from its immediate ancestor the same characters as are shown by that, it will remain specifically unchanged, and up to a certain point it may (and apparently often does) even substitute some new and slightly different characters for some ot its own, like a leaf pubescent below for a leaf glabrous on both sides. But if it take more, or more seriously different, characters, it will be regarded as a new species, and will begin as one or a few individuals. And so on, through the stage of a doubtfully new genus to the stage of one universally admitted as new, or even up to the stage of a new family.

It is of course improbable that the characters are carried as such; more likely it is an assortment of genes which when put together in a certain way result in the production of a certain character, and in some other way yet produce a new and divergent form of that character, like a pinnate leaf in place of a simple one; or in a third way alter more than one character, and so on. It is also so frequent a phenomenon that a character may appear though not usually seen in the family, even if frequent enough elsewhere, that it is not improbable that the Pandora's box may contain the possibilities of any character. But it seems probable that in any single case the characters shown by the actual parent will be those that are much the most likely to occur, though two or three may be changed. There is fairly evidently some super-Mendelian law at work, perhaps or probably complicated, some clue to which might possibly be provided by a counting-up of all the characters shown by the five thousand genera of one species, and careful comparison with those shown by the twos and threes, &c.

If the provision of characters goes on in this way, it is evident that there is nothing surprising in the fact that a character that we are apt to regard as specially marking some genus or small group may appear in some other genus or even small group, whether nearby or at a considerable distance away. Let us take an instance from the first book that comes to hand, the monograph of *Phytolaccaceae (PR)*.

Cpls 2, ovary 2-loc. in Barbeuia (*Phytolacceae*, subtribe *Barbeuinae*, made largely on account of this character, and with no other genus, all the others of the tribe having 3-∞ cpls.)	1 Madag.
2 in Didymotheca (*Gyrostemoneae*)	5 Austr.
Cpls. 2, ovary 1-loc. in Microtea (gen. anom., Chenopod. affin.)	9 Am. trop.
Achatocarpus (gen. anom., Chenopod. affin.)	12 Am. trop.
Phaulothamnus (gen. anom., Chenopod. affin.)	1 N. Mex.

It is clear that these genera did not derive their two carpels from immediate ancestors, but by super-Mendelian inheritance from something further back.

Unisexual flowers appear, again, in *Monococcus* (1 Austr.) in tribe 3 *Rivineae*, in the whole of tribe 2, *Gyrostemoneae* (5, 5, 3 and 2, Austr.), and in the anomalous genus *Achatocarpus* (12 C. and S. trop. Am.) and *Phaulothamnus* (1 N. Mexico). All the Australian, though in two subgroups, might have acquired them from one source, but not the American also, unless that source were *far back* in the family ancestry.

This apparently casual appearance of single characters which are frequent in some other part of a family is a common occurrence. For example in *Annonaceae (Gen. Pl.)* while *Uvarieae* have all, or the interior petals imbricate, so also does *Bocagea* in *Miliuseae*. Stamens are 2-5 times the petals in a few *Sageraeas* (*Uvarieae*) and *Popowia*, and in *Orophea* (*Miliuseae*) all Asiatic species, the African *Clathrospermums* (*Uvarieae*) and the American *Bocageas* (*Miliuseae*). In their descriptions, BENTHAM and HOOKER say that for example *Alphonsea* (*Unoneae*), *Clathrospermum* (*Uvarieae*) have the stamens of *Miliuseae*, and make this kind of statement very frequently, or such a one as that genera 34, 35 (of *Gen. Plant.*) have the petals of *Phaeantheae*, 36 of *Mitrephoreae*, 37, 38 of *Unoneae*, 39 of *Uvarieae*; and so on.

The next family at which the *Gen. Pl.* opens is the *Tiliaceae*, where we find opposite leaves in *Plagiopteron*, and a few species of *Sloanieae*. Petals are absent in *Grewieae*, *Triumfetteae*, a few species of *Prockia* (trop. Am.), and nearly all of *Sloanea* (trop.), and they are united in *Antholoma* (N. G., New Cal.), while endosperm is absent in *Brownlowia*.

In *Burseraceae*, leaves are opposite and alternate in *Amyris*; petals are absent in *Ganophyllum* (cf. *Antholoma* above); stamens are opposite the calyx-lobes in *Crepidospermum*, *Filicium*, *Nothoprotium*, alternate with them in *Ganophyllum*; the ovule is solitary in the loculus in *Filicium* and *Hemprichia*.

In *Leguminosae-Papilionatae* the calyx is entire, variously divided at anthesis in *Fissicalyx* (§ 9), *Baphia* (§ 10), *Leucomphalos* (do), these two trop. Afr., while *Bowringia*, also § 10, occurs in Hongkong. It also occurs in *I* 11, *Swartzieae*, in some *Zollernias* (Brazil), *Exostyles* (do), *Aldina* (do., Guiana), *Cordyla* (trop. Afr.) and in *Swartzia* itself (65 trop. Am., Afr.) from which all the others might easily be derivatives, none having more than a few species.

In *Liliaceae*, one finds three stamens in *Heterosmilax*, *Ruscus*, *Anemarrhena*, *Hodgsoniola*, *Leucocoryne*, *Stawellia*, *Sowerbaea*, *Johnsonia*, *Hewardia*, and species of other genera; more than six stamens in *Pleea* and rarely in *Smilax*; and so on.

It is thus becoming fairly evident that all, or almost all, of the characters of a family may appear anywhere in it, and therefore that the probability is that any member of the family carries with it, dominant or recessive, all the characters of the family, or rather the potentialities of producing them, and probably also, as we have seen, characters that are more frequent in other families, perhaps even far distant in the matter of relationship. The study of characters, and of the factors to which their formation is due, as well as the study of how external conditions affect those factors, may perhaps become one of considerable importance, and we have seen above how in the light that geographical distribution is beginning to throw upon this part of the subject, a number of facts, hitherto without explanation, seem to be falling into place in the general plan of evolution.

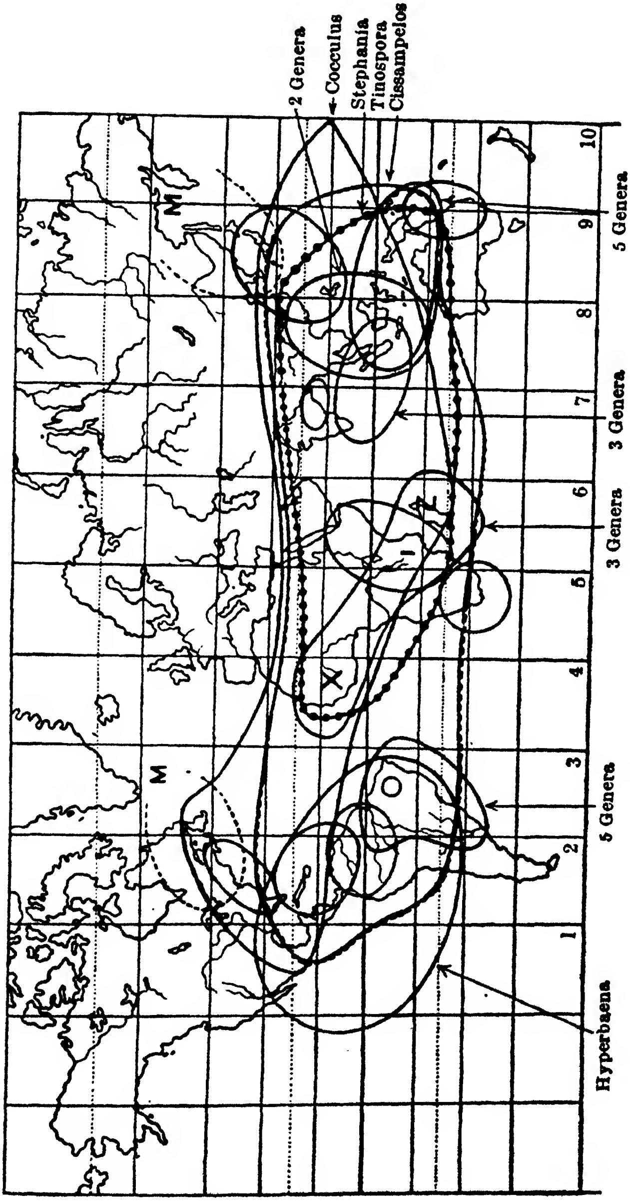
CHAPTER VII

Endemic and other genera

Going southwards from BRITAIN, one meets first endemic species, increasing in number as one goes, mainly in broken and especially in mountainous regions. After a while one also encounters endemic genera, few at first, increasing later, and further still one may even encounter families so localised that one would be sure to count them endemic. The bulk of the endemic genera belong to large families rather than to small, even in such an ancient home of endemism as the HAWAIIAN Is., where a very large proportion of them belong to the group of allied families *Compositae*, *Campanulaceae*, *Rubiaceae*, and *Araliaceae*.

Genera follow the same rules as species, and are therefore probably as a rule such as have not yet had time to spread to larger areas, especially when this has been made difficult or practically impossible by barriers like the sea or a chain of mountains. The areas occupied vary from very small, as in the case of *Itatiaia* on that mountain in SOUTH BRAZIL, *Leichhardtia* on the DAINTREE River in AUSTRALIA, *Cephalotus* at KING GEORGE'S SOUND in WEST AUSTRALIA, and so on, upwards. In NEW ZEALAND, two genera are found only in the outlying islands, while others range along the main islands for various distances from a few miles to 1000, the larger half being below the moiety of the length. If one look at the map of *Menispermaceae* here reproduced from *Age and Area*, one can see how the smaller genera are more local, obeying the law of size and space, while the largest (especially *Cocculus* and *Cissampelos*) occupy the bulk of the entire range of the family.

We have dealt with endemic genera at some length in *Age and Area*, Ch. XVI, p. 169, and esp. pp. 175-83, and



Outline Distribution of Menispermaceae
12 genera at X, 5 at Z. M = Menispermum
(By courtesy of the Royal Society)

need not repeat what has there been said. As people usually only consider as endemic those on small areas, of course the bulk are monotypes, and the numbers taper away very rapidly upwards. In MADAGASCAR, for example, where there are a great many, they show (figures of 1922) 191/1, 37/2, 10/3, with a maximum at 20. The phenomena that they show are exactly paralleled by the non-endemic genera, giving great support to our supposition that endemism is simply a miniature representation of distribution in general, which is chiefly controlled by the laws of ASA, working upon the material supplied to them by the law of divergent mutation in its various manifestations.

There is no sound basis upon which to build any theory or a satisfactory distinction between things that are endemic, and those that are not so, for no two writers seem to agree about the extent of area that an endemic species or genus may cover. This is partly due to the false impressions made by the varying scales of maps, where, for instance, the whole of INDIA, or even of S. AMERICA, is shown on one page, like the comparatively infinitesimal area of ENGLAND. While in RIO, we were asked by one of the most famous of British botanists to get him a plant from the higher levels of ACONCAGUA, more than a thousand miles away, in CHILE, to say nothing of the dense tropical forest between, and of the ascent.

If age alone were operative in this case, one would still tend to get very much the same distribution as actually exists, when one allows for geological and climatic changes, and for the action of barriers, whether more or less permanent, like sea or mountains, or temporary, like the boundaries between different ecological associations. The table given on p. 180 in *Age and Area* with the figures on p. 181, shows how mechanical is the basis of all geographical, as distinguished from local ecological, distribution. In face of such results, it becomes very difficult to uphold relicdom or local adaptation (other than that which everything must possess in order to survive at all) as an explanation of endemism, whether for species or for genera.

As we have seen in the tables of *Ranunculaceae* on pp. 30-31, and shall see again even more strikingly in the case of *Acanthaceae* in a later chapter, there is no possibility of drawing a line anywhere between endemics and non-endemics, except at the personal choice of the author, for as one goes up the list, the small and local genera are followed by genera that steadily decrease in numbers, and increase in area occupied, until at the top one comes to the actual leaders of the family. The laws of ASA are obeyed as closely as is possible, or almost exactly by the genera at the bottom, which do not come into serious differences of conditions, because by reason of their small age they occupy but small areas. As they grow larger, and occupy more space, possible differences of conditions increase, until when they reach the size of say 20-30 species they begin to come within the range of great geological and climatic changes of long ago, for their age is great enough to take them so far back. Thus, with our present very limited knowledge, speculation must begin as the genera with which we are concerned increase in size, so that with genera larger than say twenty species, we must bring geology, climate, and other conditions into the matter, and when possible trace the conditions under which the genus began its life.

Endemics belong mainly to mountainous and broken countries, as a reference to the map of *Siparuna* (p. 224) will show for a single case, and one to that of the *Menispermaceae* above. Great numbers also occur on islands, but in general islands are also mountainous, and one cannot disentangle the two factors. The proportion of endemics also increases as one goes southward, and the increase seems to go well south of the equator, reaching a maximum somewhere about the tropic of Capricorn. It is not unlikely, as to a large extent endemics mark the progress of invasions, that the current of invasion, as HOOKER has said, ran largely from north to south.

The endemics of mountains are less related to the species of the plains, in warm countries, than are those of islands to those of the nearest mainland. This is probably due to the fact that travel could often take place, or had to take place, along the higher levels of the mountain chains. One must not forget that isolation has probably something to do with the formation of endemics (*cf. AA*, pp. 17, 148, and *Evol.*, pp. 25-7, 101).

Like the species, endemic genera belong mainly to the large families. Of approximately 1879 endemic to the islands of the world, not including AUSTRALIA, nearly

90% belong to the first 40 families in world-size, while about 150 small families have no endemics upon islands at all, they having been in general too young to have reached any islands. It is thus extremely probable that the genera are formed by single mutations in the same way as the species. This is confirmed by the fact that hardly any endemic genus does not belong to an important subgroup of its family, when such a group exists; one does not often find an endemic genus in a small and insignificant group. Here again, the result is simply due to the operations of the law of doubling, by which evolution appears to work. A small group necessarily has but few offspring, while a large has many, and large groups are usually headed by large genera. This shows everywhere; let us take the *Connaraceae*, the latest monograph of which *(PR)* is lying upon my table. Placing the genera in order of size, and mentioning the position of each in the subgroups (tribes), we get :—

Connaraceae in order of world size

Genus	World size	Tribe
Connarus	121 spp.	Heading the *Connareae*
Agelaea	46 spp.	Heading the *Agelaeeae*
Santaloides	45 spp.	Heading the *Byrsocarpeae*
Cnestis	37 spp.	Heading the *Cnestideae*
Rourea	32 spp.	second in Connareae
Byrsocarpus	17 spp.	second in Byrsocarpeae
Ellipanthus	13 spp.	Heading the *Castanoleae*

and other genera of 12, 10, 8, 8, 6, 4, 4, 4, 4, 3, 2, 2, 2, 1, 1, 1, 1

All the tribes given in the list belong to and are all that make up what taxonomists consider to be the sub-family *Connaroideae*, while one small genus *Jollydora*, with three species in WEST AFRICA, forms by itself alone the other subfamily *Jollydoroideae.* The two sub-families are thus distinguished :—

Jollydoroideae :	seeds two in indehiscent follicle
Connaroideae :	seed one in dehiscent follicle

Here we have a striking double divergence, appearing late in the life of the family, for *Jollydora* has only three species, though it is West African like most of the family. But, upon structural evidence only, without reference to the size or the geography of the genus, it is considered to be different enough to make a sub-family, though it must, fairly evidently, have been the offspring of one of the other West African *Connaraceae*, and therefore related as closely as possible to *one* of the *Connaroideae*. Its present position is therefore not genetically natural, though such as will enable its easy identification. But the grouping of the family is artificial. A genetic grouping does not, under present conditions, lend itself to the great purpose of most classifications—identification. At a certain very early period in the life of the *Connaraceae* when there were only four genera, *Connarus* to *Cnestis*, with perhaps 4, 2, 2, and 1 species, there were already four subgroups represented ! Such an early formation of subgroups as this, which we shall see to be the rule, shows how families follow the rule of early divergence that we have seen so strikingly manifested by the families that contain two genera each, only, a list of which was given as Appendix III in *Evol.*, p. 199.

Schellenberg's classification frankly adopts geographical separation as a means of dividing some of his groups, and this is certainly a step towards a natural system of classification though perhaps mainly dictated at present by its convenience as a way of splitting up a family upon natural grounds. The smaller the area with which we have to deal, the easier is it to identify the plants upon it, as is familiar enough, though the reason for, and the meaning of, the greater divergences (which make classification simpler) under such conditions has escaped notice. The question now comes up—can sufficient structural differences be found between plants of the old world and of the new in the same genus or group, always to enable us to separate them, or must we go on with the whole genus, as at present, with what little help we can draw from the geography? Here, *Connarus* is the only genus large enough to occur in both worlds, and its third section, *Euconnarus*, seems to occur only in the old world, the second only in the new, but the first section, *Connarellus*, has about half its 30 species in each. Any character found in a family seems capable of turning up anywhere that a member of the family may be found, and there seems no certainty of finding any character confined to any particular region, with no discontinuous occurrence somewhere else. Characters that mark what we regard as a good and reasonably large group are almost sure to turn up elsewhere than in that group. They are then put down as exceptions, but they are exceptions to man-made, not to natural, rules.

Though geographical propinquity, or the reverse, is evidently a character that cannot be neglected if we are to arrive at a natural classification, it will make the classification by characters—at present we use only structural characters—much more complicated and difficult, if it is to be a natural classification also. In fact, it looks as if a natural classification would prove to be almost so complicated that for a real and practically useful one we shall have to fall back upon something artificial. Our present system, by putting together, for example (p. 107), as closely allied all those species of *Rhamnus* which show C5, A5, and distinguishing them from those which show C0, A4, evidently violently divorces the two closely related species of the CEYLON hills, and also those of the MADRAS hills, to say nothing of similar divorces all over the whole range of the genus. Both the sub-genera thus made at once show a very discontinuous geographical range, whereas they cover the ground very well if one add them together. The more that we try to break up a family or genus into subgroups, by structural characters only, the more do these subgroups show what we have called in Chapter IV discontinuity of character or of structure, and if we force into these subgroups, as we do, all those plants that agree with what we have arbitrarily chosen as characters for those subgroups, then we commonly get geographical discontinuity, for which we can find no reason, and though sometimes this may be explained by the presence of an overriding genus that covers both localities, this is not always the case.

One can no longer use one or two marked characters, as has hitherto been the custom, as showing, when they are the same in two species or genera, that these are necessarily closely related, for we have seen how strongly marked the tendency is, for divergence between parent and offspring to appear. We shall see as we go on that what shows in the *Connaraceae*, where the early closely related genera mostly belong to different subgroups, shows in practically all families where the distinction of these subgroups is by morphological characters and differences. Here there is a parent genus *Connarus*, and all or nearly all its earliest descendants are placed each in a different subgroup from that to which it belongs itself. From the genetic point of view, which is supported by the geographical, they must be the closest of relatives, largely in fact parent and child, but from the taxonomic point of view, which at present is simply the structural, they are all very definitely separated, each into its own subgroup. The next chapter will go into more detail, and give a table showing the actual facts for all the leading families, facts which cannot be gainsaid, and which it is perhaps worth specially noting, were obtained, as most of thediscoveries in this book have been obtained, by prediction. This endless possibility of prediction has lent force to the setting out of the new principles here advanced, and has formed them all into a connected whole.

With characters showing as they do, not necessarily inherited from parent to child, but liable at times to some complete and divergent change in that passage, it is clear that we cannot construct a natural classification upon a structural basis alone. On the other hand, it is equally clear that a classification which followed the evolution of plants by the doubling law, and therefore was a " natural " one, would probably show so many changes back and forward from character A to a, or from B to b, or even from A to B, and so on, that it would be impossible to use it as a means of identification of plants, and until we have a far more complete and thorough knowledge of characters and their incidence, would be impossible to construct. It will be better to go on with our present system, artificial though it will be in parts, and anywhere liable to be so, and to regard a really natural system of classification as a dream of the future, as we regard the formation of a gene and chromosome map. On the other hand, the arguments that go on as to the relative value of this or that character in the placing of a genus, especially when they are not based upon actual figures of frequency of occurrence, seem often to be very largely a mere waste of time.

We are as yet without any standard against which to value characters. We cannot say whether, for example, the distinction of the sub-genera in *Homalium*, single antepetalous stamen/stamens in antepetalous bundles, is larger or smaller as a mutation than the distinction between the two Hawaiian *Portulacas* (one wide, one endemic), stamens 7-12/∞, or the distinction between the two species of the endemic genus *Tetraplasandra*, stamens 3-4 times the petals/6-8 times. In general it would seem as if the distinction was probably of much the same value whether of wide and endemic with large or small genus, of the species of small genera, or of subgenera. The value is really as much imparted by age as by any factor.

Endemic genera of Ceylon. Let us now consider some of the 25 endemic genera of CEYLON, using the placings of TRIMEN and HOOKER (125), and begin with *Schumacheria* in the *Dilleniaceae* (l. c., vol. 1, p. 10), which is worth a little consideration. TRIMEN puts it next to *Acrotrema* in his key :—

Filaments dilated upwards (*Delimeae*) .	1. Delima	2. Tetracera
Filaments not dilated upwards (*Dillenieae*)		
Carpels 3; anthers opening by slits		
Perennial herbs		3. Acrotrema
Shrubs		4. Schumacheria
Cpls 4-20; anthers by pores; trees	5. Wormia	6. Dillenia

The characters are the usual *divergent* characters upon which keys are based, in fact, without which keys could hardly be made. The difference which our work brings into former conceptions of relationship is that divergence in some feature or features, which was supposed to mark wide separation if it were a "large" divergence, need not necessarily mark anything wider than the difference between closely related species or genera. *Schumacheria* in any case comes fairly near to *Acrotrema* in many characters, like the sheathing broad-based petiole, the strong lateral veins of the leaf, the ∞ stamens, not dilated upwards, the anthers dehiscent by slits, the three carpels, &c. But it differs in three important characters; it is a shrub, while *Acrotrema* (7 spp. CEYLON, one showing many forms, 1 MADRAS; 1 MALAYA) is the only herbaceous genus in the family; it has monadelphous stamens, posterior in the flower, instead of regular or triadelphous, and its carpels are 1-ovuled, not 2 or more. These characters have hitherto been supposed to outweigh those of agreement, even with the geographical argument added, which is that *Schumacheria* is an endemic genus in the heart of the " *Acrotrema country* ", and therefore probably a very close relative, while genera that have its unusual characters in common with it are far away, thus showing " structural " or " character "-discontinuity. Great stress has been laid upon the herbaceous nature of *Acrotrema*, and this genus is commonly given a group to itself, but a herb is a perfectly natural divergence from a shrub, and the two occur side by side in many genera in many parts of the vegetable kingdom. We have shown in the last few chapters that argument from structural similarity will not bear the load that is often placed upon it, and that geographical continuity is just as important, unless there be an overriding genus to cover wide gaps, as described in (**151**).

Prominently displayed among the characters of *Schumacheria* (fig. in **125**, Plate II), however, is a monadelphous column of stamens on the posterior side of the flower, and thus in strong contrast with the usual regular, or sometimes triadelphous, androeceum, found in most *Dilleniaceae*. It turns up again in the largest, and probably oldest, genus, *Hibbertia* in AUSTRALIA, NEW CALEDONIA, &c, but even there in only part of the genus, the sixth section, *Pleurandra*, though there is a suggestion of it in the fifth section, *Hemistemma*. The first four sections show little or no sign of such a thing. Nor does it show anywhere else in the family, though it turns up in BRAZIL in the genus *Luxemburgia* of the allied family *Ochnaceae*, and there is a suggestion of it in the family *Lecythidaceae*, which is largely Brazilian. If one call in destruction of transition forms to connect these great discontinuities of character, one has to call it in upon a simply incredible scale, including the destruction of many species of *Schumacheria* itself, to bring the genus down to the small and local thing that it now is, and which, if it were never any bigger, could not be closely related to anything in BRAZIL, by reason of its youth, and the great age of the separation of the two great land masses. We have no evidence for any such destruction, and even then we must have a great deal more of it to connect with *Hibbertia*, which is also a difficult proposition, with no overriding genus to help us. It is in a very high degree improbable, therefore, that these appearances of this very peculiar character have any connection with one another except through some very far back ancestor, which of course means that the character must have been handed down through other ancestors that did not themselves show it, though the potentiality of producing it was in their make-up. Given some combination of conditions of which at present we have no idea, it appeared in the places where they were operative. As a general rule, character discontinuity like this is fairly wide, and it is often so wide that (as here) it probably goes right back to the head of the family. Hence my suggestion that the head may carry with it, in a kind of Pandora's box, all the characters (or potentialities) that may afterwards appear in any member of the family. In this case, the change in *Hibbertia* was not accompanied by such marked changes as in *Acrotrema*, and the species with the peculiar androeceum were left in *Hibbertia*, while in *Acrotrema* a new genus was produced. Here again we have one of the phenomena which produce what it is becoming the fashion to call a complex of genera; in this case it is possible that the family *Dilleniaceae* is combining with *Ochnaceae* and other families to produce one.

In these cases of occurrence of peculiar characters in two or more genera of a family, when they occur at great distances apart, and there is no overriding genus (151) to connect them, it not infrequently happens that one or both of the bearers is very small (young), probably if not certainly too young to allow of transition forms or of direct descent the one from the other. Any common ancestor that carried the character could often not have been an *immediate* ancestor, so that there must have been intermediate ancestors that were not carrying it. One soon finds, as the writer found 40 years ago, that the distribution of characters is an intricate set of permutations and combinations. The only way in which both could receive the character from an immediate ancestor is by having as such some overriding genus, covering both localities sufficiently early and giving rise to the same character in two separate mutations, in which case the origin of the character would be polyphyletic. The important characters are fewer in number than the plants that show them, so that nothing but permutations and combinations could produce the results shown. The actual characters go in what we may call series, or sets, like stamens 5, 10, 15, ∞, 2, 3, didynamous, &c, &c, where the changes are often inconceivable except as sudden mutations. In fact the combinations are so complex that the only common ancestor from which all characters could, and must, have come, is the actual leader of the family (in size or age), in which we must always imagine that all but one character in any series is lying dormant or recessive. At each dip into the Pandora's box the most common result will probably be no change worth very special notice in any character—result, another member of the same species. The next most common will be a change in a few characters—result, a new species. The next a new genus, and so on. There are slight indications that a character recently acquired in the ancestry is perhaps somewhat more likely to appear in any new genus than the one that it diverged from and superseded at a previous birth. But for anything that we can tell, there is nothing to prevent an old character being taken back at the very next birth in the family. This is confirmed for example by the remaining important difference in *Schumacheria*, the single ovule in the carpel in place of the two or more in *Acrotrema*. Some *Hibbertias* in Australia, and some *Dillenias* in the Malay Archipelago, show one ovule, but nothing in Ceylon, and again it looks as if the character in *Schumacheria* had been derived from a remote ancestor. Any member of a family must carry in itself the potentiality of producing any character that may appear in that family.

A great part of this family seems artificial in its grouping. Let us for example take the species of *Tetracera* given in Engler (1st ed.). Each bracket includes the range of one species.

§ 1. Empedoclea	2 spp.	(Bahia) (Minas), adjacent Brazilian states
§ 2. Eutetracera	6 in A	(E. Brazil), (Trinidad, French Guiana) (Antilles to NE. Brazil), (Surinam), (Madagascar), (Sumatra, Borneo)
	3 in B	(Minas, Fr. Guiana), (trop. Afr.), (N. Austr., NE. New Guinea)

	6 in C	(E. Brazil), (Mexico), (Borneo), (Indomalaya), (Further India), (W. Afr.)
	6 in D	(Rio de Janeiro), (do), (W. Afr.), (Further India, Malaya), (Queensland), (do)
§ 3. Delima	2 spp.	(Further India, Malaya, China), (Fr. and Dutch Guiana).

The few species discovered since the date of this list do not fill the enormous gaps there shown. The second section illustrates especially well the widespread and important feature in taxonomic work, that the more a family or genus is split up into smaller divisions, the more marked does the geographical divergence between their members become, in most cases, thus apparently indicating that divergences of character may be the same at different places.

The second section above is divided into its four groups by the distribution or absence of leaf-hairiness. One may see the same thing in one genus in one country, in many Ceylon genera, Trimen making rather a feature of hairiness in his flora. Thus in *Vernonia* there are two wides of great dispersal, *cinerea* (palaeotrop.), hairy on both sides of the leaf, and *arborea* (Indomalayan), glabrous above and finely but densely felted beneath. There are nine endemics in Ceylon, and a tenth reaching the Nilgiris in India, none of which show these characters, even though they are almost certainly directly descended from the wides. The Nilgiri species, and four Ceylon, are glabrous or slightly hairy on both sides, two roughly hairy, and the other three show glabrous above/tomentose below, finely pubescent/densely felted, and cottony/white with fine wool. No gradual selection could produce such characters, localised in such a way.

The geographical relationships of these *Tetraceras* are particularly bad,. showing much structural discontinuity. Those in 2A are scattered over the continents, and so are most of the rest, with little geographic continuity. But *if one run them all together*, the total area of dispersal is much better covered (*cf. Rhamnus* on p. 107). The American species will then be Rio, Minas, Bahia, E. Brazil (2), Guiana, Trinidad, the Antilles, Mexico, a practically continuous stretch of country which might easily have been covered by a single line of descent, but which is here broken up among the whole of the six divisions of the genus. The four American species discovered since the publication of Engler, in Peru, British Honduras, Trinidad, and Brazil, help to cover the American space better. The more that we break up any group, family or genus, upon our present structural lines, the more incongruous do its geographical relations become, and the more do they demand the destruction of connecting links in vast profusion, if we are to regard any structure as arising out of something like itself. Some of the facts that I have observed, here and elsewhere, go so far as to suggest that not only has the same character been inherited at different places and in different connections, but that perhaps there has not even been an adhesion to the same genus, and that something like what BOWER suggested in the ferns, that a fern might go through an *Acrostichum* (or other) stage, may take place; for example an *Acrotrema* might go through a *Schumacheria* stage, and again go back to *Acrotrema*. Some *Dilleniaceae* show such a combination of characters that one puts them in *Tetracera regardless of geography*, while others may drop out of the genus for lack of one or more of the obvious characters that mark it, though there is no particular reason why these characters should be any more fixed than others. We must get more into the way of regarding characters as a whole. At some place in a family, characters A, B, and C may be well marked, and we call that group of plants the genus X; at another place E, F, G may be well marked in a number of forms, so we call them the genus Y, and so on. But the whole set of characters seems more or less fluid, and apparently any of them may change at any time, though some seem more likely to do so than others, under certain conditions at any rate. Upon our suppositions, something happened in CEYLON to the parent of the first *Schumacheria*, which belonged to another genus, probably *Acrotrema*, and rearranged the sexual nuclei in such a way that certain characters were no longer produced, but replaced by something divergent, so that characters that were new for that geographical region, like shrubby habit, and a posteriorly developed androeceum, appeared. The very next mutation may change a *Schumacheria* into something else probably causing the origin of a new endemic genus.

Everything seems to indicate that taxonomy based upon structural characters only cannot be reconciled with geographical distribution, nor with evolution by divergent mutation. Our present interpretation of taxonomic facts depends upon certain assumptions, one of which is that any character must have been directly inherited from an ancestor that showed something like it, from which it might be derived, and not from one quite different from itself, as a simple is different from a compound leaf. This divergence was one of DARWIN's great difficulties, now being better recognised, and when we find that species with structural affinities are so often so discontinuous geographically, we are evidently coming to a deadlock. From this the work described above seems to offer us a way of escape, even though it may mean scrapping what we may have hitherto regarded as almost axiomatic.

In many cases, overriding genera will afford explanation of geographical discontinuity, but there are a great many where this is not the case, and where we must probably put down the affinity to the independent appearance of the same character, in widely separated places. It seems to be an independent inheritance from a far back ancestor, most probably the actual head of the family.

But if polyphyly like this is possible among the younger genera that chiefly show such discontinuities, it is difficult to produce any reason why it should not also have occurred in the older genera, though of course much less often, as they are much fewer in number. An element of uncertainty is thus introduced into all our taxonomic work as at present conducted, and the same thing may be said about the results that are now beginning to show in genetic work. For a natural classification both this and geography must be added to morphology; it seems to the writer that without these additions it is impossible to make a classification natural.

The next CEYLON endemic genus is *Trichadenia* (*Flacourtiaceae*, *l. c.* I, 75) with one species, distinguished by its undivided calyx that opens by an irregular separation about the middle, throwing off the upper part as a cap. It also has plicate cotyledons, and only five stamens, and belongs to the tribe *Pangieae*, largely distinguished by an adnate scale on the inner side of the petal. The only other CEYLON member of this group is the widespread Indo-malayan *Hydnocarpus* (35 spp.) which has two CEYLON species, both endemic (*cf.* ALSTON in TRIMEN, *l. c.* VI, p. 15).

The peculiar throwing off of the calyx in *Trichadenia* is practically unique in the family, though *Prockiopsis* (tribe *Oncobeae,* 1 sp. MADAG.) throws off the whole calyx as a cap. The two genera are both monospecific (young) so could not have had direct connection across the INDIAN OCEAN, and are widely separated, both structurally and geographically. It is thus clear that their calyx characters must have been independently acquired, from parents that in all probability did not themselves possess them except in a recessive condition. Now that we have seen what mutation can do in the production of endemics (young beginners) differing widely from their immediate parents, there is no difficulty in accepting polyphyletic origin like this. *Gynocardia* (*Pangieae*) with one species from ASSAM to TENASSERIM, has a calyx that tears into sepals, but it is probable, again from the geography, that this character was also independently acquired.

Pangieae are divided into the group that we have just considered, and another group composed of the single genus *Kiggelaria* with seven species in S., E., and trop. AFRICA, where there is little or no likelihood that *Hydnocarpus,* which is fading out at the CEYLON level, ever appeared, especially as neither itself nor *Kiggelaria* appear in MADAGASCAR. The latter owes its inclusion in a separate group to the opening of its anthers by apical pores, or short slits, against long slits, and a fruit usually dehiscent as against indehiscent. But though thus isolated structurally as well as geographically from the Asiatic *Hydnocarpus* group, the characters of the two overlap. Structural discontinuity in fact, as proves to be so very commonly the case, refuses to agree with geographical discontinuity, and as the latter is an unquestionable fact that requires explanation, while the former is mainly an important fact *because we have assumed* that close similarity of structure necessarily goes with close relationship, regardless of geography, it is clearly the former that must be wrongly based.

As it is evident that selection cannot explain the constant occurrence of the same characters in different places (*cf.* also Testcase XXIV in *Evol.*, p. 138), as usually they have no conceivable adaptational value, there seems nothing for it but to imagine them each produced at a single mutation, but anywhere in the family. Hitherto, the family has been supposed to have a " tendency " to produce certain things, and anatomical or structural necessity has been supposed more potent than selection in the case of occurrences like this. (*Cf. Evol.*, top of p. 120, pp. 123-4, and Testcases XXIII and XXIV, p. 138.)

It seems likely that our suggestion that any member of a family may be carrying all the characters (or more probably the potentialities or the factors), and may produce them at any time, as illustrated by the facts of teratology, is perhaps the most probable solution of this problem for the present. Something happened to the progenitor of *Schumacheria* or of *Trichadenia*, which caused their peculiar characters to come out, but the same thing might, under the same or similar circumstances, happen to any of the family.

Incidentally, it is worth while to look at the floral diagrams of five *Flacourtiaceae* given in ENGLER (1st ed., p. 5) to see how impossible it would be to produce these by selection, or in fact by anything but by straight mutation. Another good illustration will be found in *Phytolaccaceae* (*PR*, p. 10).

The next CEYLON endemic genera are three *Dipterocarpaceae*, and we shall begin with a table of the whole family, arranged by world size (curve on plate, p. 33).

Subfam. I. *Dipterocarpoideae*

Genus	World size and dispersal	Tribe	Found in Ceylon
1. Shorea	100 Indomal.	Heading *Shoreae*	5, all endc.
2. Dipterocarpus	70 Indomal.	Heading *Dipterocp.*	5, all endc.
3. Hopea	55 Indomal.	2nd Shoreae	3, all endc.
4. Vatica [1]	48 Indomal.	Heading *Vaticeae*	4, all endc.
5. Anisoptera	18 Malaya	2nd Dipterocp.	nil
6. Balanocarpus	16 Indomal.	3rd Shoreae	1, endc.
7. Stemonoporus	13 Ceylon	Heading *Vaterieae*	13, endc. genus
8. Doona	12 Ceylon	4th Shoreae	12, endc. genus
9. Cotylelobium	5 do, M. P., Borneo	2nd Vaticeae	1, endc.
10. Pachynocarpus	5 Malaya	3rd Vaticeae	nil
11. Pentachme	5 Burm., Malaya, Phils.	5th Shoreae	nil
12. Parashorea	4 SE. Asia	6th Shoreae	nil
13. Dryobalanops	4 Born., Sum.	Heading *Dryobalan.*	nil
14. Vateria	3 S. Ind., Ceyl.	2nd Vaterieae	1, endc.
15. Monoporandra	2 Ceylon	3rd Vaterieae	2, endc. genus
16. Cotylelobiopsis	1 Borneo	4th Vaticeae	nil

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[1] Incl. Synaptea. M. P. = Malay Peninsula. Sum. = Sumatra

Genus	World size and dispersal		Tribe	Found in Ceylon
17. Isoptera	1 M. P., Borneo, Phils.	7th	Shoreae	nil
18. Dioticarpus	1 S. India	8th	Shoreae	nil
19. Vateriopsis	1 Seychelles	4th	Vaterieae	nil
20. Scaphula	1 Burma	3rd	Dipterocp.	nil

Subfam. II. *Monotoideae*

Genus	World size and dispersal		Tribe	Found in Ceylon
21. Monotes	13 trop. Afr.			
22. Marquesia	3 trop. Afr.			

This is a very interesting table, and shows as usual how the larger genera have the larger dispersal, and are best represented, and contain the heads of the subgroups. CEYLON has 45 species, and the heads of four of the five subgroups, in the genera 1, 2, 3, 4, 6, 7, 8, 9, and only 4 species in all the rest. As MALAYA has a somewhat similar but larger representation, we may imagine that the family began somewhere between the two, but nearer to MALAYA, and the separation is now so broad and deep that it is evidently very old.

Beginning with the division into the two sub-families, the first with anther firmly united at base to a short filament, with resin and balsam passages, the second with moveable anther inserted at middle on a long filament, and no passages, we get what is evidently a sound division, for *Dipterocarpoideae* are tropical Asiatic, fading out with one species in the SEYCHELLES, while *Monotoideae* are purely tropical AFRICA, the two not meeting anywhere, even in MADAGASCAR, and *Monotes* being so large that it could only have come from one of the four at the top. But the union, if it ever existed, must be so far back that geological help must be mainly relied upon, and the botanical evidence shows nothing to suggest that they should be kept in the same family. The anatomical difference is the same as that between *Anacardiaceae* and *Corynocarpaceae* (*Anacardiaceae* p. p. BENTH. and HOOK. f.), but evidently older, and must be mutational.

Taking this dispersal as it stands, it is clear that the geographical distribution of the genera, as usual, completely disregards the taxonomic grouping, so that the classification does not represent the real affinities, except at times, and then more or less accidentally.

Shoreae, with the largest head, is the largest group, with seven apparent descendants (for we can no longer feel sure that every one of the seven really belongs to the group), and to define it we must give it a combination of characters, the most important probably being the calyx imbricate in bud, and the two, or three, sepals enlarging to wings. But one finds the imbricate calyx again in the *Vaterieae*, which however have an equal calyx, not winged even in fruit, and in the *Dryobalanopseae*, where the equal calyx later becomes 5-winged. While most of the *Shoreae* have three wings, one subgenus of *Shorea* itself (the oldest and largest genus, be it noted) has two, and another has five.

In *Dipterocarpeae*, there are only two others that show the characters of the leader. As this is the second genus in the family, one may imagine that its genetic descendants are perhaps really more numerous, but that in the mutations that formed them they perhaps lost the particular characters that mark the subgroup. And so on.

The *Vaterieae* form a somewhat improbable group. *Stemonoporus*, as a CEYLON endemic, could hardly be its real head, and is probably a part of *Vateria*, to which it is united in the *Flora of British India*, thus centring the genus in CEYLON, while *Monoporandra*, the other endemic in the group in that country, would take its natural place as an endemic in the " *Vateria* country ".

CEYLON, with about half the genera of the family represented in it, shows the heads of four of the five sub-groups, the only one not represented, *Dryobalanopseae*, having only one small genus, in MALAYA. In so small a family, this shows up very well the underlying artificiality of our present system of classification. This same kind of thing is an universal phenomenon. It is clear that only those things are put in *Shoreae*, for example, which *happen* to have the two characters mentioned above, and that these characters may be found singly in other places (pp. 134-6). We have drawn certain lines of distinction in taxonomic work, to divide families or other groups into smaller divisions, and having done so, we find that the incidence of any single character frequently crosses these lines in an apparently arbitrary way, so that at bottom our system is largely artificial, and in places natural, just as was the case with the Linnean system, from which the writer was taught his botany only 70 years ago. In *Diandrae*, for example, one found *Circaea*, *Veronica*, and *Anthoxanthum* side by side, while the *Tetradynamae* was the single, and well established, family *Cruciferae*. The wide separation that always shows between the leading genera of a family, which are really very closely related indeed, goes to show that our present system of taxonomy is too narrowly based to form a natural classification, which would in actual fact be so complicated as to be of little use.

The work upon endemism has shown, almost beyond doubt, that in a genus with WE only, in any country—much the commonest way in which endemism is shown—the wide is the parent of the endemic, and this is confirmed by the division of the characters of the wide between the two endemics in WEE. Everything, whether in species or in genera, goes to show that any character may turn up anywhere (probably within certain limits, which as yet we do not comprehend). A character like the posterior androeceum of *Schumacheria* may be recessive for a long period, turning up again quite unexpectedly. It is possible that mere lapse of time may have some influence in the matter.

The next CEYLON endemic genus is *Julostylis* (*Malvaceae*), in the tribe *Hibisceae*, where it was probably derived directly from *Hibiscus* itself, leader of the family, which has 11 species in CEYLON, seven of them common or very common. It is distinguished from the others of the tribe by having only 10 stamens in two rows against their ∞ in many rows, again an evident mutation character. *Thespesia*, the only other member of the tribe, is a dry-country and coast plant, and *Julostylis* is common in the moist low country, where several *Hibiscus* grow. The top five *Malvaceae* by size are :

Hibiscus	160 warm	11 Ceylon.	Heads *Hibisceae*
Abutilon	120 warm	5 Ceylon.	Heads *Malveae-Abutilinae*
Malvastrum	85 Am., S. Afr.	—	Heads *Malveae-Malvinae*
Sida	75 cosmop.	6 Ceylon.	Heads *Malveae-Sidinae*
Pavonia	70 warm	3 Ceylon.	Heads *Ureneae*

and there are also in CEYLON *Wissadula* (25 trop. especially AM.), *Thespesia* (5 warm *), *Urena* (3 warm), *Dicellostyles* (2 CEYLON and SIKKIM HIMALAYA, perhaps a case of polyphyletic development of characters), and *Julostylis* (1 CEYLON, endemic). In fact the only group of *Malvaceae* not found in Ceylon, for *Hibisceae* and *Ureneae* are not divided into subtribes, is the first tribe, *Malopeae*, which is very badly constructed from a geographical point of view, its head being *Palava*, a small genus of five species in Chile and Peru, and the others *Malope* with three Mediterranean, and *Kitaibelia* with one on the lower Danube. This must be a case of polyphyletic development of the peculiar mutation character of carpels in vertical rows that marks this group.

Pityranthe, the next genus, with one species, in *Tiliaceae*, is placed in the *Brownlowieae*, whose characters, chiefly (K), and anther-thecae confluent after dehiscence, are evidently such as have been found to mark *a number of genera*. But these eight genera also show, in one or more,

petals present or absent
stamens free, or united at base
stamens all fertile, or some sterile
anther spherical or two-headed
ovary 2- to 5-locular
ovules 1, 2, or 4 or more in each loculus
panicles terminal or lateral, &c.

It has evidently just happened that this group shows two of the many characters that are possible, while to get a group that is really natural much more comparison of characters is necessary, more characters must be used, and geography, genetics, and statistics must be brought in. The mere sizes of the eight genera show that the group is probably an accidental one. They are 10, 10, 6, 4, 1, 1, 1, 1, ranging from Cuba to Polynesia.

Before leaving the Ceylon endemic genera it is worth while to note, in the family *Orchidaceae*, the variation of number of endemics, which are here plentiful, with the size of the widely dispersed genera in the family.

5 Genera	down to	200 spp.	have 21 wides,	21 endcs.	(av. per gen.	4.2)
6		100	14	19		3.2
5		50	7	10		2.0
12		25	13	9		0.75
19		10	21	11		0.58
4		5	4	1		0.25
7	below	5	7	1		0.14

and three endemic genera of one species each.

The falling off in arrivals of genera below 10 in this island is interesting.

Other interesting problems appear if we glance at the endemic genera of other countries. Let us take New Zealand, where we find *Tetrachondra*, where the first species found (in New Zealand) was placed in *Boraginaceae* (**23**), and then a second species was found in Chile. The difficulty thus opened was temporarily shelved by making it into a new family *Tetrachondraceæ*, and supposing that all the links that connected the two across the great distance that separates them have been killed out, though it is rather remarkable that just one local species should be left upon each side. But in a case like this, if we do not accept the simpler explanation of polyphyletic development, we are dealing with a thing whose previous history is practically lost. One does not seem to gain by the prevalent fashion of making new families. *Corynocarpus* in New Zealand and Norfolk I. is another case, which used to be considered as a somewhat " abnormal " *Anacardiaceae*. *Every genus is liable,* in dichotomous formation, *to need a new group for itself.*

Other interesting New Zealand endemics are *Alectryon*, *Entelia*, *Hectorella*, *Rhabdothamnus*, *Teucridium*, &c. Special interest attaches to *Myosotidium*, very isolated with its one species on the far-out Chatham Is. east of New Zealand. The only other *Boraginaceae* there is *Myosotis spatulata* Forst., but is placed in tribe *Lithospermeae*, while *Myosotidium* is placed in *Cynoglosseae*, which has no other representative either in the Chathams or in New Zealand proper, again evidently a case of polyphyletic development. Our present grouping, which necessarily depends upon divergence, or one could not make keys, but also assumes that a character can only be gradually acquired, or gradually got rid of (whether by small steps or by very small ones does not matter), is evidently an illogical and artificial one. We place a plant in a genus, or in a tribe, by our estimation of degrees of divergence.

As a rule an endemic genus is found to belong to the same tribe as one of the wides among which it is living, but this is not always so, and there is then a tendency to erect a new family. Sometimes this is done for several genera, as in the case of *Buxaceae* (*Euphorbiaceae* p. p. Bentham and Hooker), where it has already been found necessary to make three tribes :—

Buxeae	Sarcococcus	5	Ceylon, India, Sumatra
	Pachysandra	4	Alleghanies, Japan (*cf.* p. 89)
	Buxus	25	palaeotemp., W. I., the latter being sometimes placed in a separate genus
Stylocereae	Notobuxus	1	Natal
	Styloceras	3	Andes of Colombia and Bolivia
Simmondsieae	Simmondsia	1	California

One does not often meet a more impossible geographical distribution. It is clearly another case of the same mutation occurring in different places, but producing the ovule of the order *Sapindales*, not of *Geraniales*, in which *Euphorbiaceae* is placed. It is also another example of how breaking up into smaller structural groups destroys the geographical and curve continuity.

Let us now glance briefly at the endemics of the HAWAIIAN Is. which are looked upon as the chief support of the theory of relicdom. The chief thing to strike one in (62) is the absence of any Monocotyledons among them, and though a few have since been made by splitting, this has also been applied to the Dicots, whose prominence remains as great as ever.

Nearly all belong to large (old) families and genera. In (62) 8 belong to *Compositae*, 5 *Campanulaceae*, 4 *Rubiaceae*, and 3 *Araliaceae*, or 20 to this group of allied families, while the other ten families that contain endemics have only 16 among them. One of these, *Begoniaceae*, is almost entirely composed of the one great genus *Begonia*, with 800 species. The tribes to which the endemic genera belong are also usually important. In the *Compositae*, five belong to *Heliantheae*, and *Lipochaeta* (not counted as endemic) has 11 of its twelve species in the HAWAIIANS, the other in the GALAPAGOS. Counting this, the *Heliantheae* have 56 out of the 70 species of *Compositae* found. In BRITAIN they are represented only by *Bidens*, with 150 species, but the leader of the group. There are no *Cichorieae* upon these islands, nor *Cynareae*, nor *Vernonieae*. *Senecioneae* are only represented by *Senecio* itself, with one species on one island, and another doubtful as to locality, so that if the genus, as the oldest of the *Compositae*, led the way to these islands, it must have mutated fairly soon into some other group. And this looks like a possible explanation of the fact that the only member of *Heliantheae*, other than the endemics, present is a solitary species of *Verbesina* (80 spp. warm AM.) upon one island.

The *Heliantheae*, though their head, *Bidens*, is one of the smallest heads with its 150 species, form one of the largest tribes of *Compositae*, with (roughly) the following composition 76/1, 39/2, 14/3... 10/10... 3/25... 90 100 150, or 216 in all. The *Senecioneae*, on the other hand, with their gigantic leader, *Senecio*, with at least 2000 species, form quite a small group. But the distinction is largely that the pappus of *Senecio* is, and that of *Bidens* is not, hairy, a very simple character, but one only possible, in the perfection in which it is shown, by the work of mutation. It would seem quite possible that *Heliantheae* might really be a subtribe of *Senecioneae*, with *Bidens* as the leader, but a much younger group than the parent tribe, as shown by the size of the leader (3-4 species-generations younger than *Senecio*).

Let us now go on to consider some of the endemics individually.

Isodendrion (*Violaceae*) has three species, found on 5 islands, and on 2 and 1, all having OAHU in common. It is distinguished from *Viola*, the head of the family, and the only other genus of it in the islands, by its equal petals without spur or sac, and by the absence of an appendix at the end of the anther. Both are evident mutation characters. The maximum dispersal of five islands is well below that of *Viola* (all), and shows the greater youth of *Isodendrion*. *Viola* was evidently its parent, though it belongs to tribe *Violeae*, the endemic genus to *Paypayroleae*. We shall return in the next chapter to the consideration of this structural divergence, which is one of the well marked features of evolution.

The next two genera are in *Caryophyllaceae*—*Schiedea* with 17 species (on 4, 3, 3/2, 12/1 islands), and *Alsinidendron* with 1 upon OAHU, both belonging to tribe *Alsineae*, while *Silene*, the only other Caryophyll upon the islands, belongs to *Sileneae*, and has only four species (4,2, 2/1). It is thus a bit of a puzzle to trace the descent of the two endemic genera, though *Silene*, as the actual head of the family, is much the most probable. The dispersal indicates more or less equal age, while *Schiedea* has four times the number of species.

It is quite possible that the first two or three mutations of *Silene* resulted in the loss of petals—the chief distinguishing mark—and provided more potential parents for the larger number of species of *Schiedea*, and also for the other petal-less genus *Alsinidendron*, which is distinguished from *Schiedea* by the number of its staminodes, and the union of the stamens at the base. All the work that we have been doing in the last few years seems to indicate that cross-mutation such as we have just suggested plays a not unimportant part in evolution.

It should be profitable to investigate the flora of the HAWAIIAN IS. with especial reference to the individual islands, where the eastern are larger than the western. The two columns here given show the rough position of the seven most important:

West	East
N(iihau)	K(auai)
	O(ahu)
	M(o)l(okai)
L(anai)	Ma(ui)
	H(awaii)

The letters not enclosed in brackets are used as abbreviations.

The Caryophylls occur on these islands as follows, taking them always in the order K, O, Ml, Ma, H, L, N

Silene	K, Ma, H, L		Ma, H	Ml	Ma	K	K
Schiedea	K, O, Ml, Ma	O, Ml, Ma	O, Ml	K	K		
			Ma, H	O	O	O	O
			Ma, L	Ml	Ma	H	N
Alsinidendron	—	—	—	O			

Of these 34 occurrences K shows 6, O 8, Ml (a rather small island) 5, Ma 8, H 4, L 2, N 1. The greatest number of occurrences is upon the eastern and central islands, fading out to the others, and again giving a general impression of possible cross-mutation from *Silene*. I have done much work on these lines, but it will now, I fear, never be ready for publication, so these indications of the lines of it have been given.

The next family showing endemic genera, again a large (old) one, be it noted, is *Rutaceae* with *Pelea* (20 spp.), *Platydesma* (4), both endemic, and *Zanthoxylum* (6), a genus with only about 20 species in E. ASIA and N. AMERICA, united by BENTHAM and HOOKER with *Fagara*, which with its 200 species is regarded as the head of the family, and is much more likely to appear in the HAWAIIAN Is. than a small genus.

Another family which presents many points of interest is the *Rubiaceae*, of which eleven genera with 48 species (to which have probably to be added many more *Coprosmas* (cf. **111**) occur; these are (endemics in italics):

Genus	Tribe	Spp. in world	Spp. in Haw. Is.
Kadua	*Oldenlandieae*	16	16, all endc.
Gouldia	*Mussaendeae*	5	5, all endc.
Gardenia	*Gardenieae*	80	2, both endc
Plectronia	*Vanguerieae*	100	1, wide (all islands)
Bobea	*Guettardeae*	5	5, all endc.
Psychotria	*Psychotrieae*	500	2, both endc. (Kauai I)
Straussia	*Psychotrieae*	5	5, all endc.
Coprosma	*Anthospermeae*	50	9, all endc.
Nertera	*Anthospermeae*	10	1, wide (all islands)
Morinda	*Morindeae*	50	1, endc.
Richardsonia	*Spermacoceae*	10	1, endc.
			48

No fewer than nine of the 19 tribes of the *Rubiaceae* are represented in these 11 mostly rather small genera, of which four are endemic, three of them having each a tribe to itself, but a tribe, be it noted, that *occurs elsewhere.* The representation is different from what shows in northern EUROPE. The only large head of a tribe here is *Psychotria*, the leader of all the *Rubiaceae*, but represented only by two endemics upon the rather outlying island of KAUAI. There are two genera that each have one wide (only), but upon all the islands. Of these, *Morinda* (100 spp.) is the only one big enough to have so large a following, and it is not impossible that it should be the parent. But perhaps the most likely thing is that *Psychotria* mutated on arrival, and again later, giving rise to many of the other forms, while two of its descendants show its own characters, or that all the endemics are descendants of the three oldest genera, *Psychotria*, *Morinda*, and *Coprosma*, and that *Plectronia* and *Nertera*, though widely dispersed, are later arrivals. The mere presence of so many tribes, with generally one representative each, and that not always endemic, is a very difficult thing to explain upon the theory of relicdom. But this, and many other similar problems will remain simply matters for speculation for the present, until we begin to gain some knowledge of the laws of incidence and of transmission of characters, and there is plenty of work waiting to be done in the simpler problems that do not involve so much ancient history.

CHAPTER VIII

Divergent mutation in some of its manifestations

We have now seen what great changes may result from a single mutation. Rarely does it seem to change a single character only; it changes others in varying degree, so that in looking at the result, which is all that we can do as yet, it becomes very difficult, if not impossible, to say what the parent was like. We have now no longer any basis for certainty in saying that a given character in B, say a pinnate leaf, was descended from something in A, its parent, that was like it. A may have had a simple leaf, and nothing but mutation, to which such a change appears to be easy enough, will pass from one to the other. It cannot be done by gradual stages. Even with the most complete possible knowledge of the conditions, we cannot at present predict, with even an approach to probability, what will be the next mutation undergone by any single species. If, as the late Dr C. Balfour Stewart thought (*Evol.* pp. 47, 182), the mutation division is electrically controlled, we can hardly hope to find out much about it until our methods become very refined. And when we remember that even a dozen characters (or factors for them) allow of many millions of combinations, it is clear that we must first find out some of the laws that govern incidence of character.

It is not only in endemics that divergence shows itself in the ways that we have described in the last chapters. It is just as evident in any small genera, whether considered endemic or not, especially if the country be outlying. I have worked over the characters of many such genera, finding in the keys to their species ample evidence of what we may call incompatible divergences, transitions between which are impossible. If one go back into ancestry, all divergences must go back ultimately to a common ancestor. In the enormous majority of taxonomic differences, there is nothing upon which natural selection could get a grip to make a transformation even possible, so that there is nothing for it but to consider that in these cases the ancestor was carrying *both* characters, or the factors for them, with one of them in a kind of recessive condition, while the then dominant one was displayed. Such, for example, would be the case with leaves alt./opp., flowers 5-merous/4-merous, stamens 5/10, ovary apo/syn-carpous, endosperm/none, &c. There are such numbers of cases, too, where the same markedly divergent character appears in different places, and evidently independently, that one cannot put them down to selection. The explanation we have just proposed appears much more reasonable.

From the 1047 small genera that I have examined for characters, I have extracted the following examples, all rather local genera, of 2-4 species, to illustrate the way in which these mutational divergences show in all kinds of structural features. With very few exceptions, all the 1047 genera show marked mutations among their early species, just as do the genera in the families with two only, given in App. III of *Evol.*, p. 199.

Genus	Spp.	Divergent characters shown	
Sphenostemon	2	Tree	Shrub
Hyobanche	2	Parasitic on Euphorbia	Not parasitic
Verreauxia	3	Stem leafy (2 spp)	Leafless
Fresenia	2	Leaves opp., glabrous	L. alt., villous
Cyanella	3	L. flat (2)	L. terete
Dendrocousinia	3	L. petiolate (2)	L. sessile
Acidoton	2	L. spiral	L. distichous
Adolia	3	Stip. thorns recurved	Straight (2) [1]
Begoniella	3	Terminal raceme	Axillary cyme
Sarcocolla	3	Heads of fls. (2)	Solitary fls.
Boschniakia	2	Bracteoles 0	Bracteoles 2
Ceratandropsis	2	Fl. deep yellow	Dull red and white
Galopina	2	Fl. ☿	Fl. ♂ ♀

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[1] This is a common phenomenon in *Rhamnaceae*, and is probably polyphyletic. As in some cases one thorn is curved, the other straight just beside it, it must be due to mutation.

Genus	Spp.	Divergent characters shown	
Scaphocalyx	2	K splits on one side	Into four at top
Charpentiera	2	Sepals acute	Obtuse
Hemimeris	4	Corolla with spurs	With pouches
Clivia	3	Perianth curved (2)	Straight
Tetraplasandra	2	Sta. 3-4 times pets.	6-8 times pets.
Coccosperma	4	Ovary 1-loc. (2)	Ovary 2-3-loc. (2)
Homonoia	3	Ovary smooth (2)	Tubercled
Notothlaspi	2	Style very short	Long
Heterophragma	3	Caps. corkscrew-like	Straight
Tristiropsis	2	Angles of fr. blunt	Sharp
Vaillantia	2	Horn on back of fr.	No horn
Scyphanthus	2	Fruit sessile	Stalked
Zanonia	2	Few seeds, thick wing	Many seeds, thin wing
Carpacoce	2	Fruit 2-seeded	Fr. 1-seeded
Notospartium	2	Pod straight	Torulose, falcate
Pteropogon	2	Fruit ribbed	Not ribbed
Peganum	4	Capsule, 3-4-loc.	Berry, 2-loc.
Petersia	2	Receptacle glabrous	Hairy

The earliest species of genera to arrive in BRITAIN will in general be those that will later be the most widely distributed there, and being in general the earliest species in EUROPE, will be at least as widely distributed there as are any species of their genus. Being the earliest, they will also be, as we have seen, the most widely divergent structurally [1]. When a genus only contains two species in BRITAIN, therefore, these will tend to be very widely separated, as a brief inspection of the flora will show, and the same thing may be seen in CEYLON or elsewhere. This divergence is well enough known, and has been put down to the fact that there are only two, but this would not *always* separate the two unless there were some other rule behind it, which we have just pointed out—the mere age of the two species, which by making them early formations in the genus, ensures their divergence.

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[1] In fact, so markedly divergent are the characters of the widely dispersed things in BRITAIN, that the writer, and his daughter, Mrs ANDERSON (Geography School, Cambridge) are proposing a very simple flora for their easy identification.

If we look at such a genus as *Ranunculus*, one of the oldest genera in Britain, which has no fewer than six species that reach the greatest possible distribution of 112 vice-counties, we find that they can be easily separated by a very simple key, so long as it has only to deal with these six :

Flowers white; all leaves rounded; lobes broad	hederaceus
Flowers yellow	
Leaves undivided	
Petals 5 or less	Flammula
more than five	Ficaria
Leaves divided or deeply cut	
Calyx reflexed on peduncle	bulbosus
spreading, not reflexed	
No runners	acris
Runners creeping, rooting	repens

A few other species in Britain might be caught in this key, as they differ from these by " smaller " divergences; thus *R. Lingua* comes in beside *Flammula*, but has a stout beak to the carpel, instead of a point. But the six 112s can be seen in this key to be widely divergent, and nearly all of them range Eurasia, and two also North America.

The success of these large genera in Britain is in fact largely due to their age (law of age and size), which enabled them to be at the entrance of any corridor leading to Britain at an early period, and thus to miss few chances of getting there soon. Of the buttercups, *Ranunculus aquatilis* L., *Flammula* L., *repens* L., *sceleratus* L., *lingua* L., and *nemorosus* DC. (no longer British) occur in Mrs Reid's list of Cromerian plants (**106**, p. 156) of the later Pliocene, so that it is clear that *Ranunculus* was a very early genus in Britain (" to him that hath shall be given "), and evidently, even if the later British conditions killed it out there, it would not be killed out to such a distance as to be unable to return early, among the first. As giving a good idea of the vicissitudes undergone by plants in regions so near the pole, Mrs Reid's paper should be read from p. 145 onwards. Age is evidently of vastly greater importance than any adaptation. No species can survive without local adaptation to the place where it is living, but it will acquire this as it goes, without its necessarily involving any morphological change, as in fact these *Ranunculi* clearly show by being common in all parts of BRITAIN, though the conditions differ so greatly in its 112 vice-counties. They had the necessary time available to become suited to all of them.

In BRITAIN there are 130 species in all that reach the tull possible dispersal of 112. The 93 genera that contain them, in 35 families, though they do not include either *Rubus* or *Hieracium*, show an average size of 7.4 spp. in BRITAIN, against one of 4.1 for the whole flora (including the 112s). It is clear that it is simply the largest or oldest genera that have gone the furthest. The 112s average in the world 162 spp. each in Dicots, 103 in Monocots, and there are a number of local differences between families and genera that would probably repay study in other connections. Sixteen of the 22 Monocots are grasses, and they only average 46 in size, suggesting that they may have been rather late arrivals that found conditions much to their liking. On the other hand, they are all but absent in the Cromerian list. This may be thought to indicate comparative youth, thus agreeing with the statement just made, but the list shows so many marsh and water plants (all its Monocots, for example) that it is probably a rather one-sided representation of a pliocene flora.

In fact the distribution of plants in BRITAIN goes closely with their distribution in the world, when each allied group is taken separately. We have shown (law of size and space) that world distribution goes mainly with size of genus, and one soon finds that distribution in BRITAIN does the same. The genera that reach 111 or 112 vice-counties in BRITAIN have an average world size of 149; those reaching 61-70, although helped by the presence of the two gigantic genera *Astragalus* (1600) and *Salvia* (550), reach only 140, and the genera reaching 1-5 reach only 27 in world size.

We have seen in the testcases in *Evol.* that the evidence is almost overwhelming that shows that evolution went in the direction family-genus-species, not, as Darwinism would have it, in the reverse way. On the whole, with the passage of time, the mutations that mark it have decreased in what we may call emphasis. The further back that one goes, the "larger" do the mutations appear to be, but it would seem more likely that this means that they affect more characters, than that they make larger differences in single characters. But if this rule runs right back through evolution, we have at last a clue to the meaning of the great differences that we see between such classes as the algae and the mosses, or the ferns and the conifers, and we shall no longer search for *transitions* between them, or for missing links, though there *may* have been organisms between that had mixtures of characters, some from one side, some from the other.

In this connection, the following letter from my friend the late Prof. D. H. SCOTT, F. R. S., which at the time he authorised me to publish, is of interest. I asked him what he thought about HOOKER's statement of 1859 that " there are no known fossil plants... intermediate in affinity between recent classes or families ", and his reply was " this statement is more open to discussion. The *Psilophytales* have already been placed by different botanists in the *Pteridophyta*, the *Bryophyta*, and the *Thallophyta*, so I suppose we must admit that they show some intermediate characters. I used to regard the *Pteridosperms* as intermediate between ferns and true *Gymnosperms*, but now think they were an independent line, parallel to cryptogamic ferns. But the fact remains that they are vastly more like cryptogams than any seed-plants previously known.

" The *Cordaitales* combine certain characters of *Conifers* and *Cycads*, but are not intermediate in the sense of being transitional. I think that their features point to a common origin, but this has been disputed recently.

" Neither *Sphenophylls* nor *Bennettiteae* can be called intermediate between recent groups. There is thus some force still in this particular remark of HOOKER's—we find new branches more often than common stocks. "

This agrees well enough with what we have already said, and shall further say, about the handing down of characters, that the potentialities of all characters exist in the heads of families, and even further back, and that under certain circumstances that as yet we do not in the least understand, these characters may appear—apparently anywhere. Their appearance is manifested by a divergent mutation, which, as one comes down from classes to species, becomes smaller, apparently by affecting fewer characters at once.

All our work goes to show that there is no serious difference in rate of spread, in large space and in long time, between genera that are allied to one another like the members of a smallish group of any one family—all will have much the same reaction to outside influences. The survival of the parent as well as the offspring results in the formation of the familiar hollow curve for any family of reasonable size, though the taxonomic (structural) divisions of the family rarely show anything of the kind, unless very large. The new form produced anywhere will of necessity be suited to its environment enough to survive and reproduce, or it will at once be killed out. But whether it anywhere goes in front of its parent in the distribution will depend upon local circumstances, and it rarely happens over any large front.

The difference between parent and child, as we have just seen, may be of any kind, and sometimes that between two species of the same genus is so marked—as in *Rhamnus*—that we call it sub-generic. In *Rhamnus* this divergence seems constantly to appear, in any region where the genus is found, and the difference in the stipular thorns, mentioned under *Adolia* in the list above, is common all through the family. But the separation into two sub-genera is undergone, not only by the two closely allied species in CEYLON (p. 107), but also by two in MADRAS, and in other places. Thus, at the very start, two species, as closely allied as is possible (parent and child) are artificially divorced from one another, and placed in separate groups (sub-genera) in our classifications. Suppose now that these same two distinctive characters were shown, not by the two halves of a genus, but by the two halves of a family, there can be no doubt that they would be used as sub-family characters. We have had no standard by which to go to judge why any given character should sometimes mark one kind of distinction, and sometimes another. It is now clear that what really matters is the *age* of the character, for if old, it will usually be shown by more descendants than if young, and thus may be useful in one place for a species only, in another for a genus, a tribe, or even a whole family. High value in one family gives no indication whatever that the same thing will be of high value in another.

The genus that by a larger mutation than usual, probably one affecting more characters, begins a family or genus, will of necessity be carrying with it a great variety of characters [1].

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[1] When a statement like this is made, it should be understood in general that the word characters should not be taken literally;

These apparently include all possibilities of divergence that are open to any one character, like stamens in one or more whorls, di- or tetradynamous, only 2 or 3, &c, or leaves simple or compound, alternate or opposite, &c. At each fresh mutation, a species will change some of its characters, but not all, or even most; but according to how many are changed, and how "important" we consider them, the result will be a new variety, species, genus, &c. The monograph of any large genus will show what a great variety a single genus may exhibit, and we do not know that it will not exhibit still more at the next mutation. A small genus, by reason of its small numbers (youth), cannot show such a thing.

The earlier mutations in any line seem as if on the whole they were larger than later[1] ones, though it is difficult to be sure what we really mean, with our present ignorance of the incidence of characters. But it is not unlikely that a recently acquired character may show some difference in constancy of inheritance according to how recently it was acquired.

Unless, therefore, the divergences between two genera in a very small family are very conspicuous, we do not divide the family into two subgroups, for there is no special need for such a complication; we simply employ the divergence as two lines in the key. But in a large family it is a very great convenience, and often a necessity, first of all to break it up into large groups by characters that show throughout these groups, and are therefore of great age, and persistent in the heredity. They are of course due to the early mutations of the oldest genera in the family, which are now the leaders of the sub-groups. These first sub-groups are then broken into smaller ones, if necessary, by characters that were more

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it is more probable that, as we have already said, what is really carried are certain factors, or potentialities, which when put together in a certain way, produce a certain result. The one word characters is used to save this great circumlocution.

[1] Here again the expression "larger" is not necessarily to be interpreted literally. We cannot say whether a mutation that changes a 4-merous to a 5-merous flower is larger or smaller than one that changes a simple to a compound leaf, and so on. It is perhaps more probable that a "larger" mutation is more commonly one that changes more characters, rather than one that changes characters more.

recently acquired in the inheritance, and that mark smaller groups, and so on, till again we come down to the two lines in the key that mark some divergence, that however " important " it may be in itself, has only recently appeared, and only separates one genus from one or a few others.

It therefore follows that one may predict that as the large structural differences, marking large divisions, are inherited from far back, and the smaller, or rather the less common, from more recent ancestors, most of the oldest and largest genera will show characters that divide the family into its principal tribes or other divisions that may be used. As these divisions are shown by the earliest genera, which on the whole will be the earliest arrivals anywhere, the flora of any one country will tend to show great divergences among its members, as we have just seen for early species in BRITAIN. If we look at the British *Leguminosae*, for example, we find the 17 genera divided among the tribes *Genisteae*, *Trifolieae*, *Loteae*, *Galegeae*, *Hedysareae*, and *Vicieae*, or six out of the ten tribes of the *Papilionatae*, while four of these show 3, 2, 1, and 1 species with a distribution of 112, the other two of 86 and 68, or all well above the average. It is quite impossible to explain such phenomena in terms of selection.

Or if we take the British *Umbelliferae*, we find there representatives of *Hydrocotyleae*, *Saniculeae*, *Scandicieae*, *Smyrnieae*, *Ammineae*, *Peucedaneae*, and *Dauceae*, or seven tribes out of a possible twelve, the missing ones being small (young) and rather local, though all but *Mulineae* (mainly American) occur further south in EUROPE. JANCHEN (73) gives tribes in 40 families of the European flora, and in these 40 EUROPE contains no fewer than 192 tribes. This is a world wide phenomenon, which can not be accounted for by selection, or by the " upward " course from species to family that we have hitherto postulated for evolution.

Following out the prediction just given, we shall now give, in order of size, the 61 families with more than fifty genera. As more division is needed, and used, in large families than in small, we have taken the first six genera by size in families down to 250, six for each family, three to 100, and two below (list of genera, in App. I). The great crowd of families comes below 50, but even at the very bottom, the list of families of two genera each, given as App. III in *Evol.*, p. 199, shows that divergence is just as well marked in them. We have used the tribe here, as the best marked of the divisions; when tribe and sub-family are the same, we have used the termination *-oideae.*

Families in order of size, down to 50 genera, with the tribes to which their leading genera belong in order of size

1.	Comp.	1179	Senecioneae	Cichorieae	Cynareae
			Vernonieae	Astereae	Eupatorieae
2.	Orch.	726	Dendrobieae	Pleurothallid.	Bolbophylleae
			Epidendreae	Ophrydeae	Vandeae
3.	Legum.	675	Galegeae	Acacieae	Cassieae
			Mimoseae	Genisteae	*Galegeae*
4.	Gramin.	548	Paniceae	Andropog.	*Paniceae*
			Festuceae	*Festuceae*	*Festuceae*
5.	Rubi.	496	Psychotrieae	Galieae	Oldenlandieae
			Ixoreae	*Psychotrieae*	Gardenieae
6.	Ascl.	352	Asclepiadeae	*Asclepiadeae*	Tylophoreae
			Tylophoreae	Gonolobeae	*Tylophoreae*
7.	Crucif.	344	Drabeae	Arabideae	Lepideae
			Arabideae	Alysseae	Heliophileae
8.	Umbel.	334	Saniculeae	Ammineae	Peucedaneae
			Hydrocotyleae	*Hydrocotyleae*	*Ammineae*
9.	Acan.	273	Justicieae	Ruellieae	Strobilantheae
			Barlerieae	Thunberg.	Odontonemeae
10.	Lili.	269	Asparagoideae	Smilacoideae	Allioideae
			Asphodeloideae	Scilloideae	*Asphodeloideae*
11.	Scroph.	259	Rhinantheae	Verbasceae	Digitaleae
			Calceolarieae	Cheloneae	*Rhinantheae*
12.	Euph.	251	Euphorbieae	Crotoneae	Phyllantheae
			Acalypheae	*Acalypheae*	*Phyllantheae*
13.	Palm.	219	Metroxyleae	Cocoeae	Areceae
14.	Apocyn.	202	Plumiereae	*Plumiereae*	*Plumiereae* [1]
15.	Labiat.	200	Salvieae	Ocimeae	Stachyeae
16.	Melast.	193	Tamoneae	*Tamoneae*	Tibouchineae
17.	Sapind.	160	Paullinieae	Thouineae	*Paullinieae*
18.	Rut.	153	Xanthoxyleae	Diosmeae	*Xanthoxyleae*
19.	Ros.	142	Potentilleae	*Potentill.* [1]	Prunoideae
20.	Gesner.	129	Cyrtandreae	Didymocarpeae	Aeschynantheae
21.	Eric.	122	Rhododendreae	Ericeae	Vaccinieae
22.	Bignon.	121	Tecomeae	Bignonieae	*Bignonieae*
23.	Borrag.	119	Cordioideae	Heliotropioid.	*Heliotropioid.*
24.	Annon.	114	Uvarieae	Xylopieae	*Uvarieae*
25.	Cyper.	111	Cariceae	Cypereae	Scirpeae

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[1] Different sub-tribes here.

26. Arac.	108	Anthurieae	Philodendreae	Areae
27. Flacourt.	104	Homalieae	Casearieae	Flacourtieae
28. Chenop.	102	Atriplicieae	Salsoleae	Chenopodieae
29. Solan.	99	Solaneae	Cestreae	
30. Verben.	93	Verbeneae	Viticeae	
31. Myrt.	92	Myrteae	*Myrteae* [1]	
32. Menisp.	91	Cocculeae	Tinosporeae	
33. Sapot.	90	Mimusopeae	Palaquieae	
34. Anacard.	89	Rhoideae	Semecarpeae	
35. Malvac.	87	Hibisceae	Malveae	
36. Gentian.	86	Gentianeae	*Gentianeae*	
37. Aral.	83	Scheffllereae	*Scheffllereae*	
38. Amaryll.	81	Agavoideae	Amaryllideae	
39. Saxifrag.	80	Saxifrageae	Ribesioideae	
40. Caryoph.	79	Lychnideae	Diantheae	
41. Morac.	78	Ficeae	Dorstenieae	
42. Campan.	78	Campanuleae	Lobelioideae	
43. Malpigh.	73	Malpighieae	Banisterieae	
44. Cucurb.	70	Melothrieae	*Melothrieae* [1]	
45. Stercul.	70	Hermannieae	Sterculieae	
46. Icac.	68	Icacineae	*Icacineae*	
47. Meliac.	67	Trichileae	*Trichileae* [1]	
48. Bromel.	66	Tillandsieae	Pitcairneae	
49. Irid.	66	Ixieae	Moraeeae	
50. Amarant.	64	Gomphrenoideae	Amarantheae	
51. Celast.	64	Evonymeae	Eu-celastreae	
52. Zingib.	63	Zingibereae	Costoideae	
53. Laur.	60	Cinnamomeae	Litseeae	
54. Rhamn.	60	Rhamneae	*Rhamneae*	
55. Ranunc.	59	Anemon.	Helleb. [2]	
56. Prot.	57	Grevilleae	*Grevilleae*	
57. Guttif.	55	Hypericeae	Garcinieae	
58. Tili.	55	Grewieae	*Grewieae*	
59. Convolv.	53	Ipomoeaeae	Convolvuleae	
60. Onagr.	52	Epilobeae	Fuchsiaeae	
61. Urtic.	51	Procrideae	*Procrideae*	

Names of sub-groups given in italics are cases where the same sub-group appears twice. There are 34 of them, out of 186 (18%).

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[1] Different sub-tribes here.

[2] There is some doubt as to whether *Clematis* or *Delphinium* is really the larger, and as the latter belongs to another tribe than *Ranunculus*, and is therefore the more probable, we have used it here.

A list of the actual genera is given as appendix I, and there are many partial lists (*cf.* Index, under Leaders).

This result strikingly bears out our prediction. No less than 152 out of 186 genera, or 81%, have each its own tribe. Thus, even when a family contains only a few genera, most of its tribes will already be marked out, though at that early stage they would probably not have been recognised as such. This seems an almost conclusive proof of the truth of our theory that evolution worked " downwards " from family, not upwards from species. However divergent the earliest genera may be, they will be closely related, often as parent and child; this is discussed at more length in *Evol.*, test-case XX, p. 134. We can see little to contradict our supposition that any character may be changed at any mutation, so that as a family grows larger, the newer genera will tend to fall away from the standard type of the big genus that is giving its characters to the sub-group. If an " important " character is lost at some divergent mutation, there will follow disputes about the position of the new genus thus formed, and if the divergence is very marked, the tendency at the present time will be to give it a separate family. But until we know what the actual parent was, and what the next mutation is likely to be, it would seem safer to follow the more cautious methods of BENTHAM and HOOKER.

This close relationship of the early and divergent genera of a family makes it clear that our present system of classification is based upon characters that do not necessarily go with, or mean, close relationship; the system, therefore, has much in common with the artificial system of LINNAEUS, and great changes will have to be made before we can call it natural or genetic. A genetic system would probably be too complex for ordinary work, and it will be better to adhere to a more or less artificial system for that.

Let us now go on to study a single large family in the British flora in the light of what has been said. As judged simply by number and frequency of genera and species, *Compositae* seem to centre north of the equator, and they are well represented in BRITAIN by 42 genera out of a flora of 475. As early genera in a family tend to be very divergent, we shall also expect many sub-groups in BRITAIN, and actually there are eight out of the 13 in the family. Their presence has nothing to do with selection, but is simply an effect of the early divergence. Let us begin by taking the first twenty genera by world size :

Genera of Compositae in order of size, divided into British and non-British (set in) with the tribes headed by them

World size		Tribe	Brit.	Spp.	Max. Disp.	Ceylon
1. Senecio	2000	Heading *Senecioneae*	Br.	10	112	C.
2. Hieracium	800	Heading *Cichorieae*	Br.	10[1]	111	
3. Centaurea	650	Heading *Cynareae*	Br.	12	112	
4. Vernonia	650	Heading *Vernonieae*	—	—	—	C.
5. Aster	500	Heading *Astereae*	Br.	2	70	
6. Eupatorium	450	Heading *Eupatorieae*	Br.	1	99	
7. Helichrysum	350	Heading *Inuleae*	—	—	—	C.
8. Baccharis	300	2nd Astereae	—	—	—	
9. Artemisia	280	Heading *Anthemideae*	Br.	4	111	
10. Cousinia	250	2nd Cynareae	—	—	—	
11. Crepis	240	2nd Cichorieae	Br.	6	112	C.
12. Cirsium	225	3rd Cynareae	Br.	8	112	
13. Chrysanthemum	180	2nd Anthemid.	Br.	2	112	
14. Erigeron	180	3rd Astereae	Br.	2	70	C.
15. Mikania	175	2nd Eupatorieae	—	—	—	
16. Bidens	150	Heading *Heliantheae*	Br.	2	87	
17. Gnaphalium	150	2nd Inuleae	Br.	5	112	
18. Saussurea	150	4th Cynareae	Br.	1	27	
19. Achillea	125	3rd Anthemideae	Br.	2	112	
20. Anthemis	125	4th Anthemideae	Br.	3	77	

The other four tribes of *Compositae* are too young in their leaders to come into this table. They are *Arctotideae,* leader *Berkheya*, with 80 species; *Mutisieae, Perezia,* 75; *Helenieae, Pectis,* 60; and *Calenduleae, Osteospermum,* 40. They are all comparatively small and local groups.

Thus no fewer than 15 out of the first twenty *Compositae* by size in the world occur in BRITAIN, and the largest have the most species. In all they have 70 out of the 126 British species in all 42 genera, leaving only 56 for the other 27 smaller genera. While the leader of all, *Senecio*, has 2000 species, the number of species in the whole 27 smaller genera is only 993, or not quite half. One might perhaps expect that *Senecioneae*, with so gigantic a head, would be the largest tribe of all, but one must remember that as the table just given shows, most of the earlier descendants of *Senecio pass automatically into other tribes*, so that the group is but small, except for the head. This, by the way, is a very general phenomenon with the tribe that depends upon the head of a

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[1] Nominal.

family, though it is not quite universal. The first sixteen members of the tribe are given :

Tribe Senecioneae of Compositae, in order of size in the world

		World size	Subtribe	Brit.	Spp.	Max.	Disp. Ceyl.
1.	Senecio	2000	Heading *Senecioninae*	Br.	10	112	C.
2.	Othonna	80	Heading *Othonninae*				
3.	Liabum	60	Heading *Liabinae*				
4.	Arnica	50	2nd Senecioninae				
5.	Cacalia	40	3rd Senecioninae				
6.	Gynura	40	4th Senecioninae				C.
7.	Cineraria	35	5th Senecioninae				
8.	Euryops	35	2nd Othonninae				
9.	Ligularia	35	6th Senecioninae				
10.	Werneria	35	3rd Othonninae				
11.	Doronicum	30	7th Senecioninae				
12.	Gynoxys	25	8th Senecioninae				
13.	Cremanthodium	20	9th Senecioninae				
14.	Culcitium	20	10th Senecioninae				
15.	Erechtites	15	11th Senecioninae				
16.	Petasites	15	12th Senecioninae	Br.	1	110	
	and 2/12, 10, 4/8, 7, 6, 2/5, 2/4, 6/3, 8/2, 26/1, one of these British						
	Tussilago	1	Senecioninae	Br.	1	112	

Duplicates begin at 40.
CEYLON occurrences are put in, to be referred to later.

This table is of interest, both taxonomically and geographically. The three topmost members all head subtribes, and as all three must be closely related, the subtribes are artificial to the same degree as the tribes. The great gap below *Senecio* is probably to be explained by the fact, shown in the first table, that its early mutations all gave rise to members of other tribes, or even possibly of satellite families.

The next tribe, the *Cichorieae*, gives a very different result. This tribe, with its leading genera, is very well represented in BRITAIN, its large head, *Hieracium*, and most of its other genera, being characteristic of cool temperate regions. There are five subtribes, but of these one has only a genus of three Mediterranean species, and another only two genera, one of seven in JUAN FERNANDEZ, and one of one in TAHITI, so is an evidently polyphyletic group, with no parent in its own set.

Tribe Cichorieae of Compositae, in order of size in the world

		World size	Subtribe	Brit.	Spp.	Max.	Disp. Ceyl.
1. Hieracium		800	Heading *Crepidinae*	Br.	10[1]	111	
2. Crepis		240	2nd Crepidinae	Br.	6	112	C.
3. Lactuca		100	3rd Crepidinae	Br.	5	76	C.
4. Scorzonera		100	Heading *Leontodontin.*	Br.	1	1	
5. Hypochoeris		60	2nd Leontodontin.	Br.	3	112	
6. Sonchus		50	4th Crepidinae	Br.	4	112	
7. Leontodon		45	3rd Leontodontin.	Br.	3	112	
8. Picris		40	4th Leontodontin.	Br.	2	66	
9. Microseris		40	Heading *Cichorinae*				
10. Tragopogon	+ 1	35	5th Leontodontin.	Br.	2	94	C[2]
11. Taraxacum	+ 1	30	5th Crepidinae	Br.	4	112	
12. Mulgedium	+ 1	25	6th Crepidinae	Br.[3]	1	2	
13. Two at 20				none Br.			
14. Four at 15				none Br.			
15. Lapsana	+ 2	10	2nd Cichorinae	Br.	1	112	
16. Cichorium	+ 1	8	3rd Cichorinae	Br.	1	68	
and 1/7, 3/6, 4/5, 1/4, 9/3, 12/2, and 27/1, one British							
Arnoseris		1	Cichorinae	Br.	1	24	

The first duplicate of any of these numbers, *Microseris* (AM., &c) appears at 40, and the numbers gradually increase, rapidly at the last, as the figures show.

Thus all *Cichorieae*, from *Hieracium* at 800 down to *Picris* at 40, are British, and down to this point there are no duplicates of numbers, though *Microseris* (AM., AUSTR., &c) appears there, and *Launaea* (warm countries) appears at 35. The numbers of duplicates rapidly increase from here downwards, ending with a great display of "ones". We may obviously predict that if growth goes on in the dichotomous way we have postulated, there will be no duplicates, unless perhaps by accident, at the top of the table, but they will begin lower down, when the first dichotomy or two have given rise to new branches of descent, in which two births may take place about the same time. These duplicates will tend to be well separated both taxonomically and (because by that time the family will be spreading in many directions) geographically. Taking in the *Compositae* the genera of 30 species, of which there are 18, we find them to be scattered all over the world, and to belong to ten of the thirteen tribes;

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[1] Ten is taken as a nominal number of species.

[2] *Launaea* at 35 (1 sp., coast plant) is the only other genus of the tribe in CEYLON.

[3] *Mulgedium* often taken as *Lactuca*, p. p.

and in smaller genera these features become even better marked. One will therefore expect representation in a country to go largely with the mere size of the genera, as the figures for CEYLON given in many papers well show, and the general absence of small genera in BRITAIN confirms, as we have just seen in *Cichorieae*.

Such figures as these, added to the many we have already given, make the supposition that distribution in large areas and long time depends upon adaptation seem inapplicable. Adaptation has a great deal to say about details of distribution upon small areas and for short times, but the conditions that require different degrees of adaptation vary from place to place, and from time to time, so that in large areas and in long time they can only produce very slight and general effects.

The dispersal of the *Cichorieae* in BRITAIN shows that the group was evidently born (as its leader, *Hieracium*, shows) in northern palaeotemperate conditions not very different from those of BRITAIN, to which its members could easily suit themselves, much in the order of their size or age, while but few of the very small members of the group—only *Lapsana*, *Cichorium*, and *Arnoseris*—were born sufficiently near to BRITAIN to reach it before it was too late.

Let us now go on to look at some of the other groups, and take the third, the *Cynareae*. Not only is the group younger (smaller leader), but its leader is a markedly Mediterranean genus, flourishing in rather warmer conditions than in BRITAIN.

Cynareae in order of size, showing sub-groups, and British representation

	World size	Subtribe	Br. Spp.	Max. Dispersal
1. Centaurea	650	Heading *Centaureinae*	Br. 12	112
2. Cousinia	250	Heading *Carduininae*	E. Medit., C. As.	
3. Cirsium	225	2nd Carduininae	Br. 8	112
4. Saussurea	150	3rd Carduininae	Br. 1	27
5. Echinops	80	Heading *Echinopsidin.*	S. Eur., As., Afr.	
6. Jurinea	60	4th Carduininae	Medit.	
7. Serratula	40	2nd Centaureinae	Br. 1	64
8. Carduus	35	5th Carduininae	Br. 3	89
9. Carthamus	25	3rd Centaureinae	Medit. Afr. As.	
10. Onopordon	25	6th Carduininae	Br. 1	61
11. Carlina	20	Heading *Carlininae*	Br. 1	85
and Arctium	4	Carduininae	Br. 4	92

Duplicates begin at 25. No *Cynareae* in CEYLON.

Again the British genera are at the top of the list; those near the very top have the most species, and the species have the widest dispersal. All four sub-tribes have their leaders in these first eleven genera, and all but *Echinopsidinae* occur in BRITAIN. The leader of this group, *Echinops*, has two species in FRANCE, and its one follower is very small. The non-British genera tend to be Mediterranean, like *Centaurea* itself.

The American genera, apart from a few (large genera) *Centaureas*, *Cirsiums*, and *Saussureas*, are of interest. They are *Rhacoma* (12 W. I. and trop. S. AM.) which is large for its somewhat detached position, and *Centaurodendron* (1 JUAN FERNANDEZ) perhaps too small and too isolated to have sprung from any other member of the group. These genera are possibly due to parallel mutations which gave to them the characters of *Cynareae*.

Vernonieae, the tribe beginning with the fourth genus, which is tropical, has no British representative, but *Vernonia* itself, with 12 species there, many common, and nine of them endemic, is the commonest native *Composite* in CEYLON. Its tribe is rather small, and it is only accompanied by the common tropical weed *Elephantopus*.

The next group, *Astereae*, has genera that are not so well separated as some. The leader being smaller (younger) and mainly American in dispersal, cannot be expected to be so well dispersed in BRITAIN, nor to have many followers there. The group actually shows :

Tribe Astereae in order of size in the world

	World size	Subtribe		Br.	Spp.	Max.	Disp. Ceyl.
1. Aster	500	Heading	*Asterinae*	Br.	2	70	
2. Baccharis	380	Heading	*Baccharidin.*				
3. Erigeron	180	2nd	Asterinae	Br.	2	70	C.
4. Aplopappus	125	Heading	*Solidaginin.*				
5. Olearia	100	3rd	Asterinae				
6. Solidago	100	2nd	Solidagin.	Br.	1	111	
7. Brachycome	60	Heading	*Bellidin.*				
8. Conyza	60	Heading	*Conyzin.*				C.
9. Felicia	60	4th	Asterinae				
10. Pteronia	60	3rd	Solidaginin.				
and 3/50, 45, 40, 2/35, 2/30, 7/20, 5/15, including							
Bellis	15		Bellidin.	Br.	1	112	
and 3/12, 9/10, 3/8, 4/7, 10/6, 9/5, and so on							

Duplicates begin at 60; 100 is a " lumping " figure. The other subtribe, *Grangeinae*, is a scattered group of six very small genera; *Grangea* itself occurs in CEYLON.

The next group, *Eupatorieae*, and another, the *Heliantheae*, are both chiefly American, and are represented in each case only by one or two species of the leader, *Eupatorium* or *Bidens* (*cf.* **106** p. 157, where the interesting fact may be noted that both occur in the Cromerian plants).

The *Inuleae*, more an old world tribe, shows :

Tribe Inuleae in order of size in the world

	World size		Subtribe	Br.	Spp.	Max. Disp.	Ceyl.
1. Helichrysum	375	Heading	*Plucheinae*				
2. Gnaphalium	150	Heading	*Gnaphalinae*	Br.	5	112	C.
3. Inula	100	Heading	*Inulinae*	Br.	2	59	
4. Antennaria	85	2nd	Gnaphalinae	Br.	1	89	
5. Blumea	80	2nd	Plucheinae				C.
6. Anaphalis	50	3rd	Gnaph.				C.
7. Helipterum	50	4th	Gnaph.				

and also in Britain *Pulicaria* (30 spp. 2nd *Inul.*) and *Filago* (12 spp. 2nd *Filaginin.*, the first being *Evax*, 15).

Other subtribes are *Tarchonanthinae*, *Angianthinae*, *Relhaninae*, *Athrixinae*, *Buphthalminae*, all with small leaders.

Finally there comes the tribe *Anthemideae :*

Anthemideae in order of size, showing British genera &c.

	World size		Subtribe	Brit.	Spp.	Max. Dispers.
1. Artemisia	280	Heading	*Anthemidinae*	Br.	4	111
2. Chrysanthemum	180	Heading	*Chrysanthem.*	Br.	2	112
3. Achillea	125	2nd	Anthemidinae	Br.	2	112
4. Anthemis	125	3rd	Anthemidinae	Br.	3	77
5. Matricaria	50[1]	2nd	Chrysanthem.	Br.	2	111
6. Tanacetum	30[2]	3rd	Chrysanthem.	Br.	1	108
and Diotis	1[2]		Anthemidinae	Br.	1	10

There are only the two subtribes here.

Divergence within the genus. Just as the early genera of a family diverge from one another so much that they form the heads of most of the tribes and subtribes at a very early time in the history of the family, so also, within any one genus the bulk of the species that are first formed, and that will therefore, upon our contention, be the most widely

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[1] Duplicates at 125,50 (lumping) at 30,1 coast plants.

distributed of all, diverge so much from one another, structurally, that they tend to occupy different taxonomic sections of the genera. If, for example, we take the three species of *Galium* (*verum*, *palustre*, and *Aparine*) that have the maximum dispersal of 112 in Britain, and that outside of Britain (*cf. Ranunculus* on p. 13) cover the whole of temperate Eurasia, we find them to belong to the sections *Eu-galium*, *Trachygalium*, and *Aparine*, while the one species that reaches 111 (*cf. LC*) and at least covers Europe, *G. saxatile*, belongs to *Leptogalium*, and the next, *G. Cruciata* at 98, to the section *Cruciata*. Thus the five most important sections of *Galium* are represented by the five most widely dispersed species in Britain and only at 94 does *Trachygalium* find its second representative in *G. uliginosum*.

Similar phenomena are very common. If in every British genus of Monocots where the sub-divisions are given in NP/1, and the specific names are mentioned (which is not always the case), we take the two leading species, we find them in 13 out of 17 cases in separate sections, a proportion not unlike that of the genera that belonged to separate tribes.

One may even carry this line of investigation down to the subspecies, and find the same phenomena showing themselves. Let us look at the British *Hieracia* (*LC*). If we take the 15 that have the largest dispersal in Britain, we find them to be :

Subspecies	Dispersal	Subgenus	Group
H. vulgare	111	2, Pilosella	§ 10. Pilosellina
umbellatum	48	1, Euhieracium	§ 8. Umbellata
Schmidtii	39	1, Euhieracium	2. Oreadea
Lachenalii	33	1, Euhieracium	3. Vulgata, § a
anglicum	28	1, Euhieracium	1. Cerinthoidea
stictophyllum	23	1, Euhieracium	7. Tridentata
argenteum	23	1, Euhieracium	2nd Oread.
maculatum	22	1, Euhieracium	3. Vulgata § b
scanicum	22	1, Euhieracium	2nd Vulg. a
caesium	21	1, Euhieracium	2nd Vulg. b
obliquum	20	1, Euhieracium	9. Sabauda
prenanthoides	18	1, Euhieracium	6. Prenanthoidea
crocatum	18	1, Euhieracium	2nd Umbell.
rubicundiforme	18	1, Euhieracium	2nd Cerinth.
gothicum	17	1, Euhieracium	2nd Trident.

Thus all the groups but 4, 5, and 11 are represented in this list of the most widely dispersed *Hieracia* in Britain. Group 4 has a leader at 16,5 has only two species, very doubtfully native, and 11 (belonging to the second subgenus, *Pilosella*) has only one species of dispersal 6.

Similar phenomena occur in *Rubus*, but were evidently older, as the dispersal is much greater, averaging 78.6 for the first fifteen, while the *Hieracia* only averaged 30.7, though *Rubus* looks as if it would perhaps be slower in distribution.

Species	Dispersal	Section	Sub-section	Group
R. idaeus	111	Frutescentes	Idaei	No groups
Selmeri	86		Fruticosi	4. Villicaules
polyanthemus	84		Fruticosi	3. Rhamnifolii
caesius	82		Fruticosi	14. Caesii
Lindleianus	81		Fruticosi	2nd Rhamn.
plicatus	80		Fruticosi	1. Sub-erecti
dasyphyllus	79		Fruticosi	12. Koehleriani
radula	78		Fruticosi	9. Radulae
rusticanus	76		Fruticosi	5. Discolores
rhamnifolius	76		Fruticosi	3rd Rhamn.
leucostachys	71		Fruticosi	7. Vestiti
mucronatus	70		Fruticosi	8. Egregii
saxatilis	70	Herbacei	no subsect.	no groups
pyramidalis	70	Frutescentes	Fruticosi	2nd Vest.
corylifolius	65 (v. 69)		Fruticosi	2nd Caes.

Thus of the 16 groups or divisions in the *L. C.*, there are eleven represented in these first fifteen most widely dispersed species (or rather sub species). The phenomena, both here and in *Hieracium*, exactly reproduce what we have seen throughout. The missing five groups have leaders in Britain of 61 (group 6), 38 (11), 31 (10), 26 (2), and 24 (13).

If, as we have suggested, *Rubus* is older in Britain than is *Hieracium* (both have 111 as their maximum dispersal), then we should perhaps find confirmation in the fossil record. Looking at the five lists of Pliocene plants given by Mrs Reid in (**106**) we find no *Hieracia* recorded at all, while in all the later four there are species of *Rubus*, including *R. idaeus* in the Cromerian.

If one were to take the trouble to measure the areas of dispersal of all the many *Hieracia* and *Rubi*, one would probably find that most of the species mentioned above as leaders in Britain had also the largest areas of any in their particular groups. The point of special interest is that these species are divided from their " equals " by the largest divergences *available at that stage.* It is another proof that the great characteristic of evolution is divergence.

Hieracium and *Rubus* do not seem to be in process of producing new species and genera based upon the very small subspecies at present so numerous, but rather seem to be continually producing more and more new subspecies, and especially so *Hieracium*, the younger, apparently, of the two. Forty-one of its subspecies show 1 vice-county as a dispersal, while in *Rubus* the ones are in what are regarded as varieties of the subspecies. New genera, if produced, will appear by sudden mutation, taking the whole step, probably, in a single operation. We must get into the way of recognising that evolution is working " downwards ", not upwards as we used to think, and is continually forming more and more new things, of lower rank on the whole, as compared with their immediate ancestors, than the things that were formed further back in descent. The difference probably lies in the greater number of characters that were liable to simultaneous change in older forms, and the shrinkage will presumably go on till all have come down to Jordanian species. Some supposition like this will provide the simplest explanation for the great divergences that are shown among the groups of plants that in general preceded the flowering plants, like algae or ferns.

We may now go more into the realm of distribution. In the composition of the associations of plants that make up the flora of any given region, the chief factor operative is necessarily the local adaptation of the plants. Suppose a country composed only of moor and fen, then it two plants, one of moor, one of fen, arrive at the frontier, each will find its way gradually into its appropriate place, as it gradually acquires more and more local adaptation. But a plant of the forest will simply be stopped at the frontier, unless it can slowly adapt itself there, or form a new species (under the stress of the local conditions) that is adapted to living in one of the two types of habitat that are available.

But in actual fact most countries contain a great variety of habitats, but in different proportions; one may contain much forest, one much fen, and so on. But in BRITAIN, for example, given a little time to make the local adaptation, there is probably some place where most plants found in

FRANCE, other than such as the high alpines, could succeed. The fact that so great a number of French plants are not found in BRITAIN is attributable, not to the climate or the soil but merely to the fact that there has not been the time available for the necessary local adaptation, which has to take place step by step. A few have reached sufficiently far north to reach BRITAIN, had the CHANNEL not been formed, but the great bulk of the French plants that do not occur in BRITAIN will be found further to the south in FRANCE. It is in general simply a question of age; all the plants are obeying the law of age and area, one of the laws of ASA. We have seen in *Cruciferae* (p. 51) the striking way in which the genera of French crucifers that reach BRITAIN surpass those that do not, in size (age) in the world, size in FRANCE, and area occupied. In large areas and in long time distribution is mainly determined by the laws of ASA. As YULE and the writer said in 1922 (159) the vital factors cause only deviations this way and that from the dominant plan of evolution.

When to this we add the fact that generic distinctions are chiefly simple structural characters, with whose appearance selection can have had little or nothing to do, and which in most cases have little or no use-value, we shall not expect selection to have anything seriously to do with dispersal in long time on large areas, where there are many different associations of plants. If one look at such a flora as BENTHAM (9), where something is usually said about the generic characters, one will soon appreciate their unimportance for use-value. Dispersal is governed in general by the laws of ASA, and the development of each new genus from a preceding one which persists after the birth, gives all the genera of a family, down to almost the last, different ages, though, as we have seen, the numbers begin to overlap about 40 in the *Compositae*, with different figures in other families, according mainly to their size.

It is evidently to some extent a mere question of time, or age, before a genus gives rise to a new genus, or to more species, a species to sub-species, and so on. Probably, however, some stimulus of change of conditions in some way (*cf.* my working hypothesis, p. 96) is also required, for we see so many more new (endemic) species in broken and mountainous country than under the comparatively uniform conditions of open plains. But if this be the case, we shall expect to find more varieties in the older species that have larger areas. If we take, from HAYWARD (58), the varieties recorded in the British (Dicot) flora, we find that

314 gen. of 1-4 spp. with 521 spp. have 85 vars., 16% of the sp.
53 gen. of more with 452 spp. have 127 vars., 28% of the sp.

a marked agreement with the prediction.

That the behaviour of the *Compositae* is typical may be inferred from the table on p. 173, but we may take one more instance from the *Umbelliferae*.

Order by size	Spp. in world		Tribe	Gen/Spp. in trib.
1. Eryngium	220	cosmop.	Heading *Saniculeae*	6/303
2. Peucedanum	180	*, S. Afr. Am.	Heading *Peucedaneae*	63/803
3. Pimpinella	110	*, S. Afr.	Heading *Ammineae*	130/872
4. Bupleurum	100	*, S. Afr.	2nd Ammineae	
5. Azorella	100	S. Am., N. Z.	Heading *Mulineae*	17/215
6. Hydrocotyle	75	cosmop.	Heading *Hydrocotyleae*	13/171

All but *Azorella* are British. The other tribes are headed by genera of 60, 45, 40, 35, 8, 5, 3.

Suppose that now we take the *Ammineae* as the largest group, we find

1. Pimpinella	110	Heading	*Carinae*	Br.
2. Bupleurum	100	2nd	Carinae	Br.
3. Ligusticum	60	Heading	*Seselinae*	Br.
4. Seseli	60	2nd	Seselinae	Br.
5. Apium	45	3rd	Carinae	Br.
6. Bunium	35	4th	Carinae	Br.
7. Oenanthe	35	3rd	Seselinae	Br.
8. Aciphylla	30	4th	Seselinae	
9. Carum	25	5th	Carinae	Br.
10. Conopodium	20	6th	Carinae	Br.
11. Cnidium	20	5th	Seselinae	
12. Selinum	16	6th	Seselinae	Br.

There are only the two subtribes in this group.

Such phenomena are the rule, and it is now clear that instead of reaching them by a series of deductions, one might have realised at once that they *must* occur, and that our classification was therefore artificial to a considerable extent.

The above form really a somewhat remarkable set of lists. They show how well the *Compositae* and *Umbelliferae*, and the same is true of most other families, obey the laws of divergent mutation in the dichotomous formation of new genera in evolution, and the laws of ASA in their dispersal. The first few genera evolved in a family are largely heads of tribes, and the first offspring of these are largely heads of subtribes, and so on. It is very difficult to reconcile with any system of selection, or of gradual development by means for example of small mutations, the fact that it is among the largest genera at the tops of the families that the heads of all the tribes, subtribes &c, are formed. The same is the case, too, with the largest areas of dispersal—both seem to go mechanically with simple size (age), and the laws of ASA are operative throughout.

It necessarily follows from all this that in the flora of a given country the genera representing a family will be determined, not by any supposed adaptation, but primarily by their closeness of reaction to the laws just mentioned. Local adaptation can obviously be attained only after arrival, though a plant will hardly arrive at all if it have not sufficient local adaptation to survive. The plants that first arrive, therefore, will in general be those nearest to the frontier, and of these probably most will be those with the greatest dispersal, the oldest in general in the family concerned. The oldest of all will evidently be the most likely of all to lead the way, and the rest will follow roughly in order of their dates of birth, if one take enough to get a good average, for of course a plant born on the near side of the oldest will probably get a good start of one born upon the far side. We have already seen how in over 70% of the families of the British flora, the first (world) genus is present, followed a good way behind by the second (pp. 27, 191).

If we take the proportions of species and genera in each tribe to the size of the leader, we obtain some interesting results, which are repeated in other families, but it would take up too much space to set them out in full. The oldest tribes with the largest leaders do not show genera and species proportionate to the size of the leader, for one may expect that many of the early genera born from the leader will themselves be the leaders of other tribes. Thus the six uppermost tribes of *Compositae*, whose six leaders in all have

5050 species, have 482 other genera with 6006 species in all, or 1.2 species for one in the leader. The seven lowermost tribes, whose leaders only add to 1060, and are thus very much younger, show 674 genera with 5586 species, or 5.2 species for one in the leader, a great difference [1]. But, as we have seen in the table on p. 173 the early descendants of *Senecio* all went to head other tribes. It must be realised that *the closest genetic relationship is at the top of any family, among its first few genera, where on the other hand the structural divergence is the greatest in the family.* But no two genera in any tribe, unless they happen to be parent and child, will be so closely related as the two first genera of the family, which usually belong to well separated tribes or subfamilies. And the same kind of thing shows among the species within a genus. *At each stage, as one goes upwards, close relationship tends to be marked by wider and wider structural divergence.* Thus the regularity of the figures, as shown in the hollow curves &c, which is excellent so long as a family is treated as a unit—the descendants of a certain genus X—is destroyed by the more or less artificial breaking up that a family undergoes in the attempt to classify it upon structural grounds alone.

It will be noticed that just as the leading genera of *Compositae* show a great proportion of leaders of tribes, so the leading genera of the tribes show many leaders of sub-tribes, and so on. But it not easy to say exactly in what the differences in these mutations consist. If we find a certain character that marks a big genus showing through much of the rest of the family, we admit its rank, *in that family*, as tribal or sub-family, but the rank is owed, not so much to anything in the size of the mutation, as to its mere age. If it were of more recent formation in the family, the same mutation might only mark a group of genera, or one genus, or even only one or two species, and yet be identical in size with what elsewhere is a tribal or even a family character. Only detailed examination of the particular family with which we are dealing will tell us what any particular character is worth in that family, and the results are practically valueless for dealing with any other family.

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[1] This counting was made at a different time from others above, and numbers are continually being altered.

Probably individual mutations, that form species, genera, tribes, or families largely differ in the number of component parts, if one may use the expression; one that forms a genus will involve more structural features than one that only forms a species. The more characters that A and B show in common, the closer in general will be their relationship. But at birth of a new form, some of the characters of the parent will be lost, and replaced by *divergent* characters in the offspring, as we have seen with endemic forms and with the genera at the head of a family or a tribe; and the divergence is commonly incompatible in such a way that it can only have been formed by a straight mutation, as for example the great difference between the two great divisions of *Acanthaceae* (next chapter) is in the aestivation, one being imbricate, the other convolute.

So far the matter is fairly simple, but we must not forget that the number of species is greater than that of characters, so that differentiation depends largely upon permutations and combinations of the latter. In *Rubiaceae*, the inferior ovary of *Psychotria*, the leader of the family, was passed on to nearly all the rest, and is a family character there, while in *Saxifraga* it is not even a generic character, and in *Gaertnera* (*Rubiaceae*) the mutation that produced the genus gave it a superior ovary, which for long caused it to be placed in *Loganiaceae*. Many examples of this kind may be found in a large family like *Rubiaceae*, as we have already pointed out (**146**, p. 624; *Evol.*, p. 118, 178). But all these characters that thus appear in this apparently casual way are characters that elsewhere may be of great importance, such as a superior ovary (*Gaertnera* in *Rubiaceae*, for example), a different number of stamens, and so on in great variety. Their importance anywhere depends on their age, and therefore upon the number of descendants to which they have transmitted the character, and especially when the display of the character is not geographically interrupted. Had *Gaertnera* been accompanied by a number of palaeotropical descendants (it contains 30 species itself), instead of what is actually the case, that the superior ovary is only shown elsewhere in *Pagamea* with 8 species in BRAZIL and GUIANA, we should have regarded the group as not belonging to the *Rubiaceae*.

What really seems to happen is that genera &c are produced by a kind of shuffling of characters whose potentialities are already carried by the parent. The new ones produced may even, as in *Gaertnera*, be quite new *for that family*, and in a large family like *Rubiaceae*, where 500 opportunities for generic change have been offered, quite a number of such characters have appeared, as we have already pointed out in detail in (146). As yet, just as in human birth, however well the parental characters may be known, it is impossible to predict what will appear at the next mutation, for though the bulk of the characters will be directly parental, some are sure to come from further back. In animals, where sex is much more in evidence, change goes on much more rapidly, so that it looks as if sex were an arrangement ensuring this rapid divergence.

Just as in a single human family there may be considerable mutual divergence, so is there in the offspring of any genus of plants (its species), bringing in sometimes, though rarely, characters only seen in other genera which may be only distantly related. Until we can trace some of the laws which, like Mendel's law, run through character-inheritance, we shall, however, be working very much in the dark.

The first genus of a new family necessarily begins as a single species of very local dispersal, in fact endemic to its birthplace. It must at birth have been reasonably adapted to growth there, or it would not have survived. As yet we have no idea whatever as to the number of non-survivors, whether through any lack in their adaptation, or through sheer bad luck. But in general one may surely expect enough adaptation to survive to reproduction, and it will always improve. But here is at once the first factor that may interfere with the regularity of the figures in the curves, which are largely concerned with size in the world. This character of size in the world (number of species), and its connected character of area occupied and its continuity, both of them figuring in the laws of ASA (p. 23), though hitherto neglected almost entirely, are of very great importance. This was brought home to the writer when in 1889 he began to prepare facts of generic sizes tor his *Dictionary*, and soon began to realise that there were laws underlying their distribution. Using the Hookerian conception of species, he made allowance for synonyms by a careful estimation of the relative space that they occupied in the *Index Kewensis*, which in those days gave synonymy. He counted the actual species in small genera, usually lumping after five at 8, 10, 12, 15, 18, &c, but in the larger he measured the actual space occupied, and allowed for the synonyms, increasing the proportion when the authors were notoriously "splitters". Thus all these figures were prepared upon one plan, and that they have been regarded as very useful and reliable is shown by the way in which they are used in so many places. For the new edition of the *Dictionary* which it is hoped to publish when this present book is out, the figures are being very carefully prepared by Mr W. T. STEARN, one of the joint editors. The old ones, however, remain almost as useful as ever for comparisons, for which they are used in this book, and have the great advantage of being all prepared upon the same system throughout.

If we take a considerable number of families, we ought to get fair average results with their figures of size &c. We shall for instance expect the first genus at least to double the second in the numbers of species, and in actual fact the 28 first genera in the families down to 100 genera have altogether 12,965 species by the latest countings in my possession, and the 28 second have 6,807, while half the first number is 6,483. This is surprisingly near to expectation, and as the second must have had fewer vicissitudes to undergo, one can hardly wonder if it be a trifle in excess. This result, therefore, may be added to the many proofs already given in *Evol.* that this is the general track followed by evolution, while a further one is given by the tables above in this chapter, where a note is given after each, saying that duplicates only begin at 40, &c. If evolution goes by dichotomy, and in this mechanical way with little or no reference to adaptational usefulness, then, as only one genus is produced at each mutation, the family will have grown to some size before it will be likely to produce two genera at about the same time, and they will almost certainly be in different lines of descent. This also proves to be the case; if we look at the genera of 5 in *Compositae*, we find the 60 of them to be in all tribes but *Vernonieae* and scattered all over the world.

Another question that at once arises is whether a character, once acquired, is handed down to all descendants of the form that shows it. Considering the ease with which mutation can change a character, and the fact that the number of characters is apparently far less than that of the species, the answer would seem to be negative, but it is really a question for the geneticists. With no adaptational value, there seems no particular reason why it should be so retained. Our working hypothesis supposes the change to take place under circumstances that put a strain upon the nucleus, which ultimately causes it to readjust its arrangement of genes and chromosomes. This has the result of bringing it into a proper balance of adaptation to the new conditions, with the further result, which appears to be largely incidental, that a new structural arrangement is produced, and forms a new species, or genus. As mutations are dichotomous, and the parent also survives, a hollow curve (logarithmic straight line) is produced by the various sizes of genera, following the law of compound interest. The curve continually lengthens at the upper end by the production of new species, which becomes ever more rapid as the genera there increase in size, and at the lower end by the increasingly rapid production of new genera, on account of the continually increasing number of potential parents, the new genera of course always beginning as " ones ".

New problems seem all the time to be presenting themselves for solution. Why, for example, did the posterior androeceum shown in one section of *Hibbertia*, which is the leading genus of *Dilleniaceae* (p. 146) only appear again in the small and local *Schumacheria* of CEYLON, far away from the habitat of *Hibbertia ?* What was the impulse, and where and how did it arise, that brought out this very remarkable feature twice over in such separate places? And so on.

Another question of importance is to what extent the first genus of a family continues to lead, after others have begun to form and to arrive in the country concerned. In our present state of ignorance of the influences of many factors, all we can do is to make a statistical comparison of the families found for example in BRITAIN. Of the 99,44 have only one genus each, and in 28 of these, or 63.6%, that genus is the actual first genus in the family in world size. The same is the case in 68.2% of families with two or three genera, 85.7% of those with 4-10, and 92.3% of those with more genera than ten. Thus there is no certainty that the first genus will always arrive, though it might arrive if time enough were allowed. Another comparison will perhaps give a better result. All the families with one genus only show the first in 63.6%; all with one or two genera show it in 66.6%; all with one to ten in 69.7% and all the families, of whatever size, in 71.0%. Thus in about nine families, the first genus was later than first in arrival, and in the other 27 it did not arrive at all.

With regard to the 27 families that do not show the first genus, we may easily predict that the bulk of them will be found to be such as have their beginning in far-away countries, especially tropical. It would take too much space to set them all out, but taking them in alphabetical order, their first genera are *Agave*, *Tabernaemontana*, *Anthurium*, *Schefflera*, *Aristolochia*, *Cordia*, *Hydrocleys*, *Ipomoea*, *Melothria*, *Elaeagnus*, *Dioscorea*, *Haloragis*, *Boottia*, *Loranthus*, *Cuphea*, *Hibiscus*, *Ficus*, *Jasminum*, *Dendrobium*, *Gilia*, *Calandrinia*, *Psychotria*, *Gnidia*, *Grewia*, *Celtis*, *Pilea*, and *Clerodendron*, genera which are usually unfamiliar to Europeans except under glass. The genus that in BRITAIN actually leads in each of these 27 families is in general some places down in the list of sizes, indicating, on my working hypothesis (p. 96) that the conditions changed between the tropics, where most of these families obviously centre, and BRITAIN, enough to cause the formation of a new genus on one or more occasions.

The more that we break up a family, the more artificial do our divisions look. The very first one practically always takes the second genus—directly derived from the first—into another tribe, and the same kind of thing happens at later divisions. And while the whole family usually shows a good and smooth curve, the tribes made by structural characters do not show this, but become more and more irregular the more that we split them up. Divergence of near relatives is the principal factor in the making of tribes &c, and age, size, and area, hitherto almost totally neglected, are generic and specific characters of very great importance indeed.

Various minor laws, based upon the laws of ASA and upon the growth by compound interest, seem gradually to be making themselves felt, and to be bringing some semblance of order into the hitherto confused mass of facts that has made up the subject of geographical distribution. It is fairly evident that the inductive method can be applied here as elsewhere. Everything seems to point to the probability that the whole process was directed from above downwards by the production of descendants by a more or less regular dichotomy. At the same time the characters of those descendants were not primarily produced by a method of trial and error, as used to be supposed, but were handed down in some way by their ancestors, which carried the potentialities of producing them under certain circumstances that as yet we do not in the least understand.

Once produced, a new form, whether family, genus, or species, will very slowly expand its area of dispersal, and will give rise, again by some law that we do not understand, to new forms that will repeat the behaviour of the parent.

As one goes backward through the descent of things now existing, the sudden mutations to which they owe their origin seem to show a tendency to be larger at times, the largeness being mainly shown by the fact that it involves a greater number of characters, though at times one may see a mutational change, like that between two cotyledons and one, that *looks* as if perhaps it were really greater than usual. There is no doubt that the differences between the great groups are more emphatic, so that most people would without thought describe them as larger, but we have nothing at present to go upon to show that it is really the case, and for the present it is safer to consider the " larger " differences as due to change of more characters.

CHAPTER IX

The classification and distribution of the Acanthaceae as illustrating the probable growth and dispersal of a family

Let us now go another step forward with the newer problems that we have indicated. *Acanthaceae* have long been divided into four sub-families, considered as of equal rank, though we have shown in *Evol.* that size (age) is of as much importance as structural characters. Three of the four are very small, I, *Nelsonioideae* (6 genera), II, *Mendoncioideae* (5), and III, *Thunbergioideae* (3), while the fourth, *Acanthioideae*, has nearly 300 genera, and is divided into two super-tribes, A, *Contortae* (aestivation usually convolute), and B, *Imbricatae* (usually imbricate). They are headed by the two largest genera in the family, B by *Justicia* (325 warm) and A by *Ruellia* (225 warm). The former probably began the family, and its first offspring was the latter, showing the divergence of character to convolute, no great change in itself, nor one with any use-value, but here important because it was the first and oldest in the family, and was handed down to, and thus marks, the two great subgroups. We do not however know that all that show imbrication are actual descendants of *Justicia*, or those with convolution of *Ruellia*, for there may have been cross-mutation from one to the other, for anything that we can tell. These characters are common as distinctions in other families, though nowhere to quite so great an extent, for example in *Erythroxylaceae*, *Gentianaceae*, *Guttiferae*, *Oxalidaceae*, *Primulaceae*, or *Rubiaceae*. By reason of their size and age, *Imbricatae* and *Contortae* are of higher rank than the three first sub-families.

Both give good hollow curves, *Imbricatae* from 325 down to 84/1, and *Contortae* from 225 to 41/1, but regularity and geographical continuity begin to break up as we break up the family by structural features only.

The change from *Justicia* to *Ruellia* could only have been by sudden mutation, and as advantage was not in any way involved, there seems no reason why it should not be repeated, or even reversed, and there is reason to suppose that both these phenomena may be frequent (*cf. Rhamnus*, pp. 107-8). As yet, one is very handicapped in work of this kind by complete lack of knowledge of the laws of incidence of character.

Appearance of the same character in different places. Of this, useful lists are given in (10) and (35). From them we extract the following, which are hereditary, not teratological, phenomena.

Leaves usually opposite, but alternate in *Elytraria* (I in LINDAU's classification in *NP*/1) and in one *Aphelandra* (IV. 9).

Calyx gamosepalous almost to apex in *Satanocrater* (A. 6), *Physacanthus* (do) and *Phialacanthus* (B. 14). Two pairs of sepals fully united in *Louteridium* (IVA. 2) and *Spathacanthus* (IVB. 4). Ringlike edging of calyx in *Clistax* (B. 8c) and *Thunbergia* (III).

Corolla. Hygrophileae (A, 3) and most *Imbricatae* (B) have a fully two-lipped corolla. Many *Justicieae* (B, 8c) and *Odontoneminae* (B, 7b) have a trough in the inner side of the upper lip, enclosing the style. In one *Himantochilus* (B, 8c) there are similar troughs for the stamens. When the upper lip is absent, there is often a dorsal slit nearly to the base of the corolla, *e. g.* in *Acantheae* (B, 1) and *Eremomastax* (A, 3). The underlip is inrolled in *Symplectochilus* (B, 7b) and *Himantochilus* (B, 8c).

Stamens. Five occur in *Pentstemonacanthus* (A, 6); four in *Ruellieae* (A, 6), *Thunbergioideae* (III), &c; two in most *Imbricatae.* Some genera vary very much; in *Barleria* (A, 7) there may be four stamens and one staminode, two fertile, two reduced, and one staminode, two and three staminodes, or two and two. The connective is sometimes divided into two arms—a suggestion of the behaviour in *Salvia*—*e. g.* in *Strophacanthus* (B, 8b) or *Dicladanthera*

(B, 7b). The anthers usually open by slits, but though these are found in *Thunbergia*, the closely allied monotypic *Pseudocalyx* has pores. It will be remembered that porous opening appears in many places in many families.

Pollen-sculpture &c. This is the character upon which LINDAU largely bases his classification, as the patterns are completely valueless from a selection point of view. But we find smooth round pollen, with either two or three pores (this difference alone requires mutation), in A, 6, in B, 6, in B, 8a, and in some genera of I and II; prickle pollen in some of A, 2, 5, and 6, B, 2, 4, and 8a; and other kinds of pollen mixed in their incidence in the same way.

Many other features might be quoted, and the same thing may be done in any fairly large family. This appearance of the same character, and one with commonly no conceivable use-value, is one of the most widespread phenomena, which has hitherto received no satisfactory explanation, but which is to be expected if characters are handed down from above in (usually) a recessive condition, but one which may at any moment, or at any suitable conglomeration of factors, become dominant for the lifetime of the species that shows it.

Such lists as this prove that under circumstances which as yet we do not understand, the same character may appear at different places, either in the same, or as could easily be shown (as with inferior ovary), in different families. The value of the character in classification simply depends upon how many genera or species display it, or in other words, simply upon its age at the place under consideration, though we have to be careful to get species or genera as closely allied as agreement in *many* other characters can make them. Now that we know what great differences a single mutation can make in almost any character, it is clear that taxonomy, dependent as it now is almost entirely upon structural resemblance, is trying to stand upon a base which is dangerously narrow for such a superstructure as we have erected. Other criteria, at present chiefly geographical and genetic, will have to be admitted if we want to have a really natural classification.

As they stand, group B is definitely larger than A, therefore possibly the older. Disregarding the taxonomic classification altogether, except for the primary division into A and B, let us divide up these groups geographically only, when we get a rather striking result, partly shown in the table below. Scores of such tables can be, and have been, made up for the larger families and sub-families, so that one realises that geography is of great importance, not only for distribution, but in taxonomic work, and in the study of evolution. To set out all the *Acanthaceae* in detail would make an inconveniently large table, so we have given detail only for Asia, which has the smallest numbers. The tables for Africa and America match this in proportions, but are much larger.

Mainly tropical or sub-tropical, the family is also found to a small extent in warm temperate regions. A few genera are pan-tropical, and average about 130 species each, so are very old, by the laws of ASA. They are followed by rather more genera that are palaeo- or neo-tropical. The latter simply fade out into the cooler zones on either side, but the former are followed by separate groups of genera confined to Africa or to Asia, which are now divided from one another by water, or by a great expanse of land now rather unsuitable to many *Acanthaceae*. All three lists include large numbers of genera of the smallest possible size. Each begins with large ones at the top, well separated in size, and smaller ones below, increasing in numbers as they get closer and closer in size. Towards the bottom there is much overlapping of genera of the same size, and they end in a great display of " ones ". All but the pantropical show more B than A, and the numbers tend to fall off eastwards, the family making but a small show in Australia and Polynesia. In this connection, the tables and map on pp. 180-1 of *AA* are worth looking at.

The Distribution of Acanthaceae, geographically and numerically treated

	Imbricatae			Contortae	
Pan-Tropical Genera	Spp.	Tribe		Spp.	Tribe
Justicia	325	16	Ruellia	225	6
Dicliptera	100	14a	Barleria	150	7
Adhatoda (Justicia pp.)	100	16	Lepidagathis	80	7
Dianthera (do)	80	16	Dyschoriste	50	5
Pseuderanthemum	60	13	Hygrophila	40	3

	Imbricatae			Contortae	
Palaeo-Tropical Genera	Spp.	Tribe		Spp.	Tribe
Hypoestes	90	14a	Strobilanthes	180	5
Blepharis	80	8	Micranthus	12	4
Asystasia	35	11	Cardanthera	12	3
Acanthus	25	8	Neuracanthus	8	3
Crossandra	25	8	Nomaphila	10	7
Rungia	25	14a	Asteracantha	1	3
Peristrophe	15	14a			
Rostellaria	10	16			
Rhinacanthus	7	14b			
Rhaphidospora	6	12			
Nicoteba	5	12			
Monothecium	3	14c			
Asystasiella	3	11			

Asiatic Genera

Gymnacanthus	30	trop. As.	Eranthemum	25	trop. As.
Andrographis	20	trop. As.	Hemigraphis	25	Ind. Chi. Jap.
Hallieracantha	20	Mal. Arch.	Daedalacanthus	15	Indomal.
Phlogacanthus	15	Indomal.	Echinacanthus	8	Himal. Java
Leda	7	Mal. Pen.	Stenosiphonium	5	Dekkan, &c
Ptyssiglottis	6	Indomal.	Pseudostenosip.	5	Ceylon
Cystacanthus	6	Fur. Ind.	Aporuellia	4	Malaya
Filetia	5	M. P., Sum.	Gutzlaffia	3	S. E. As.
Polytrema	5	Mal. Pen.	Aechmanthera	2	Nepal, Khas.
Haplanthus	3	Indomal.	Chingiacanthus	2	China
Odontonemella	2	Indomal.	Calacanthus	1	W. India
Strophacanthus	2	Indomal.	Petalidium	1	Himal-Dekk.
Sphinctacanthus	2	E. Ben. Siam	Stenothyrsus	1	Perak
Codonacanthus	2	Khas. Chi.	Lamiacanthus	1	Java
Diotacanthus	2	S. India	Sautiera	1	Timor
Isochoriste	2	Java Angola	Ancylacanthus	1	New Guin.
Oreothyrsus	2	New Guin.	Leptosiphonium	1	New Guin.
Calophanoides	1	Indom. Chi.	Chroesthes	1	Tonq. Yunn.
Phialacanthus	1	E. Bengal			
Antheliacanthus	1	Siam			
Cyclacanthus	1	Annam			
Clinacanthus	1	M. P. Java			
Trichacanthus	1	Java			
Calycacanthus	1	New Guin.			
Jadunia	1	New Guin.			
Hulemacanthus	1	New Guin.			
Gymnophragma	1	New Guin.			
Plaesianthera	1	Ceylon			

By placing all the continents in parallel tables with that of ASIA, which is much the smallest, one obtains a very impressive table of the distribution of all the *Acanthaceae*, but it occupies too much space, and we shall continue simply with the actual numbers, for the three great continents, of the genera that are confined to them. The pan- and palaeotropical genera are given above, and the neo-tropical are the same as the American.

B (*Imbricatae*)

Asia	11/1, 7/2, 1/3, 2/5, 2/6, 1/7, 15, 20, 20, 30
Africa	25/1, 8/2, 4/3, 2/4, 4/5, 1/6, 1/7, 1/8, 2/10, 25, 30, 50
America	38/1, 7/2, 8/3, 6/4, 3/5, 3/6, 2/7, 2/8, 2/10, 12, 20, 25, 30, 45, 80

A (*Contortae*)

Asia	8/1, 2/2, 1/3, 1/4, 2/5, 1/8, 15, 25, 25
Africa	14/1, 7/2, 2/3, 1/4, 3/5, 2/6, 2/7, 1/8, 12, 15, 15, 35
America	14/1, 3/2, 1/4, 2/10, 12

Total of *Imbricatae* 152 genera with 745 spp. Average 4.9
Contortae 75 322 4.3

It is of interest to note how little variation there is in the average size of these genera. The averages for all the six groups of B and A are 5.0, 4.4, 5.1, 5.6, 4.5, and 2.7. The last is perhaps accounted for to some extent by its very small size, and the small size of its leader in the continent; its genera are probably mainly the direct offspring of the pantropical genera, a suggestion perhaps supported by the great proportion of ones, which is much too large to have come from a local leader of only 12 species.

The distribution of the " ones ", which we have seen to be the young beginners as genera (*AA*, pp. 165-7), is of interest. If we take the rough descriptions of their localities given in my *Dictionary*, we find them to be, for both A and B together, in Asia, Indomalaya 3 (one reaching China, but none occupying very large areas), Ceylon, E. Bengal, Siam, Indochina, Perak, 1 each, Java 2, Malay Penin. and Java (Timor), New Guinea 6.

Africa, parts of trop. Afr. 5, East trop. 5, West trop. 7, Somaliland 4, South Afr. 2, Madagascar 14, Socotra 1.

America, California 2, SE U. S. 2, Mexico 11, Central Am. 8, Colombia 4, Venezuela 2, Peru and Bolivia 10, Brazil 8, Cuba 4, Jamaica 2, Haiti 1.

It will be seen that in this list of 110 genera, there are no fewer than 85 that occur in mountainous country or in islands, or 80% of the total, and this proves to be very generally the case. It is shown very strikingly, for example, in *Siparuna* (map at p. 224), which shows the overwhelming proportion of endemics, in this case species, in the great mountain chain of western SOUTH AMERICA; other places show it in the same way. Endemics of course are fairly frequent in comparatively level regions, usually when covered with forest, but there is no doubt that they are far more common in broken country. Most islands are mountainous, and this type of country provides more variety in conditions, and favours isolation. With regard to mountains, one must not forget that conditions change quickly in the *vertical* direction.

Such lists as these show very clearly the operations of the law of size and space. As the newly formed genus grows, and covers more space, often perhaps travelling with the association into which it happened to be born, it will produce, though probably only after a long time, and under some stress of conditions, a new species, divergent from itself. This will repeat the behaviour of its parent, but probably not exactly, it having been born under, and therefore centring upon, different conditions; and of course, unless it has inherited enough local adaptation, it will not survive at all. How far, and in what directions it spreads, will then depend, as did that of its parent, upon its reaction to the conditions.

The new species is usually produced within, or close to, the area covered by its parent, as one may readily see if one look up the areas occupied by the species of any genus with only a very few. In CEYLON, the first species of *Schumacheria* (p. 145) reaches from GALLE in the south, through the wet south west low country, to LABUGAMA near COLOMBO, a distance of about 60 miles, while the other two species occupy smaller areas in the same region. If one look at TRIMEN's estimates of areas for the species of the endemic genera, one finds *in Dipterocarpaceae* C, RC, 2 RR, 4 R, 3 VR; 2 RR, 4 R, 9 VR; R, VR (initials stand for common, rare, very, and rather). The larger genera even make suggestions of curves, with their larger numbers at the rare end of the scale.

As new species and genera are necessarily very local, one will expect them, if formed in accordance with my working hypothesis, to be frequently, but far from exclusively, formed in new regions in which the parent has arrived some considerable time previously, as in southern EUROPE one finds so many endemic species in genera that have now reached BRITAIN. They do not occur in BRITAIN itself, at the outer limit of the genera. The endemics in fact mark the track of invasions, but follow the actual leading species at a safe distance behind. One must also remember that a species may meet with as great a change of conditions by going backwards as by going forwards, so that new forms may arise (as " ones ") even near to the original centre from which the family started. And one must further remember the very striking phenomenon about which there was a good deal of controversy at the time of the publication of *AA*. It was called " swamping " by SINNOTT, for it is commonly shown by the fact that some genus may be represented in a country by endemic species *only*, or even a family by endemic genera only, like *Monimiaceae* in CEYLON by the small endemic genus *Hortonia*. We shall deal with the subject in a later chapter.

In going back to the separation of *Ruellia* from *Justicia*, and the formation of the early pantropical genera, one is evidently going back to the very remote period when there was a land connection between old world and new, to the period when what we called above (p. 89) real discontinuity was being produced. DE CANDOLLE and others (*AA*, pp. 17, 22, 49, &c) were clearly right when they showed that water carriage was only responsible for a trifling amount of dispersal, and their figures, and those given here, make any but land connection practically impossible. Even allowing for a possible WEGENER separation, pantropical genera must usually be very old, and must have suffered a good deal of indiscriminate slaughter of species during the separation, in any case. But *Justicia* and *Ruellia* would in all probability continue to lead the way, though smaller genera would be confined to one or the other side of the ATLANTIC. But one must not forget that one or two of these might have overpassed the pantropicals so far as to equal or exceed them in number at the " landing ".

The earliest genera to reach AFRICA, or to be born there, in the northern parts at any rate, would usually be in time also to reach ASIA. The separation of these two continents was less complete and thorough than that with AMERICA, and of later date, as is shown by the smaller size of the palaeotropical genera. While the smallest pantropicals have reached at least 40 species (now), there are some palaeotropicals of only three, and *Asteracantha*, which is a marsh plant subject to less variation of conditions, has only one species in both AFRICA and ASIA. In AMERICA, on the other hand, there was no separation except into north and south, and even that is not complete, while there is good evidence to show that communication long existed across what are now the WEST INDIAN islands. Most American genera of *Acanthaceae*, therefore, may be equally well described as neotropical, whilst they fade out into the cooler zones on either side.

The Acanthaceae in the West Indies. There are a number of interesting points that can be made out about the distribution of the family, if one make predictions from the laws of ASA and of growth by compound interest, and then test them upon the facts, in the way in which, as a matter of fact, the great bulk of this book has been written.

Other evidence goes to show that the WEST INDIES are the remains of more extensive land communications that existed long ago, whether all at the same time, or not, or all in one direction, or not. As it was so long ago, the genera now found in the islands would be those that were in existence at that time, or genera which now will be large ones, though of course the nearer to the points where the breaks of communication were made, the smaller might be the genus, and if it were born a long way from these points, a very large genus might be too late to reach the islands. Genera born upon what are now the islands, too late to get to the mainland, will of course be endemic to the islands. Counting up all the figures that we could find, we obtained the following results; names are not given to the genera, but only their sizes.

Reaching the W. I., in B	325 100 100 80 80 60 45 30 20 10 6 4 3 3 1/1
Not reaching	25 12 10 8 8 7 6 5 5 4 4 4 4 3 3 3 3 2 2 2 2 2 2 2 32/1
Reaching the W. I., in A	225 80 50 40 10 4 2 2 2 and *Barleria* (150) very doubtful
Not reaching	180 (*Strobilanthes*) 12 10 2 14/1

It is clear that our expectations have been completely fulfilled. Some of the genera in these lists are endemic to the islands, and it is an obvious prediction that they will prove to be larger, and probably also more numerous, in B than in A, and this also proves to be correct, for in B they are 6, 4, 7/1, and in A only *Barleriola* with two species.

The same phenomena show themselves in the case of CEYLON as compared with INDIA, or MADAGASCAR with AFRICA. Only in the cases of the far outlying islands like NEW ZEALAND or the HAWAIIANS is there any serious difficulty in determining the source of the flora, and by simply picking out the larger genera at the source, one may get a very fair notion of what will be in an island, and even in what proportion. Distribution, as we have been showing all along, is a very mechanical process unless one take very small (ecological) areas, where selection has the principal voice in the matter.

Some general problems. The effects of the laws of ASA are more and more interfered with by outside influences as one goes up the scale from the smallest genera, the field for speculation becoming wider. During the comparatively short lifetime of genera confined to one continent, the areas concerned are much less likely to undergo serious change in size or in climate &c. But it may be worth while to point out the kind of problem upon which one happens in the more complicated problems of the larger genera.

Why, in AMERICA, where *Ruellia* is better represented than in the old world, is group A so much smaller than B, though there are fewer *Justicias?* Is there any means of finding out which genus is the direct offspring of which? Are all the descendants of *Justicia* in *Imbricatae*, or all of *Ruellia* in *Contortae?* Why does *Barleria* so largely take the place of *Ruellia* in AFRICA, and *Lepidagathis* tend to do the same by *Barleria* in ASIA? Is it possible, or probable, that *Barleria* " landed " in AFRICA with more species than *Ruellia*, or with younger species, and that something of the same kind happened on the way to ASIA? There are innumerable questions of this kind that may be brought up; these are just given as suggestions. From whence again did *Strobilanthes* come, and why has it so many species? It is a conspicuous exception to the rest of the family, as it is one of the largest genera in it, yet is not pan-tropical; except for a few species in MADAGASCAR and the MASCARENES, it is confined to the INDOMALAYAN region. HOOKER's *Flora* shows 146 species of *Strobilanthes* in INDOMALAYA, where the only pan-tropical member of the *Strobilantheae, Dyschoriste* (*Calophanes*), has only 4 species, and evidently could not be its parent.

It is interesting to look at a family displayed upon geographical evidence only, like the *Acanthaceae* above, where we have only used taxonomy in separating A and B. This display being paralleled by most large families, is clearly a phenomenon of importance, and incidentally shows that there cannot have been any appreciable selection of genera, which would imply the destruction of others. All goes to show that there is little to choose between one genus or species and another allied to it.

The group B is in general superior in number, and often in size of genera, to A. There are many " ones " at the bottom, the numbers falling off rapidly at first as one goes upwards, and more slowly later. But when one looks at the taxonomic placing of the genera, one finds many groups represented by genera that do not always overlap, or even touch, geographically. This tends to suggest that cross-mutation may be not infrequent, but as yet we have no information to go upon. The figures show that both the As and the Bs evidently developed where they are found, in each continent. It therefore becomes important to know what could have been their parents, and the geographical lists help in this task.

When one sees how clearly all these geographical relationships come out, and how each geographical section is arranged as one would expect from dichotomous production, it is clear that the geographical relationships are as important as the structural, especially now that divergent mutation seems to be the rule. Only in quite recent years has any serious notice been taken of geographical relationships at all. On the other hand, though they produce a very remarkable arrangement, they alone cannot be trusted any more than can structural alone. No evidence as to relationship can be neglected, if we are finally to arrive at trustworthy results.

The taxonomic classification of the Acanthaceae. The usually accepted system is that of LINDAU in *NP*/1, IV, 3, p. 287. It is largely based upon the very marked sculptural characters of the pollen grains, which lend themselves admirably to mutation, and to that alone, and which were adopted as fulfilling the often expressed desires of taxonomists by not being in any way useful, or possible subjects for natural selection. The classification, given in full in *NP*-1, *l. c.*, forms an instructive comparison with our geographical list. Let us begin with our usual list of the leading genera by size in the world :

The leading genera of Acanthaceae, in order of size

Genus	Spp.	Group	Tribe	Ceylon	W. Ind.
1. Justicia	325	B	Heading *Justicieae*	C	W
2. Ruellia	225	A	Heading *Ruellieae*	C	W
3. Strobilanthes	180	A	Heading *Strobilantheae*	C	
4. Barleria	150	A	Heading *Barlerieae*	C	W ?
5. Thunbergia	150	III	Heading *Thunbergioideae*	C	
(Adhatoda	100	B	Justicia p. p.)	C	
6. Dicliptera	100	B	Heading *Odontonemeae*	C	W
7. Hypoestes	90	B	2nd Odont.		
(Dianthera	80	B	Justicia p. p.)		W
8. Lepidagathis	80	A	2nd Barler.	C	W
9. Blepharis	80	B	Heading *Acantheae*	C	
10. Aphelandra	80	B	Heading *Aphelandreae*		W
11. Pseuderanthemum	80	B	Heading *Pseuderanthemeae*		W
(Monechma	50	B	Justicia p. p.)		
12. Dyschoriste	50	A	2nd Strobil.	C	W
13. Beloperone	45	B	2nd Justic.		W
14. Ebermaiera	45	I	Heading *Nelsonioideae*	C	
15. Hygrophila	40	A	Heading *Hygrophileae*	C	W
16. Asystasia	35	B	Heading *Asystasieae*	C	W
17. Brillantaisia	35	A	2nd Hygroph.		
18. Isoglossa	30	B	Heading *Isoglosseae*		
19. Odontonema	30	B	3rd Odont.		W
20. Mendoncia	25	II	Heading *Mendoncioideae*		

Andrographideae, *Petalidieae*, *Graptophylleae*, *Trichanthereae*, and *Louterideae* are headed by genera from 20 down to 2, in order.

There are many duplicates at all numbers below 25.

It will be seen as usual that the leading members of the family by simple age are, as one would expect, leaders of most of the tribes into which the family is divided. They are therefore, at birth, although they belong to four subfamilies and fourteen tribes, as closely related as is possible for so many. Later members of these tribes, however, as they become smaller and smaller, tend to become steadily wider and wider apart in their relationship. Speaking generally (for of course any two of them may be as closely related to one another as is possible) the " ones " show the smallest degree of possible relationship, the few large genera at the top the greatest. The separation, in fact, simply goes with the divergent system upon which they are evolved. The great lines of taxonomic division are marked out in the very earliest stages of the growth of the family. Relationship goes with the actual position in the dichotomous system, *whatever the actual structural features may be.* Genetic connection is vertical (parent to child) rather than horizontal (cousin to cousin).

Pollen-patterns. It is almost inconceivable that these can be produced in any other way than by sudden mutation, and it is therefore of interest to study their incidence, which is outlined for the top genera on p. 208, and given in full detail by LINDAU in various papers. Though the first twenty genera must be closely related, they show a very great variety in the pollen. It is clear, here as elsewhere, that the mutations that produce the characters of the early genera may easily be, and in fact most often are, of sub-family or tribal rank, by reason of simple age in the family. The distinctions between these tribes are *necessarily* dependent upon the mutational changes that took place between father and son at some remote period. As only one new species or genus appears to have been born at one time, it is even possible that two or more tribes should be headed by brothers, born from the same parent, and that none of them should belong to the same tribe as that parent. A small genus in one tribe is not likely to be closely related to any ot another tribe, unless the leaders of the tribes happen to be themselves small. The leader of any tribe may be the actual son of a rather larger genus in a different tribe. As a tribe grows larger, more characters will almost necessarily appear, and these may be, and in fact often are, characters that appear elsewhere in other tribes, so that polyphyletic composition may be frequent enough. To try to harmonise genetic relationship with taxonomy has some resemblance to trying to make ropes out of sand, and it would seem better to regard the two as separate aims, both of which have to be reached.

Distribution of pollen patterns among the leading Acanthaceae

Using LINDAU's names to save space, we find :

Knötchenpollen in *Justicia*, including *Adhatoda*, *Dianthera*, and *Monechma* (subgenera), and in *Beloperone* (*NP*/1, *l. c.* fig. 110, P, Q, R, p. 281).

Wabenpollen in *Ruellia* (probably the first mutation) (fig. 111, F, G, p. 282, *l. c.*), *Barleria*, *Lepidagathis*.

Rippenpollen in *Strobilanthes* (110, G, H, J), *Dyschoriste*, *Hygrophila*, *Brillantaisia* (and *Pseudobarleria*).

Furchenpollen in *Thunbergia* (110 B, 116 N).

Spangenpollen in *Dicliptera*, *Hypoestes*, *Pseuderanthemum*, *Odontonema* (110 K, L, M).

Spaltenpollen in *Blepharis*, *Aphelandra* (129D), *Ebermaiera*

Rahmenpollen in *Asystasia* (110, N, O) (and in *Anisacanthus*).

Gürtelpollen in *Isoglossa* (111 D, E).

Glatter, runder Pollen in *Mendoncia* (110 A).

There are also Kammradpollen, Stachelpollen, and one or two more kinds, rare, and found only in a few of the very small genera. It is clear that almost every variety of form has been produced in the first twenty closely related genera, and must have been due to well marked mutation.

If characters are mutational, it should in time be possible to obtain some suggestions of the way in which they are distributed, or of their incidence. It is evident that when a family is young, the divergences of character in its early genera are very marked, as we have now seen in these last chapters, and in *Evol.* p. 199. Their mere age has enabled them to show themselves in many descendants. The incidence of the pollen patterns in *Acanthaceae*, which is evidently a mutational character allowing of no transitions or intermediates, and which is so distinct and well marked, should afford a good subject for genetic investigation. Between *Justicia* and *Ruellia*, the first two genera in the family (father and son), there is a complete change, and yet others to *Strobilanthes* and *Barleria*, the following genera, though *Barleria* goes back to the *Ruellia* pattern—a fact that can no longer be accepted as an unquestionable proof of descent from *Ruellia*.

Mutations show such variety, and are of such different age, that as yet it is idle to think of placing them in any very well marked degrees of rank. But there does, upon the whole, seem to be a well marked increase of divergence as one goes upwards from varieties to larger groups. This increasing divergence has hitherto been regarded as due to the destruction brought about by competition (natural selection), which has killed out the less efficient transitional forms (on the older view) or intermediates (upon the newer). But, as we have been pointing out for the last forty years, this is an illogical standpoint. The really severe competition is not between widely divergent forms, but between those that are most closely allied, and physically closest together as was long ago pointed out by OLIVER WENDELL HOLMES when he said that religious quarrels were never so bitter as when the differences were almost imperceptible, unless perhaps when they were quite so. There will be great competition between two sellers of the same evening paper in the same short street, but not between one in Holborn and one in Piccadilly Circus, or one in London and one in Glasgow, where conditions have brought about a different evening paper. Still less will there be competition between London and New York, where yet another important condition, the time, is different. One may almost venture to say that the more the divergence increases, the more is the competition reduced, and that the great need is to strike out new lines by new mutations. There is no need to fear that all may be used up; a dozen characters will mutate into millions of combinations.

Geographical difficulties also appear with characters. The same character may appear, not only in two or more groups, but in regions that are separate from one another. Thus Spaltenpollen (using LINDAU's term) is found in *Ebermaiera* (*Nelsonioideae*) in INDOMALAYA and BRAZIL, in *Blepharis* (*Acantheae*) largely African, and in *Aphelandra* (*Aphelandreae*), which is American only.

There are also cases of tribal difference with the same pollen character. *Hygrophila* and *Brillantaisia* (A 3) show the same pattern as *Pseudobarleria* (A 4) and *Strobilanthes* (A 5). *Dicliptera* and *Hypoestes* belong to B 14a, while *Pseu-*

deranthemum is B 13, and *Odontonema* is B 14b. There is considerable variety among the smaller genera near the foot of the family, but what we may see among the 20 leaders in their 14 tribes goes to show that one pollen character, or probably any other character, is useless as a distinguishing mark unless backed up by many others. This well known axiom in taxonomy is now showing itself more susceptible to a proper explanation. If we imagine that characters are handed down from the ancestry, probably as potentialities, one need no longer look upon it as a surprise, difficult of explanation, if any character turn up anywhere, as it was when they had to be formed by selection, and one could find no reason for that selection.

There are many features of interest in these pollen patterns, were space available to go into the matter. The important thing in the present connection is the evidence that they give for the acquisition of characters by heredity from ancestors, though very often these same ancestors showed no sign of possessing them. It is quite possible that not only must there be certain external conditions present in order to bring out a character from the potentialities that are carried, but that one character can only follow something else, or may be determined by something that has occurred in the ancestral history. There is a vast field open for investigation. There are probably some mathematical laws concerned, but the writer has so far failed to trace any, though he is always on the look out for such, and found them in the laws of ASA. The old ideas of relationship, based upon structural characters only, will have to be revised, now that it is evident that mutation goes in this dichotomous and divergent manner. The same thing may reasonably be expected to hold in animals (cf. *AA*, chap. XIX, p. 200 and pp. 237, 242), and if this is found to be the case, may not be without influence in matters of religion and politics.

The divergence, whose appearance seems to be one of the regular features of evolution, and which caused us in *Evol.* to give the book the full title of *Evolution by Divergent Mutation*, seems, upon the whole, to be more marked (?affecting more characters at once) as one goes back in time, thus suggesting a more reasonable explanation of the great divergences that mark the first early divisions into Algae, Ferns, Conifers, &c, than the attempt to explain them by selection, involving the destruction of innumerable transitional forms. The whole of the large step from one of these groups to another (including in the total any groups of reasonable size now only found as fossils) was probably taken at one operation.

Complexes. If origin of new genera occurs, as there now seems every reason to believe, by continual dichotomous formation, it is clear that on the whole, the genera should be parents according to size, the largest, the leader of the family, having the greatest number of direct descendants. These are separated from it by " greater " or by " smaller " divergences, and we give, or try to give, to what we call the " larger " the title of genera, to the smaller the title of species. It is almost needless to say that many will be so near the line that they will cause dispute.

It also seems very probable that there is little or no acquirement of new characters by the new beginners—the very small genera—through the agency of selection, which in fact is put out of court by the very small numbers concerned. Any characters that are shown by any genus must have been handed down to it from its ancestors, and the potentiality of any new character must have existed in the ancestor from which the genus that displayed it was immediately descended, but in some kind of recessive condition. It is not necessary to suppose that all characters of all plants existed in some kind of recessive condition in their primeval ancestor, but that that ancestor was carrying something that as it produced one character became thereby capable of producing a second, and perhaps a third (or more), and so on, in somewhat the same way as the genera were formed, so that the possibilities were also continually on the increase. But all characters have been formed in this way, by rules, probably complex, which remain for us to investigate. It must be remembered that the permutations and combinations of quite a small number are very many. Even twelve will give over three millions, so that there is nothing out of the way in the variety shown by nature.

In their descent, the characters behave in such a complex or intermingled way, that the genera that are thus formed are liable, *when they grow large*, to make what we may term a complex by showing, in some of their species, characters that we are accustomed to regard as belonging to some other related genera. The genus A may start very well, with a cleancut set of characters which are all its own, and then will gradually grow larger, cover more country, come into more varied conditions, and produce more species, and perhaps new genera. These genera may perhaps inherit from their more distant ancestors characters that until that time have been confined to other genera. This at once brings in complications, and it is very common also to find that the new appearance of the character is not geographically connected with any of its older appearances. In *Grumilea*, for example, which is often made a separate genus in the tribe *Psychotrieae* of *Rubiaceae* on account of its ruminate endosperm, the effect of accepting this as a generic character is to bring into the genus different groups of species that show such endosperm, but are not connected at all geographically, the intervening space being filled only by species of *Psychotria* which do not show such endosperm. Cf. the subgenera of *Rhamnus*, p. 107.

If the view that we are here putting forward be adopted, that the big genera are carrying the potentialities of all the characters that may be seen in the family, the matter is simple enough. The small and comparatively recent members of the *Rubiaceae* show certain characters that mark *their few species*, but as they grow larger, they produce, out of the Pandora's box, more and more characters in so far as these are forthcoming there, and as the number of species exceeds the number of available characters, there will tend to be duplication of individual characters every now and then. The result of this is the complex frequently seen with a large genus. Baillon in fact was justified in his remark that it would save a lot of labour and trouble to unite the whole group of *Psychotrieae* as one genus.

What happens in the formation of a complex is perhaps something like this. *When young*, the genera that now compose it were probably quite separate in their characters. Genus A might begin with characters 1, 2, 3, 4, 5 taken from the parent, genus B with 6-10, but in some of the later mutations (for of course all would start as single species, so that there would be little difficulty in defining their characters; it is only as new species begin to bring in more characters that the difficulty of defining the genus increases) a character or two belonging to another genus of the group might put in an appearance in some of the species. At first local, these species would grow and produce new ones, and if the character proved persistent, would soon complicate matters as to the generic rank of the genus or species concerned. To explain the matter reasonably, some system by which all characters are directly handed down from above seems the most simple.

The overlapping of characters seems to increase with age, and often to have nothing to do with geographical propinquity. *Dianthera*, one of the largest of the *Justicia p. p.* genera, and accepted as a genus by LINNAEUS himself, its author, is distinguished from *Justicia* proper mainly by blunt (as against spurred, or at least acute) anther loculi, and by its American dispersal as against chiefly old world. But there are exceptions in most of the characters given, and the anther loculi in *Dianthera* are at times acute. With a few exceptions, however, *Dianthera* is a well marked and well located genus. But the most important feature of these phenomena is probably the way in which some of the characters of *Justicia* are liable to turn up again in unexpected places in other genera, and that without any reason that one can at present comprehend. It is this phenomenon that we have usually in view when we talk about a complex, and its simplest explanation seems to be that all characters that may show anywhere in a family are handed down from the head of the family, and are not picked up in a casual way by selection of those plants that show the most advantageous variations. It is hardly too much to say that there is little or no evidence of any advantage being possessed by one genus over another, and still less one family over another. Their differences in size and in dispersal are due to their obedience to the laws of ASA, as has now been abundantly shown in *AA*, *Evol.*, and the present book.

Looking through the genera of any family that are arranged in order of size, one usually notes genera at frequent intervals that are p. p. of the head of the family, *e. g.* of *Justicia*. Their placing depends upon the general judgment of taxonomists, for they possess some, but not all, of the characters of *Justicia*, sometimes more, sometimes fewer, and we are trying to indicate that the phenomenon depends upon the laws that regulate the incidence of characters, all being the descendants, direct or indirect, of *Justicia*, from which they inherited characters. Genera are artificial divisions, made at what seem to be the more marked points of separation, and often depend upon judgments arrived at only after much dispute, and often not universally adhered to.

Taking together all the figures that we have given, including those for average size of genus in each tribe (p. 215), and for number of genera in each, it is evident that the arithmetical regularity, so conspicuous in the whole family, or even in the sections A and B, soon disappears when structural taxonomy is brought in to divide up the family. The same thing is true of the geographical distribution, which becomes more incongruous with every fresh division. All families seem to behave in the same way in this respect, becoming confused when our present subgroups are made, yet adding up to an arithmetical regularity in most cases, and with distribution about as continuous as is allowed by the geological and other changes that have affected the past history. It is evident, therefore, that it is our system of subdivision that is at fault, by reason of the artificiality that we have shown to be present, and which is due to its being based upon structural characters which are liable to divergence at any mutation. To be natural, a system will have to pay much greater attention to distribution, and to the curves formed, especially the logarithmic (*cf.* p. 262, below, also *AA*, pp. 241-3, *Evol.* p. 33). A thorough study of incidence of character, and of the rules that govern it, is needed, and it is quite possible that a genetic and morphological study of the pollen patterns in *Acanthaceae* would be remunerative.

The tribes of Acanthoideae. Our present classification does not agree with anything but the structural characters of its subjects, and requires wholesale and widespread destruction of transitional forms, and these not necessarily in the same neighbourhood, but often over great areas of the world (why?). But it also does not agree with the arithmetical curves that have been shown to be the rule, unless in this case one add up all the taxonomic groups into one, and deal with the family as a whole. In this connection it is instructive to lay out the actual sizes of the genera (by my *Dict.* as usual) as they are arranged by LINDAU, and in the actual order in which he places them by structural relationship. Taking only group IV, we get :

Tribe	Genera by size	Average size	Nº
IV. A, 1	2, 1, 10, 1, 1, 1	2.6	6
2	2	2	1
3	12, 35, 40, 1, 1, 6	15.8	6
4	4, 1, 12, 1, 1, 15	5.6	6
5	5, 15, 8, 50, 4, 1, 1, 2, 25, 5, 5, 1 180, 1	21.6	14
6	1, 5, 6, 2, 3, 1, 8, 1, 1, 1, 2, 225, 25, 5, 2	19.2	15
7	1, 2, 80, 12, 150, 2, 12, 1, 10	30	9
B 8	5, 1, 80, 25, 7, 5, 25	21.1	7
9	1, 1, 1, 20, 1, 80, 10, 1, 1	12.9	9
10	15, 20, 2, 15, 6, 3	10.1	6
11	3, 1, 2, 35, 3, 1, 4, 3	6.5	8
12.	5, 6, 10, 12, 2, 5, 5, 6, 3	6	9
13	2, 60, 6	22.6	3
14a	15, 8, 25, 100, 90, 2, 2	34.5	7
b	1, 5, 6, 30, 2, 1, 1, 1, 1, 8, 1, 1, 2, 8, 1, 3, 1, 3, 25, 3, 7, 2, 1, 1	4.8	24
c	4, 3, 1, 3	3.75	4
	or all three together, 10.5, 35		
15a	1, 1, 2, 1, 2, 5	2	6
b	6, 2, 2, 30, 2, 1, 10, 1, 4, 4, 3	5.9	11
16	2, 5, 6, 1, 325, 1, 10, 25, 45, 2, 1, 7	35.8	12

If the sizes of genera in the tribes are arranged in order we get :

35.8, 34.5, 30, 22.6, 21.6, 21.1, 19.2, 15.8, 12.9, 10.1, 6.5, 6, 5.9, 5.6, 4.8, 3.75, 2.6, 2,2.

a very great range of sizes, for which there is nothing whatsoever to account.

One criticism that may be made is that in this list we have left out all new genera since published, but these are nearly all twos and ones, and could hardly be parents.

To look at the numbers just given, and the same thing may be seen almost anywhere, one would never suspect that they were definitely connected upon an arithmetical plan —the law of compound interest. The divergences that take place rob a purely structural arrangement of its naturalness, and the same character may turn up almost anywhere, with the necessary combination of circumstances. If the characters of a family are all in the keeping of its original parent, this is what we should at times expect, though one must not forget what we suggested as to increase in number of possible characters from older genera downwards. There is probably some mathematical rule controlling it, but the writer has not been fortunate enough to stumble upon it.

The first three sub-families. These are but trifling in size, compared to those we have considered; they contain

I. *Nelsonioideae* (ovules ∞; retinacula papilla-shaped)		
Ebermaiera (Staurogyne)	45	Indomal., Brazil
Elytraria (Tubiflora)	5	warm countries
Nelsonia	1	palaeotrop.
Zenkerina	1	W. Afr.
Ophiorrhiziphyllum	1	Martaban
Ixtlania	1	Mexico
II. *Mendoncioideae* (ov. 4; seeds not exceeding 2; drupe; no retinac.)		
Mendoncia	25	trop. Am.
Afromendoncia	5	trop. Afr.
Lirayea	1	trop. Afr.
Gilletiella	1	Congo
Monachochlamys	1	Madagascar
III. *Thunbergioideae* (ov. 4; capsule; retinacula papilla-shaped)		
Thunbergia	150	palaeotrop., espec. Africa
Pseudocalyx	1	Madagascar, Nossi-bé
Meyenia	1	East Indies

However natural these groups might be, they are very small, and cannot be regarded as in the same rank as even *Contortae*. They are based purely upon structural features, and it is clear at a glance that their geographical relationships are rather impossible. The differences in character are principally those between a capsule and a drupe, and between few and ∞ ovules, both of them common mutational differences between groups of genera or species, large or small. As regards the drupe and capsule, *cf. Evol.* pp. 122-126. One cannot fit these groups into any system of evolution by dichotomy, at least without enormous destruction, which is put out of court by the very small size of most of the genera, and their lack of geographical relation. They are convenient divisions for the identification of plants, but probably nothing more; it would seem much more probable that the peculiar divergent characters had been handed down from the ancestry, and that at some point a double divergence gave rise for example to *Nelsonia*, and at another the same thing gave *Ixtlania*.

General. We have suggested the incidence that an inductive study of dispersal seems likely to have upon our taxonomic studies. Classification, as such, may of course be based upon any characters that occur in different places and with different degrees of frequency. But if it aim, as at present it does, at being a genetic and natural classification as well, it clearly cannot afford to leave out the great amount of evidence furnished by geography and genetics, and cannot continue to depend, as it does now, almost entirely upon structural evidence.

We are not suggesting that our present system is all wrong or all unnatural, but simply that the way in which the leaders behave makes a " natural " classification almost an impossibility at the present time. They give the general structural characters to the subdivisions of families, tribes, genera, and even of species, but they themselves show the closest possible relationships, though structurally so different. Sub-families and tribes simply owe their origin to the fact that the mutations that took place when the family was very young produced characters that remained more or less fixed in inheritance, and so were handed down to an important proportion of the later genera of the family. The same characters, however, if they appeared later in the life of a family, would be handed down to fewer descendants, and would be regarded as less important in that family. But till we have some knowledge of the laws of incidence of character, no more definite statement can be made. A natural grouping we must have, as we must have chromosome maps, but the object of such things is not the identification of the plants themselves, and for practical purposes of this kind it will be much better to have some kind of artificial system, but one that is universally agreed to, working at the " natural " system as a separate branch of botany; most enquirers simply want to find out the name of a plant, and something about it. When any structural characters are liable, as we have now seen, to be suddenly and completely lost, in passing from father to son, a natural system becomes a very difficult thing to construct. It is like trying to classify the population of a town by physical or mental characters, and expecting to get their relationships by the same process.

Growth upon the dichotomous system which we have shown to be the rule means that at every stage—every birth of a new form—the new chain of descendants starting there should ultimately be exactly like the one starting from the stage just above. Each should form a hollow curve, giving a logarithmic straight line, which is just what our groupings, formed upon structural characters, fail to do. The two are incompatible.

When the mutation giving rise to some new form is unusually well marked, we consider the new form as the head, or type of a family, tribe, genus, or species, according to our valuation. As there is no certainty that the chief characters of any one thing will all be shown by all of its immediate descendants, an element of great insecurity is introduced into the making of monogeneric families, &c, by breaking away from the more cautious procedure of Bentham and Hooker; some of the new families, like *Lardizábalaceae* or *Phrymaceae*, are of rather dubious standing.

The Growth of the Acanthaceae. Justicia and *Ruellia*, being the largest genera in the family, were presumably its oldest, and the first important event to occur in its history was the splitting off of the latter from the former by an early, divergent, but simple, mutation, the results of which show in the fact that practically all members of the family have their aestivation either imbricate or convolute. Thus the very first mutation split the family into its two chief subdivisions, and we have already seen in Chapter VIII, and App. III of *Evol.*, p. 199, that this is the rule throughout the whole taxonomy. Thus, *in the Acanthaceae*, but not necessarily anywhere else, the divergence between imbrication and convolution has become a sub-family or super-tribe character. It owes this position simply to the fact that it was a very early divergence to occur in the family, and once formed, was largely so persistent in the heredity that practically all the family show one or the other type of aestivation. The same identical change may be found in many other families, as for example in *Gentianaceae* it distinguishes some of the *Gentianoideae* from others of the same sub-family, while in yet other families it may occupy an even lower position, simply because there it is of more recent acquisition or occurrence. Whilst on the whole characters of the essential organs of the flower are the most likely to be of early or of more permanent acquisition, and therefore of great importance, *any* character may at times be found in this position. As yet, we have no knowledge of the rules of character-incidence. Any character that by its divergent forms will divide a family into two main portions is gladly seized upon for that purpose. It is the age of the character *in its family* that matters, when reflected, as it is in many cases, by inheritance in many smaller genera.

Being in a tropical family, and therefore perhaps, not so liable to invasions of fatally cold weather, and being, as the oldest genera, by much the most widely dispersed into various regions and conditions, there was little likelihood of any complete extermination of *Justicia* or *Ruellia*, once they had passed the very early stages. But in the changes that went on in the early and long-drawn-out stages of the family, it is by no means impossible that *genera that had not spread so far as these two* (*i. e.* younger genera) might be exterminated, so that they are now found only, if at all, as fossils. These fossils, however, would only represent a *sideline*, and must not be supposed ancestral to any living *Acanthaceae*, unless they were themselves widespread (old), and even then only with some doubt. In this connection, YULE's description of a " cataclysm " in (**158**, p. 23), should be read, where he shows that upon a scale representing the life of the vegetable kingdom, the last glacial period, estimated as of the nature of 20,000 years, would appear to be absolutely sudden, yet from a dispersal point of view, it produced its effects in many directions and at different times.

As each genus, when it is formed and has reached some little size and importance, tends to give rise to another, the lines of descent will continually increase in number, and that more and more rapidly the older the family grows. Thus in the early days, and of course always among the now large genera then produced, there are very few lines of descent, so that the production of genera of the same age and size is unlikely. But as we come further down the list, the probabilities of such things will continually increase, and duplicates, of the same general size and age, will begin to appear, as one may see in the lists of the *Compositae* in Chap. VIII. Below this point they will rapidly increase, till at the very foot there is a large display of " ones ", which probably remain longer in that stage, when they are just beginners, than in the stage of two, or of higher numbers. The hollow curve, forming the logarithmic straight line, is thus automatically and inevitably produced.

The top genus will likely produce descendants at a rate a good deal quicker than the next (say about double; *cf.* p. 335) and so on all the way down, so that a considerable fraction of a family may be the direct and immediate offspring of the original parent. It would therefore seem not improbable that the hollow curve of genera that are geographically connected, like the *Acanthaceae* of one continent, or part of a continent, or an island, &c, is really also a curve of those that are genetically connected, complicated by the intrusion into that continent, or other area, of more than one of the widely ranging big genera near the head of the family.

Justicia and *Ruellia* will get a long start of their descendants, especially the former, but sooner or later they will themselves give rise to new descendants, and the mutations by which they are formed will almost certainly take them into other new subgroups. The new genera will repeat the behaviour of their parents, but at a considerable distance behind, for their early stages must evidently be passed through very slowly, until they have established themselves in some numbers and upon a reasonable amount of space (*cf.* *AA.*, p. 34). This process will be repeated as time goes on, the family continually growing larger, as the parent survives as well as the offspring; and all produce new species, so that all the genera will grow continually in size, the older of course growing more and more rapidly as they increase in size, which means also in potential parenthood. While a genus of one species is increasing to two, a genus of 50 *may* become one of 100, and so on; hence the wide separations between numbers of species in the large genera at the tops of the lists, for example in any of those in Chap. VIII, and the large overlapping at the foot of a list, where the increase is not in species, but in genera, whose births are due to the ever-increasing potential parents.

The process of growth of a family is thus at bottom a fairly simple one, but it is of course almost at once liable to the complications introduced by the occurrence of barriers, whether physical, climatic, or ecological. We have already said a good deal about this in *AA*, pp. 12, 13, 16, 20, 21, and especially Chap. V, p. 32. In the earlier days of a genus, when it is small and local, it will not have to undergo much variety in conditions, but the variety will continually increase as it spreads into more and more new places and conditions, until gradually its obedience to the laws of ASA, which would be very close when it was small and young, will be more and more interfered with by new conditions, barriers, &c, &c.

This must suffice as a brief sketch of the probable process of growth and dispersal. It is not altogether unlike the distribution of slops that one may see going on at the back of an old-fashioned cottage. A large pailful (corresponding to the larger and older subgroup of the *Imbricatae*) is thrown out, and goes a long way in various directions, while the smaller pailful (*Contortae*) which follows it goes more or less the same way, but does not reach so far (as we have seen above), though at some spots, for some probably trivial local reason or accident, it may go even further than its predecessor.

CHAPTER X

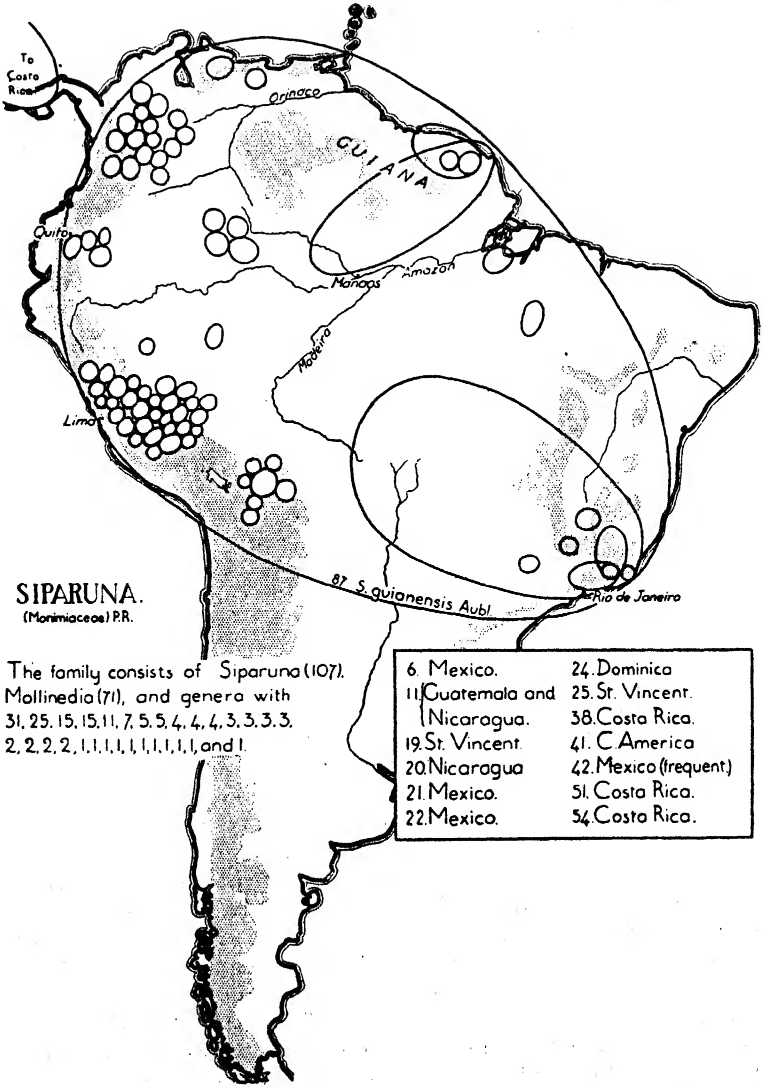
The classification and distribution of the Monimiaceae

We have shown that small genera, being young and more or less confined to one continent, are less likely to have been interfered with in their obedience to the laws of ASA and of dichotomous division; and in this connection it will be worth while also to look at a small family, the *Monimiaceae*. It is classified, structurally and geographically, upon pp. 228 to 230, and when we compare these groupings, it is evident that each was drawn up without reference to the other. To begin with, there is no large genus like *Senecio* or *Justicia* that leads the family over most of its range. The nearest approach to such a thing is *Siparuna* (map at p. 224), which covers most of the American dispersal, but does not occur in the old world. It is followed in BRAZIL by the second genus *Mollinedia*, differing chiefly in the fact that its anthers open by slits, not by valves. These are the marks of the two sub-families, into which *Monimiaceae* are divided.

These characters, as so constantly occurs, not only separate the second genus (though sometimes only the third or fourth) from the first, but being handed down to a number of descendants, they give the characters to two separate sub-families, though themselves evidently those of father and son. This simple fact, abundantly demonstrated in Chap. VIII, that the leaders of the subgroups of a family are mainly to be found in the few, and obviously closely related, genera at the head of the family, is almost enough to prove our theory of "downward" evolution from family to species; and the dispersal area of *Mollinedia*, which only goes beyond that of *Siparuna* at its southernmost part, where the conditions of life are rather different, fits in well with this theory, though taxonomically the two genera, as we shall see, are widely separated.

All the 36 genera which we now consider as belonging to *Monimiaceae* show one or the other of these divergent anther openings, together with sufficient general resemblance in other structural features to make it not improbable that they are all of one family. We therefore use this divergence, evidently very old in the family, and one which has persisted in the inheritance, as the main mark of the two sub-families, and it must be particularly noted that it occurs in the two oldest genera, whose regions of occurrence overlap. *Mollinedia* must have been born at some region south of the birthplace of *Siparuna*, at a time when that genus comprised only two to perhaps five species. The most widely dispersed, and therefore probably the oldest species, *S. guianensis*, covers the whole range of the genus in S. AMERICA, and one may expect the birthplace of *Mollinedia* to be somewhere within its range.

The dispersal of *Siparuna* is shown in a general way for South America, its most important centre, in the map at p. 224. It also reaches Mexico and the West Indian islands of Dominica and St Vincent (probably therefore by way of Trinidad). The striking feature in its dispersal map is the great crowd of localised endemic species at various points in the Andes, especially near the Isthmus of Panama, and in Peru. These are not shown in the map in their exact location, but are massed together in such a way as to give a good general idea of their dispersal. But it is fairly evident here that in so mountainous a country, the most recently formed species will not only be very slow in spreading on account of their small number of individuals, but will also be severely handicapped by the rapid and local changes of conditions, such as of soil with its composition and consistency, of slope with its direction and its degree of insolation, of water supply with its frequency and its differences at different times and places, and so on. To all these differences a new species will have to adapt itself as it spreads. Much time must therefore be allowed, and it may be a very long while before the species escapes from its beginnings, which are always a case of specialisation and localisation.



SIPARUNA.
(Monimiaceae) P.R.

The family consists of Siparuna (107). Mollinedia (71), and genera with 31. 25. 15. 15. 11. 7. 5. 5. 4. 4. 4. 3. 3. 3. 3. 2. 2. 2. 2. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1, and 1.

6. Mexico.
11. Guatemala and Nicaragua.
19. St. Vincent.
20. Nicaragua
21. Mexico.
22. Mexico.
24. Dominica
25. St. Vincent.
38. Costa Rica.
41. C. America
42. Mexico (frequent.)
51. Costa Rica.
54. Costa Rica.

Upon my working hypothesis (p. 96), the birth was at some place where unusual conditions were encountered. As the present dispersal of *Mollinedia*, while largely included in that of *Siparuna*, goes beyond it mainly to the south, where it reaches MONTEVIDEO instead of RIO, one may imagine that perhaps colder winters formed part of the stimulus that gave birth to it. But taxonomically it belongs to *Monimioideae-Mollinedieae*, while *Siparuna* belongs to *Atherospermoideae-Siparuneae*, though evidently so closely related. They are thus not only in separate tribes, but in separate sub-families. Their chief difference, the way in which the anthers dehisce, is a perfectly simple mutation, which could hardly be anything else. *Siparuna* evidently carried the slit-opening as a recessive character, or potentiality, and gave it to *Mollinedia* full-blown. Had it been later in appearance in the family, it might only have been a separation mark of two tribes, or even of two genera, or only of two species. Its rank here as a sub-family mark is merely due to its age *in this family*, and gives no guarantee that it is of this, or of any other value, anywhere else.

This is the usual type of family formation, as the lists of the positions of leading genera, given on pp. 173, 174, clearly show. So far, there is no great difficulty about the grouping of the *Monimiaceae*, but as we begin to break it up upon structural grounds, the geographical and arithmetical difficulties continually increase.

But if *Siparuna* and *Mollinedia* thus stand in the relation of father and son, as seems practically certain, and if in our taxonomy we separate them so widely as we do, being in most cases compelled to put the first two genera of a family into different tribes, or even into what we consider as sub-families, it is clear that our classification, as at present accepted, is artificial. A divergence comes at every mutation, and sometimes we regard the resulting new genus as belonging to the same group as the parent, and sometimes as belonging to, or forming, another group. Yet in origin and in genetic relationship the two are apparently the same. But we consider the characters in one case as being more "important" than in the other, when the difference between the two cases is rather that in one the divergences happened to appear in characters that we were using as marks of a subgroup, and in the other case not so, but affecting something else, which we are inclined to imagine as "less important", though we have no reason for making the assertion, other than their different degree of occurrence in the family, which as yet we do not properly understand, though it is evidently largely a function of age. It is primarily age that gives importance, and the nearer that we are to the largest or oldest genus, the head of the family, the more likely is the divergence to be of subfamily or tribal rank. In fact, one may in a general way say that the nearer to the top that a genus is, and therefore the more species that it comprises, the higher is its rank, for it will have correspondingly more descendant species and genera.

It is clear that each genus in turn is the head of the group that contains all its genetic descendants. Thus the first genus A gives rise all the time to species of A, but also, at intervals, to what we regard as new genera, and call successively B, C, D, &c. But we have little or nothing to go upon, *rightfully* to call these particular new species (as they *are*) of a different rank from those that we consider as simply new species of A. When there are many descendants showing these particular characters, and with other descendants showing well marked differences also, we have some reason for calling B a new genus, for from a practical, classificatory, point of view, the more we can break up the vast mass of species into genera and other divisions, the better. But we lack any really sound basis for definition of genus or species.

A natural or genetic classification should really be the expression of this continual dichotomy, and obviously would be impossible to make at the present time. It is clear that we have not arrived at that stage in our knowledge of past events, and of the laws that govern such things, that would enable us even to begin with any confidence a map of past evolution, and a great amount of work will yet have to be done. Geographical distribution, structural features, genetic relationships, and other things will have to be made out for most genera, and all will have to be fitted into one harmonious whole, showing everywhere the curves of compound interest, or something closely similar. One cannot but feel that there is some general law underlying the incidence of mutations. MENDEL's law, GALTON's law, the laws of ASA and of dichotomy all point so clearly to some general mathematical law underlying the whole, that it is quite possible that when we gain some further knowledge, especially perhaps of the law of incidence of mutation, we may begin to perceive it.

But though such a system would be of great practical value to breeders and others, a natural system would be of little or no use for the actual identification of plants, and for that, which after all is one of the most important requirements, an artificial system must be used. Obviously, therefore, this should be the most convenient possible. But as yet, each new advance to the far away goal of a natural system has on the whole been a falling away from this object, and one that becomes continually worse rather than better. Even the admittedly artificial system of LINNAEUS brought together things like *Cruciferae*, or grasses, and more and more natural groupings show in each new system, but they become more and more difficult to use for practical purposes, because of the continually increasing numbers of exceptions, which are inevitable if characters are handed down from above, and in what as yet looks like a casual way. The average interested enquirer does not care about exact relationships; he wants to know the name of his plant, and something about it. We might even go so far as to suggest that a public herbarium, where at present the untrained enquirer is helpless, might have a public " enquirer's room ", with a local, or a more general, herbarium, as local circumstances dictate. In this there might be a key to the flora, with pictures showing the divergences at every stage, leading gradually down to the individual plants, which should be mounted under glass or cellophane. In this room there might be a small library of books of reference, folklore, and other subjects, and pictures and descriptions of ecological associations to which the various plants belong, and so on.

For some people, the old theory of very gradual change has been replaced by a supposition of small, but distinct, changes of less than specific rank, due to small mutations. We have seen in our consideration of teratology (p. 100) that such mutations are common enough. It is therefore probable that they do occur in a more permanent form, as we have suggested for actual specific mutations, and that they give rise to varieties, of different degrees of importance in reference to species. But there seems no evidence that other small mutations must follow in such a way that the variety must ultimately become a new species. A small variation does not usually make parent and child mutually sterile, and why should one variation only, in a series, be able to cross the sterility line? Probably it can, but if so, it will probably be one that would have made the specific difference by itself alone, without needing to be led up to by smaller, varietal, mutations. The method of evolution thus suggested has always appeared quite illogical to the writer, who since 1907 (**131-2**) has always stipulated for the whole change between one species or genus and another to be made at a single mutation, though there will probably be a few cumulative cases. This theory is now well supported by evidence, such as that of the formation of most endemics, or the formation of the early genera of a family such as we have seen in Chap. VIII. Under any theory of evolution, two characters, however divergent they may be, have got to unite somewhere in the past, and if, as so commonly happens, they are incompatible, then one must be recessive, the other dominant, in some ancestor, or, as under selection, we must call in destruction of transitions, often upon a truly colossal scale, for which we have no evidence available.

Upon pp. 228 and 229 we have given two groupings, one taxonomic, one geographical but also with genera in order of size, while upon p. 230 we have given the usual list of the few earliest genera in the family, to show the incongruity of all these groupings. The geographical facts are more absolute than the structural, so that it is the latter that will probably be those to give way most often.

Monimiaceae, taxonomically grouped

Sub-family I. MONIMIOIDEAE (anthers opening by slits)

Tribe I. *Hortonieae*	Spp.	
1. Hortonia	3	Ceylon
2. Peumus	1	Chile
3. Amborella	1	New Caledonia
4. Hedycarya	20	Austr., N. Cal., N. Z., Polynes.
5. Levieria	6	N. Guin., Moluccas, Queensland
6. Decarydendron	1	Madagascar
7. Hedycariopsis	1	Madagascar

Tribe II. *Trimenieae*

8. Trimenia	4	Fiji, &c
9. Piptocalyx	1	N. S. Wales
10. Xymalos	2	S. and trop. Afr.

Tribe III. *Mollinedieae*

11. Macropeplus	1	E. Brazil
12. Mollinedia	80	Trop. Am.
13. Macrotorus	1	Rio de Janeiro
14. Ephippiandra	1	Madagascar
15. Matthaea	15	Malaya, Phils.
16. Steganthera	15	New Guin., Celebes, &c
17. Anthobembix	4	New Guin.
18. Tetrasynandra	3	E. Australia
19. Wilkiea	5	E. Australia
20. Kibara	30	Burma, Sumatra to Phils.
21. Lauterbachia	1	New Guin.
22. Carnegiea	1	New Caledonia

Tribe IV. *Monimieae*

23. Palmeria	10	E. Austr., N. Guin., Celebes
24. Canaca	1	New Caled.
25. Monimia	4	Madagascar, Mascarenes
26. Tambourissa	25	Madagascar, Mascarenes
27. Schrameckia	1	Madagascar
28. Hennecartia	1	Paraguay, S. Brazil

Sub-family II. ATHEROSPERMOIDEAE (anthers by valves)

Tribe V. *Laurelieae*

29. Nemuaron	2	New Caled.
30. Daphnandra	4	Queensland, N. S. Wales
31. Laurelia	3	Chile, Peru, New Zealand
32. Atherosperma	2	E. Austr., Tasmania
33. Doryphora	1	New S. Wales

Tribe VI. *Siparuneae*

34. Siparuna	120	Trop. Am., W. Indies
35. Glossocalyx	3	W. Africa
36. Bracteanthus	1	Amazon region

Monimiaceae, geographically grouped (in order of size)

America	Subgroup	Spp.	
1. Siparuna	II. 6	120	Trop. Am., W. I.
2. Mollinedia	I. 3	80	Trop. Am.
3. Laurelia	II. 5	3	Chile, Peru, New Zealand
4. Peumus	I. 1	1	Chile
5. Macropeplus	I. 3	1	E. Brazil
6. Macrotorus	I. 3	1	Rio de Janeiro
7. Hennecartia	I. 4	1	Paraguay, S. Brazil
8. Bracteanthus	II. 6	1	Amazon region

Africa	Subgroup	Spp.	
9. Glossocalyx	II. 6	3	W. Africa
10. Xymalos	I. 2	2	S. and trop. Afr.
Madagascar			
11. Tambourissa	I. 4	25	Madagascar, Mascarenes
12. Monimia	I. 4	4	Madagascar, Mascarenes
13. Decarydendron	I. 1	1	Madagascar
14. Hedycariopsis	I. 1	1	Madagascar
15. Ephippiandra	I. 3	1	Madagascar
16. Schrameckia	I. 4	1	Madagascar
Ceylon			
17. Hortonia	I. 1	3	Ceylon, SW and central
Malaya, Polynesia, Australia			
18. Kibara	I. 3	30	Burma, Sumatra to Phils.
19. Hedycarya	I. 1	20	Austr., N. Z., Polynes.
20. Matthea	I. 3	15	Malaya, Phils.
21. Steganthera	I. 3	15	New Guin., Celebes, &c
22. Palmeraia	I. 4	10	E. Austr., New Guin., Celeb.
23. Levieria	I. 1	6	New Guin., Moluccas, Qnsld
24. Wilkiea	I. 3	5	E. Austr.
25. Trimenia	I. 2	4	Fiji
26. Anthobembix	I. 3	4	New Guin.
27. Daphnandra	II. 5	4	Queensland, N. S. Wales
28. Tetrasynandra	I. 3	3	E. Austr.
29. Laurelia	II. 5	3	Chile, Peru, New Zealand[1]
30. Nemuaron	II. 5	2	New Caledonia
31. Atherosperma	II. 5	2	E. Austr., Tasmania
32. Amborella	I. 1	1	New Caledonia
33. Piptocalyx	I. 2	1	New S. Wales
34. Lauterbachia	I. 3	1	New Guinea
35. Carnegiea	I. 3	1	New Caledonia
36. Canaca	I. 4	1	New Caledonia
37. Doryphora	II. 5	1	New S. Wales

Early genera of the Monimiaceae, by size in the world

1. Siparuna	120	Trop. Am.	II. 6	Heading *Siparuneae*
2. Mollinedia	80	Trop. Am.	I. 3	Heading *Mollinedieae*
3. Kibara	30	Burm. Mal. Phils.	I. 3	2nd Mollin.
4. Tambourissa	25	Madagascar	I. 4	Heading *Monimieae*
5. Hedycarya	20	Austr. N. Z. Polyn.	I. 1	Heading *Hortonieae*
6. Matthaea	15	Malaya, Phils.	I. 3	3rd Mollin.
7. Steganthera	15	N. G., Cel., &c	1. 3	4th Mollin.

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[1] A repetition of No. 3, making the total 37 against 36.

The other two tribes are headed by genera with four species each, *Trimenia* (I. 2) in FIJI, &c, *Daphnandra* (II. 5) in E. AUSTRALIA.

It is clear that among the leading genera, with few exceptions, the heads of subgroups must be found, and equally clear that each genus in general must have its parent in those above it; proper geographical relationships must also be evident. A very early and large parental genus might by direct divergences give rise to smaller heads of subgroups. But some geographical connection, even if now extinct, is required, if we are to work upon any theory of evolution, and what is most in favour at the present time is the destruction of the connecting links by lack of adaptation or other unfavourable attributes. In the colder temperate climates, where cold periods have alternated with warmer, and the plants have surged to and fro, such a thing is more possible, but the difficulties are just as marked in tropical families, where nothing of this kind seems to have occurred recently enough to have been within the lifetime of most of their members.

We have thus got various groupings of the *Monimiaceae*, which require to be harmonised in some way, and the same thing is equally true of many other families. All the work that we have done for many years upon endemism, upon distribution in general, upon curves of origin, and so on, which is described in many papers, and in *AA* and in *Evol.*, goes to show that we have no justification for the calling in of wholesale destruction of transitional or intermediate forms. This is especially the case with the great areas that are often concerned, and when the discontinuous plants are, as most commonly is the case, so small as genera that they must either be too young to have been alive at the time of separation, or must have suffered great destruction of species to bring them down to their present small size. Not only so, but the destruction would be required in very many directions, and vast geological and climatic changes would be necessary. We shall better understand our problems by discarding as much as possible of this speculation, which is so attractive that it has always been the bane of work upon origin and distribution. We must work by inductive methods, which we have now shown to be very applicable in such cases, and work by aid of the laws of ASA and of growth by dichotomy, and with the knowledge that our present system of classification is often artificial.

Let us look at some of the many incongruities in these lists. Taking first the early genera, we find those at the top heading subgroups as usual. This of course is what one should expect, but up to the present the size of a genus as an important generic character has been entirely neglected. It is very noticeable that the large genera of a family tend to scatter themselves among any large structural groups that may be made, so that one cannot construct tribes without reference to the characters of these genera. This alone shows how much more important in classification is a large genus than a small one. Taking this list alone, it is clear that *Kibara* is too large to have sprung, at so great a distance away, from either *Siparuna* or *Mollinedia*, which are not so very much older than it is. The later genera, in fact, after the first two, have no geographical connection with them, *within the family*. They are separated by immense distances, and in two directions, from BRAZIL to MADAGASCAR, and to MALAYA and AUSTRALIA-NEW ZEALAND. But to make a natural grouping, upon genetic lines, there must either be some geographical continuity among the areas occupied, or there must have been some overriding genus of the group, or more probably of the family, *or even of some allied family like Lauraceae*, that might give rise to similar things in widely separated localities. With the vast numbers of permutations and combinations that are available, it is extremely unlikely that an overriding genus should belong to any family that was not, structurally, fairly close to *Monimiaceae*. It is fairly evident that any new form tends to inherit its characters (though a few are marked by distinct divergence) from its ancestors by something like GALTON's law of ½ from parents, ¼ from grandparents, and so on, as indeed one might almost expect.

Failing one of these occurrences, we are forced to demand great selective destruction that will kill out all the intermediate geographical links, frequently whether transitional or not. There is very little evidence indeed for such happenings, and certainly not for their occurrence in the numbers and directions desired, whilst there is enormous difficulty —geographical, geological, and meteorological—in the way of its occurrence. There is also nothing in the structural differences to show that there is any likelihood that it should happen.

The primary distinction into *Monimioideae* and *Atherospermoideae* has always been maintained, for the whole family, supposedly natural, shows one or the other type of anther dehiscence; but the members of *Monimioideae* have at times been shuffled. But one cannot make them up by structural characters so that these will agree with the geographical arrangement, to say nothing of the arithmetical.

Siparuna is the largest genus, yet has apparently only two other genera carrying its characters (*cf*. *Senecio*, p. 177), one in W. AFRICA, one in the AMAZON region, while the genus itself is purely American. *Mollinedia*, its most evident direct descendant, is widely separated taxonomically, and the rest of the American members of the family (*cf*. p. 229) are scattered over a number of tribes, two of which have only one representative each in AMERICA, in each case a monospecific genus.

Mollinedia (31 spp. RIO, 22 adjacent states, 55 altogether in BRAZIL and GUIANA, 16 PERU to MEXICO) covers less range than *Siparuna*, but mainly within the latter, only going beyond it to the south. If evolution went as we have hitherto supposed, species to family, there would be nothing specially surprising in its being placed so far from *Siparuna* taxonomically as it is, but now that it is enormously more probable that it went the other way, from family down to species, and that there must be some geographical links between genera that are related, even if only slight, the whole of the old position becomes untenable. In probable fact, the two genera are father and son, as closely related as is possible, and their ranking in different subfamilies is due to the great structural divergence that marks them. It is not possible to explain by selection, or by small mutations, why the chief divisions of a family have as their heads genera belonging to the first few (by size or age) in the family. Often the first two each head a sub-family.

To find parentage for the other American genera, except *Bracteanthus* in *Siparuneae*, within the limits of dispersal of *Siparuna* itself, is not easy, unless we disregard the taxonomic classification altogether, for, though only seven in number, they belong to the groups *Hortonieae*, *Mollinedieae*, *Monimieae*, and *Laurelieae*, and are all small (young). Those in

Mollinedieae can of course be fathered upon *Mollinedia*, but there is nothing in *Hortonieae* for *Peumus*, nor in *Monimieae* for *Hennecartia*, and they must look for parents to one of the other groups. Going by size, it is clear that the *Atherospermoideae* make no serious approach to a hollow curve, dropping from 120 to 4 in the second place, while *Monimioideae*, with a leader of only 80, show 30, 25, 20, 15, 15, 10, 6, 5, 4, 4, 4, 2/3, 1/2, 13/1, an almost equally improbable curve, especially when broken into its four tribes.

Not only should there be geographical continuity in the family as a whole, but it should also be shown by the members of any sub-family or tribe, if they are in reality descended, directly or indirectly, from their own leading genus. Thus here all the tribes with the possible exception of *Laurelieae*, which itself has no likely leader, are greatly confused when taken from a geographical point of view, as the list on p. 229 shows. The most probable explanation is that all the characters shown in all the genera were handed down by ancestors which carried them in a dominant *or recessive* condition, and that their appearances were often polyphyletic, the same character sometimes appearing more than once in widely separated genera (like *Hibbertia* in AUSTRALIA and *Schumacheria* in CEYLON, described on pp. 145, 146), so that a character might easily be shown without having anything of the same kind in its immediate ancestry. It is possible, too, that it might have an immediate ancestor showing the character, in some nearly related family like the *Lauraceae*.

Or let us take the *Monimiaceae* of MADAGASCAR in the two lists and compare them. *Tambourissa* (25 spp.), *Monimia* (4), and *Schrameckia* (1) are all in the tribe *Monimieae*, but *Decarydendron* and *Hedycariopsis* are in *Hortonieae*, and *Ephippiandra* in *Mollinedieae*. How did so many of the tribes, not always very large ones, come to be represented upon MADAGASCAR? And the question is not made easier by looking at the genera of continental AFRICA, which are only two, with independent areas, *Glossocalyx* in W. AFRICA with 3 spp. and belonging to yet another tribe, the *Siparuneae*, and *Xymalos* with 2 in S. and tropical AFRICA, in the *Trimenieae*. All the groups but the *Laurelieae* occur in this handful of genera, quite separated geographically from the rest of the family!

Another stage eastwards brings us to CEYLON, which has one isolated genus, *Hortonia*, endemic there, with three species, one with an area about 60 miles in diameter, the other two less, as one would expect if one was born from another. Finally, there is a considerable group in MALAYA, AUSTRALIA, NEW CALEDONIA, NEW ZEALAND, and POLYNESIA broken as to area, especially by stretches of sea, but at least forming a possible curve (*Kibara* 30, 20, 15, 15, 10, 6, 5, 3/4, 2/3, 2/2, 6/1). But they belong to the tribes *Hortonieae*, *Trimenieae*, *Mollinedieae*, *Monimieae*, and *Laurelieae*, all the tribes in fact but the one that contains the leader of the family. In any case *Laurelieae* with genera of only 4, 3, 2, 2, 1 is not a group that one would expect to find in CHILE and PERU as well as NEW ZEALAND, when the rest are only in eastern AUSTRALIA and NEW CALEDONIA. NEW CALEDONIA, which is much smaller than MADAGASCAR, shows more tribes than the whole of ASIA.

If we take the individual taxonomic groups, we get the same kind of complications in other ways. *Hortonieae* alone contains genera of 3 CEYLON, 1 CHILE, 1 NEW CALEDONIA, all much too small (young) to have been alive at the formation of the vast oceanic separations. The chief genus is confined to eastern AUSTRALIA and POLYNESIA and NEW ZEALAND, centring with most of its species in NEW CALEDONIA, so that it does not reach, nor even suggest that it ever reached, CEYLON or CHILE. In fact the CEYLON genus is not near any of the real *Monimiaceae*, however wide a view we may take of them. Nor, though not quite so definitely, is *Peumus* in CHILE, though *Laurelia* in *Atherospermoideae-Laureliae* occurs in CHILE, PERU, and NEW ZEALAND. Any of the six taxonomic groups, in fact, will provide almost hopeless problems for the man who works only upon structural resemblance, while the principles that we are advocating here do at least provide some hope of future understanding.

This general occurrence everywhere of so many subgroups, often only represented by one or two very small genera, which may be widely separated geographically from others of the same subgroup, makes it extremely probable that the subgroups are not natural, but artificial. Even genera or families seem somewhat artificial at times. In fact, it is quite possible, though it may be thought improbable, that new members of sub-groups may be formed at any period in the life of a family in the same way as the first members were formed in the early days of the family, by divergent mutation. On the other hand, such divergences as may give rise to what we consider to be new subgroups seem to become rarer as the family grows older. There are various explanations of this fact that are possible, and we must briefly consider them. It may be, for example, that in a certain family, certain combinations of characters only are possible, and may have already been used, or that as one comes downwards from the head of a family, the mutations become less marked. But before we can express an opinion upon these matters that will have any real value, we must have a much better knowledge of characters and their incidence. We know, for example, that the character that appears to be the principal one dividing *Acanthaceae* into A and B, or the character that divides the *Monimiaceae* into two sub-families, may appear elsewhere, where it is younger in the family concerned, and is therefore shown by a smaller proportion of the family, its descendants.

At the present time, this fact is translated into the current botanical language of the day by saying that the character is "less important" there, though no attempt was made to show why it was less important, until the writer showed that importance was an accompaniment of age. But this one particular divergence of character in the *Acanthaceae* or in the *Monimiaceae* has remained so persistent in the heredity that either one side or the other of the divergence marks one or the other of the two great divisions into which the family is split. Other characters or divergences accompany this one, however, and to say what really happens at any single mutation becomes a complicated problem, upon which it is at present very rash to give any decided opinion. Let us leave it, therefore, with a leaning towards the idea that mutations become less complex as one comes downward, as this helps to explain the great differences that mark the great groups into which plants are divided, though it is largely true that they owe much of their importance to their age, which has produced many descendants with the same general character as themselves and has given these forms a great dispersal over the earth.

It will probably be found, now, to be more difficult than before to make a genetic group. If any character of a family, or even a character as yet only known in some other family, like the superior ovary in *Gaertnera* of the *Rubiaceae*, may thus suddenly appear in that family, we have no longer any assurance that two things that show it are necessarily any more closely related than are any two others, while any mutation may produce something that breaks away from its existing structural relationship to place itself in another one. While age seems to be the most important feature of a character, we must not forget that though, for example *Ruellia* in arising from *Justicia* changed its aestivation, it also changed other characters, so that the divergences shown in them are just as old as those in the aestivation. But they seem to be less steadfast in their subsequent appearances, showing occasional new divergences to something different, while in the aestivation there have been few *new* divergences, though there may have been cross-mutations, for anything that we can tell. It is this lack of permanence in the inheritance that has caused other characters to be regarded as of less importance *in the family concerned*, while in other families they may have the greatest importance possible. With our present complete ignorance of why a divergence appears, why it is what it is, and so many other problems here concerned one cannot yet go beyond the stage of vague suggestion.

If a character is found to be common to a considerable number of species in a large genus, it is probably old, and certainly so if a number of those species prove to be of the widest possible distribution in that genus. In that case it is quite probably of the same age as the genus itself, whose number of species shows its age as compared with others in its own family. A character is simply a character, liable to divergent change by rules that we do not understand, and whose importance is given to it, in each case, (1) by its age there, and (2) by its persistence in heredity there.

To feel more sure about relationship we shall have to take into account more characters than hitherto, including geographical and genetic. How little progress, other than continual shuffling of families and genera, is likely to be made under our present system of using structural resemblances only, or, be it at once admitted, under any system based upon geographical continuity only, may easily be gathered from any comparison that is made upon the lines that we have adopted for the *Acanthaceae* and the *Monimiaceae*. Some congruity must be brought into the results given by structure and by geography, not forgetting the possible overriding genus or family, which may cause great resemblances to appear at great distances apart. The geographical facts are less easily made to support any particular theory, so that we shall have to be very careful in our handling of the whole subject. The appreciation of the possibilities of divergence at a single stroke that have now been shown to be the rule rather than the exception, alters our outlook upon such problems very materially.

A diminishing number of us can remember the flourish of trumpets with which the supposed supersession of Bentham and Hooker's *Incompletae* was greeted, and it is of interest to look at the result after many years, for they are now largely to be found in the first 15 orders of *Archichlamydeae*, which, with the exception of 5 and 10, composed only of *Garryaceae*, and *Julianaceae*, contain nothing else, and might quite well be labelled *Incompletae*. In the orders after 15 there are also families of *Incompletae*.

One cannot but suspect that the *Monimiaceae* are not a simple genetic family, and the same is true of many others. *Siparuna* and *Mollinedia* start off in proper order and position, the older spreading over a greater area, and reaching the West Indies, which the latter, apparently born further south, fails to do, though as old as many genera that have arrived there. One rather expects to find more *Siparuneae* in America, and must suppose that the genera intermediate between the one very small one that is found, and the large top genus have mutated out of that group, and are to be found in other places, even in other families, like *Lauraceae*, which probably belongs also to the *Monimiaceae*-complex. This passage of species or genera into some other group was first suggested by Bower in connection with the genera of the ferns (16).

In Engler-Diels, 11th. ed., *Monimiaceae* is placed in *Ranales*, § 4 *Magnoliinae*, and in the present connection, as showing the shuffling that goes on when the only criterion is a structural one, it is of interest to find that Hutchinson (68) places the same group in four different orders — *Magnoliales*, *Annonales*, *Laurales*, and *Rosales*, and puts the first three groups of Engler-Diels into his own *Ranales* and *Berberidales*. The tendency in recent groupings is to postpone the difficulties that we have been pointing out, and that have arisen partly on account of the use of too few criteria, by increasing the number of groups, whether genera, families, or orders. Thus, where BENTHAM-HOOKER have 120 families in 23 orders of *Archichlamydeae*, ENGLER-DIELS have 201 in 33, HUTCHINSON 213 in 59.

Probably a mutation of long ago gave rise to the *Monimiaceae* proper, a S. American family, which lost some of its members by cross-mutation into other families like *Lauraceae*, while perhaps other mutations came in from this or other allied families like *Lauraceae*, giving rise to the present *Monimiaceae* of MADAGASCAR, MALAYA, AUSTRALIA, NEW ZEALAND, &c, which are not geographically connected by other members of the family. But if it be recognised that the family is artificial, they may quite well remain in it. But we are here entering the very attractive, but deceptive, realm of speculation, and must return to the paths of induction.

Less marked structural features. A feature of the present family is the structural variety of the receptacle and perianth, showing suggestions of features that one may see in other families of this complex. Now that we have seen what mutation can do, it is clearly not impossible, even perhaps not improbable, that a feature supposed to mark one family only may at any time appear in another family, usually, one may suppose, related to the first. In fact, everything goes to show that characters are handed down by inheritance from above. Those of the immediate parent are those that are most likely to appear in the offspring (*cf.* GALTON's law, p. 232). Most characters, when they once appear, seem to be more or less adhered to for a number of generations, but in how many of these this may be the case, we have no idea at present. One cotyledon, for example, seems a very permanent character, but we cannot guarantee that it may not disappear at the very next mutation of some Monocot.

It may be worth while to look at one or two of the characters that are less widespread in the family, or in general younger, than the form of anther-dehiscence, and to compare their geographical and taxonomical incidence. There is an orthotropous ovule in *Amborella* (*Monimioideae-Hortonieae*, 1 NEW CALED.) and in *Daphnandra* (*Atherospermoideae-Laurelieae*, 4 QUEENSLAND, N. S. WALES), geographically near enough, but taxonomically in separate sub-families. Though the character does not lend itself to selection, and thus has an added "importance", it is a simple change for mutation, and must probably be of polyphyletic origin here. One of the rather impossible so-called natural families made of recent years, the *Phrymaceae*, with two genera, *Phryma* (1 E. AS., ATL. N. AM.) and *Denisia* (1 S. AFR.), depends upon its possession of an orthotropous ovule for its extrusion from *Verbenaceae* (of BENTHAM and HOOKER). The writer, before he had fully grasped the possibilities of mutation, split off *Tristichaceae* from *Podostemaceae* (138), as more natural by reason of their completely different morphological structure, a change which could not be passed over by gradual stages. He now realises that this was easily possible to mutation in such plastic material as submerged water plants, so that it is perhaps not impossible that other solitary water plants, separated by wide divergences from other plants, whether land or water, may really be closely allied genetically. The same may be the case with some of the parasites and saprophytes.

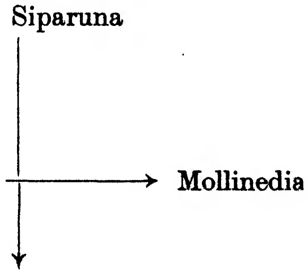
To return to our theme, let us consider the presence of glands at the base of the stamen, found in various places, *e.g.* in *Hortonieae* (*Hortonia* in CEYLON, *Peumus* in CHILE, &c), in *Monimieae* (*Monimia* in MADAGASCAR), and in *Laurelieae* (E. AUSTR. NEW CALED., N. ZEAL., CHILE, PERU). Both this character and the last, with their wide discontinuity in what are almost certainly very young genera, far too young to have been present at the formation of the PACIFIC, for example, come under the head of what in Chap. IV we called character-discontinuity, which cannot be explained by the destruction of transitional or intermediate forms. As there is no overriding genus in *Monimiaceae*, the character must be polyphyletic so far as they are concerned. As the same thing is shown by several *Lauraceae*, it has probably come down at least from the common ancestor of both, turning up independently here and there. There are a number of such scattered characters of interest in the *Monimiaceae*, but space will not allow of their discussion. For instance there are the very different male and female flowers in some species of *Siparuna*. Here we may note, with reference to complexes, that we find the *leader* of the family showing a character which is otherwise only shown by the distantly related *Laurelia sempervirens* and *Atherosperma moschata*, both, it is perhaps worth noting, in the sub-family in which *Siparuna* itself is found. Such behaviour as we have outlined in these two examples of character-discontinuity is not uncommon, and goes to prove our contention that the potentialities of all characters in a family are already existent in the head of the family, though only appearing under certain circumstances—perhaps, for example, only being able to appear after something else has happened in the mutations that go on in the family. Other examples of interesting characters are to be noted in the different types of receptacle in *Hortonia*, *Levieria*, *Trimenia*, *Xymalos*, *Siparuna*, *Mollinedia*, *Macrotorus*, *Wilkiea*, &c; the velum, shown in great variety in *Siparuna*, where some species have none, *Lauterbachia*, *Glossocalyx*, &c; the stamens, usually ∞, but only four in *Matthaea*, *Steganthera*, *Anthobembix*, united to a tube in *Tetrasynandra*, and so on. The incidence of characters in this and other (allied) families is well worth detailed study, and character-discontinuity should be studied in connection with the characters of the head of the family, as with *Senecio*, where one finds many species, or groups of species, that show characters that especially mark certain of the smaller genera of the family. While such facts as these are not unfamiliar, it is perhaps not fully realised how important is their bearing when we reverse the order of evolution to the direction family-species, when at once they fall into their proper place.

It is also interesting to study the contrasts provided by the two methods of grouping. The *Hortonieae* are headed by *Hedycarya* (20 AUSTR., NEW CALED., N. Z., POLYNESIA); half the genus is confined to NEW CALEDONIA, from which it evidently spread (terrestrially) to the rest, which lie in a circle round it at not greatly differing distances away. This is a normal dispersal, and *Hedycarya* could not have been the parent of such things as *Hortonia* in CEYLON, or probably of *Peumus* in CHILE. The hermaphrodite flowers of *Hortonia* are unique in the group and it shares opposite leaves with *Peumus*, while the alternate leafed *Amborella* (1 NEW CALED.) is probably a direct mutation from *Hedycarya*, so recent that it is endemic. *Levieria* is a doubtful mutation from *Hedycarya*, all but one of its species being confined to NEW GUINEA, which is therefore probably its birthplace, and is outside the range of *Hedycarya*. If, therefore, *Hortonieae* are to be retained as a natural group, we are left to explain the far outlying *Hortonia*, *Levieria*, and *Peumus*. None of these are individually discontinuous, but if they are genetically closely related, their mutual discontinuity, without any overriding genus in *Hortonieae*, is very great, while the genera are too young to explain it without vast destruction, for which there is no evidence, especially when we see how well *Hedycarya* has followed the usual laws.

It is therefore almost certain that these outlying genera must owe their origin to descent from one or more genera that did not belong to *Hortonieae*, and the question at once arises whether it or they belonged to *Monimiaceae* at all. This, it must not be forgotten, is a small family, allied to *Annonaceae*, *Myristicaceae*, and *Lauraceae*, and perhaps other *Ranales*. Its small size is often put down to destruction, especially by the breaking up of the land of the southern hemisphere, but more than half its species are in the two normal S. American genera *Siparuna* and *Mollinedia*. To suggest that the rest of the family are relics does not in the least agree with what has been set out above as to their dispersal and taxonomy. Similar criticism may be applied to other subgroups of *Monimiaceae*.

The distribution of species or genera. For many years we have tried to prove that the evolution of species is *downward* from the original parent of the genus, that differed so markedly from the grandparent that taxonomists finally agreed that it should be considered as a new genus. This view of course reverses the Darwinian conception, going back to the pre-Darwinian. Our book upon Evolution, seven years ago, was largely devoted to this theme, and gave many convincing crucial test-cases. We have tried also to show that the most probable mechanism of the process is that one new species is formed at each birth, and that this fact did not affect the parent, which survived the birth, and went on as before to the next birth, survived that, and so on. If the offspring, as one would expect, inherited the adaptation of its parent to the conditions of the locality, it would survive; if there were any inferiority in adaptation, it would probably be killed out at once by selection, which of course is in continual operation. If, on the other hand, there were any appreciable superiority, the offspring would be likely to get a better start than usual, so that it might ultimately achieve a somewhat greater distribution than that to which its actual age would entitle it. It is to allow for slight differences of this kind that we drew up the rule that calculations for age and area should be based on ten allies compared with ten others allied to the first. It must not be forgotten that the already established parent starts with a great advantage over its offspring. In the majority of cases, probably, the offspring of a genus will be a new species of that genus, but at times, perhaps when the stimulus of changed conditions is unusually great, it may be what we regard as a new genus, or even a new family.

The first genus of a family probably always behaves in much the same way. *Siparuna*, for example, beginning as a single species, perhaps as *S. guianensis* (see map) probably started somewhere not far from the Andes, in western Brazil. The great mass of mountain species seems to point to the likelihood that it soon reached the mountains, in which, though the broken nature of the country encourages the formation of many species, travel, especially upwards, will on the other hand be slower than upon the more level lower country. All the time, the genus is increasing by the production of more species, especially in the hills. At certain times, and perhaps more in the direct line from *Siparuna* than in the side lines of other genera (though as these grow older and more numerous they will probably, on the total, surpass *Siparuna*), new genera will appear instead of simply new *Siparunas*.



Going on from this point it is not difficult to make further predictions which, if as successful as several hundreds have now been, will give further evidence greatly in favour of our general contentions. In the first place, it is clear, and indeed it is a not unfamiliar fact, that the central part of the area occupied by a genus should in general carry the largest proportion of its species. The evolution of a genus will of course begin somewhere about the centre of its ultimate area, and it will spread in all directions, though probably conditions will soon ensure that it goes more rapidly in some directions than in others. The earliest dichotomies will probably not be very far from this centre, and the results of these dichotomies will on the whole get the start of dichotomies further away from the centre. The tendency will thus be to get the greatest proportion of the species occurring in the most central region. Going outwards from it, the numbers will automatically tend to decrease, and will cease altogether at a greater or less distance away. But one must not forget that there are two ways in which this limit may come. If it is simply the limit imposed by time in a fairly uniform country, one will expect to find it occupied only, or almost only, by the oldest species of all, provided that the edge is still under conditions not very far removed from those at the centre. But if conditions have seriously changed on the way, one will expect a new species to have formed somewhere, which is better suited to the outlying conditions, and which has probably been able to outrun the original first species. In BRITAIN, for example, families like *Malvaceae*, mainly tropical, with *Hibiscus* (not British) as the leading genus, are not led in BRITAIN by a species of *Hibiscus*, but by one of *Malva*, which is a much smaller and younger genus, but centred on more temperate-zone conditions.

The other type of termination of area in any direction is where it is due to the formation of a definite barrier to further passage, by sea, or by a range of mountains, or a desert &c. For example, in CEYLON further expansion southwards has for an immensely long time been prevented by the INDIAN OCEAN, and the result has been to allow later genera and species to overtake the first arrivals, and to allow endemic species to appear much nearer to the boundary, and in greater numbers, by reason of the time available during which the first comers have been held in position and not allowed to go any further.

All these facts give strong support to our contention that the dispersal of a species is a more or less mechanical phenomenon, once the species is formed. There is no evidence of any serious competition between one species and another, and much less between one genus and another, though the structural differences on the whole are larger.

We may make a second prediction upon somewhat different lines. Assuming, as we have now every right to do, that evolution goes by divergent mutation, then in the central region where the earliest part of the evolution of a genus went on, and the greatest number of species occur, there should be also the greatest structural variety in every way, while at the edge of the dispersal of the genus, there should only be one or two of the very oldest species, but these should show very clearly marked divergences, as we have seen above with the earliest species.

The keys that are given in monographs of course place most nearly together the species that are nearest in structural relationship, no other characters being employed, except that sometimes a block of species is marked as being for example all African or all American. It may be worth while, however, to point out that this is a comparatively rare event, the blocks of species made up by structure only being most often geographically mixed, as we are trying to make clear. In a key, the *attempt* always is first to divide into A and B, then to divide A into a and b, a into 1 and 2, and so on, till at last one comes down to the individual species. Thus if of two species, one shows the character A, one B, they will be divided by the most widespread divergence in the genus, which is also as a rule a well marked one. Two species, on the other hand, that only separate after having agreed in showing A, a, 1, &c &c, are species that agree in many characters. But on the whole it is evident that wide separation in the key means structural separation by many characters, while close proximity means separation only by a few; and a scattering of species from one geographical region over most of the key means that most of the characters have come into use in that set of species.

It is fairly evident, from the map at p. 224, that *Siparuna guianensis* is the parent, direct or indirect, of all the species in S. AMERICA, and probably at any rate the immediate parent of *S. cujabana*, which occupies the second largest area, beginning at RIO. But, as seems to be the all but universal rule, these two are well separated in the classification, by a well marked divergence, the former being in Bc—, the later in Aa—.

Suppose we look at the great crowd of species of *Siparuna* in Peru, where they are all local, except for *S. guianensis*, we find their numbers in the key to be as follows, the key numbers running from 1 to 89 (*PR*), to which new species were added in (*PR* suppl.) by a or b at proper places. The 36 species are Nos. 7, 7a, 11a, 12a, 15, 17, 18a, 18b, 26, 26a, 27, 33, 33a, 36, 37, 39, 39b, 41b, 44a, 45, 45a, 47, 49, 52, 56, 61, 66, 66a, 72, 73, 79, 81, 84, 85, 87 (*S. guianensis*), 88. *S. guianensis* is separated from its next neighbour, 88, by connate as against free styles. It will be seen that the numbers of the Peruvian species run through the whole gamut of possible characters for a species of *Siparuna*, and the phenomena here described will be found to make a very general rule for incidence of characters. It will be seen that they agree with the way in which the incidence of the characters happened in the *Compositae* (Chap. VIII).

If we look at *Mollinedia* in the same way, we find it to centre in the (mountainous) state of Rio de Janeiro, and to show 71 species in its key, with a few of a or b. Thirty-one are confined to the state, or endemic there, and they show the following numbers: 3, 4, 5, 7, 8, 10, 11, 12, 13 (so far evidently closely structurally related), 17, 18, 19, 20, 23, 33, 34, 37, 39, 44, 45, 46, 49, 56, 57, 58, 59, 60, 64, 66, 68, 68a. The numbers cover so much of the list that it is clear that the Rio species cover most of the structural variation, including many in both of the sub-genera *Exappendiculata*, without appendages to the lower tepals, and *Appendiculata*, with appendages, a simple mutation, but well marked, probably shown at the very first mutation in the genus.

If the structural characters went with the geographical separation of the species, all would be well, and structure and geography would agree, but this is just what does *not* happen, probably in the majority of the cases. For example, in *Mollinedia*, species 9 in Peru comes in the middle of a whole lot of Rio species, yet they are separated by a vast distance, mainly covered with heavy forest. Cases like this may be found in great numbers, and it is clear that structural characters do not go with the geographical distribution of forms. When there is no overriding genus from which the same character in the same family can have come in two widely separated places, it is necessary to suppose that it came from separate genera in different families, presumably of the same complex of families. Failing that, enormous destruction according to the older views is often needful, and often (across oceans, for example) at a date too far back in time.

It thus seems fairly evident that the dispersal of the *Monimiaceae* cannot be explained upon the supposition that a character is necessarily handed down in such a way that in the parent one may see an earlier stage of what occurs in the child, or that it may be, except perhaps in very rare cases, acquired by selection. Divergence at mutation, which probably has some electrical rule behind it, seems to be general everywhere, and the characters are handed down as some kind of potentiality from above. The family is probably largely artificial, with a polyphyletic origin. We shall consider this matter further in the next chapter.

CHAPTER XI

The classification and distribution of the Araceae

We have now seen many interesting new, and at times unexpected facts, like the early branching out of the head of a family into the heads of sub-families, tribes, and subtribes; and we have seen the same thing in a genus, even down to the leaders of sub-species in such things as *Rubus* or *Hieracium*. All goes to show that in all this evolution there must be one chief governing law, regulating the formation of new subdivisions, which, it seems to the writer, must be the law of dichotomy by divergent mutation.

The point must also be stressed that all these things have necessarily followed from the law of age and area, discovered by induction from the accumulated facts of dispersal. The rest has been deduction, which, as the writer grew in confidence that he was getting upon the right track, was replaced by simple prediction, which has proved successful, without a failure, in hundreds of cases. The great bulk of the present book is made up of the results of such deductions and predictions, whose verification has involved much work, while the time in recent years has been largely occupied in marshalling the results, and writing them up into a connected whole, this work, however, being often interrupted by the incidence of new deductions, which had to be fitted in with the old. All this work has given the writer great confidence in the general correctness, not only of the original law of age and area, but also of the next stage, the laws of ASA, of the third stage, the law of divergent dichotomous mutation, and of later deductions from all of these.

It may interest some people to know what the writer has gradually found to be the best way in which to make these predictions, which are really deductions made by the use of the sub-conscious mind. Instead of sitting down to think out deductions, which are apt to refuse to come at demand, he is accustomed to soak his mind, if one may employ such a phrase, in some subject such as size and space, and leave it. After a greater or less time, up to three or four months, deductions begin automatically to come up, most often at times of waking in the night. For about 45 seconds to about three minutes, but *not more,* one grasps the deduction and the steps that led to it, which sometimes involved more than one premise. He therefore carries slip notebooks, with pencil, in his pockets, has one beside the bedlight, and one on every table used, to write down the deduction before it fades, which it soon does, beyond the possibility of recall. The notes are attached to sheets of paper, and the often arduous labour of verification is put in hand later. The period during which deductions come up may last as long as three months, and the greatest number ever noticed in a night was five. I have long ceased to keep count, but estimate that I have made about a thousand in the last ten years, and not one of these, to my continual surprise, has failed of verification upon examination of the facts, themselves often collected by those who have been my opponents. In general, therefore, it would seem that the premises, such as the laws of ASA and of dichotomous divergent mutation, must be correct. Naturally, the subject being biological, the correctness of the deductions does not necessarily go into every detail or every instance, so that it is not difficult to find objections in single cases. But it has gone, throughout, by decided majority vote, as is shown for example in many of the tables. After the verification has been done, the necessary account of the result has been put together, and the files have been sorted under heads, until at last the material for a book was complete.

Such work has given the writer great confidence in the general correctness of his theories, and however undesired the new viewpoints may be, it will be realised that distribution, hitherto made largely a field for profitless but fascinating speculation, shows itself as capable of inductive and deductive treatment as any other branch of biology, and that its neglect has left large arrears to be made up. It must at the start be realised that distribution and evolution go together of necessity, so that the writer has had to study the latter as much as the former, and it is the final result of this study that is here presented, with much evidence in its favour, which if required could be greatly extended, as the laws which are here brought out seem to be of universal applicability.

The branching out of the head of a family into lines that now represent its classification, and at the earliest opportunities, was discovered by this method, and when once seen, was evidently a necessary consequence of divergent mutation. It is in turn a great support to that theory, which with its continual dichotomy produces the hollow curve. The characters of A, the first genus, and B, its first offspring, will be handed down to two different lines of descendants, most often different sub-families or tribes. One or other of the two chief divergent characters of A and B usually shows in all their descendants, and the importance of these characters is simply due to their *age in the family*; in other families the same pair of characters may only mark the distinction between two small groups, even perhaps only genera or species. The same kind of divergent mutation goes on at every subsequent mutation, continually dividing the family into more and more, and smaller and smaller groups, down to small sub-species. Mutations at the top of a family seem to be larger, *on the whole*, and those above family rank larger again, but the interesting problem is one for the geneticists.

The original parent A starts with an outfit of characters of all kinds. Some, but not all, change to divergent characters at the first mutation, which let us suppose produces another genus B. The next genus again will probably be C, a direct descendant of A, rather than B1, but it may be the latter, the probability in favour of C resting upon the fact that A will get a long start while B is becoming established and ready to mutate. It is not at all unlikely that several of the early genera of a family may be direct descendants of the actual leader. On the whole, the early genera will tend to go into sub-families or tribes different from the one that contains the head, but not necessarily so; it depends upon the particular characters that may be chosen for the mutation.

Classification as we know it is a more or less mechanical result of divergent mutation, for it is only upon such divergences of structure that we can at present base a classification. The first divergences to appear will be those that show between the earliest genera of a family, which are now, of course, the largest genera in that family. These divergences will thus tend to be inherited by the largest number of descendants, so that their features will mark the first divisions of the key, those separating sub-families or tribes. Later divergences will separate smaller divisions, and so on downwards. There is little or no evidence that the first divergences are necessarily " larger ", for it depends largely upon the family; the same divergence may mark a sub-family in one case, and only a genus in another. But the first divergences are the oldest, and therefore mark a larger part of the family than do the later ones. When one fully grasps the meaning of this dichotomous divergent mutation, it is evident that it automatically brings changes into our notions of classification. This of course can only be founded, if it is to be practical, upon the divergences that exist. So long as we believed these to be gradually acquired *upwards* (towards larger and larger divergences), so long could our classification be regarded as more or less closely approaching natural. But now that we see the evolution of the plants beginning with the wider and larger divergences, and working *downwards* towards smaller and smaller, it is evident that our classification requires much revision to make it " natural ", for a large divergence may easily carry the child into another tribe, and in fact, in the early stages of a family, most often does so. Divergence is no longer due to continually increasing selective destruction of intermediate or transition forms, but is impressed upon the child at its birth. If development is downwards, the smallest genera are the youngest, and it is the oldest and largest, like *Senecio*, *Ranunculus*, or *Carex*, that contain the relics !

Of the 61 leading families given on p. 173, one may see that at the first mutation the first and second genera became the heads of the first two tribes in 47 cases, and not so in only 14, though even then they sometimes headed different sub-tribes. But before a family has grown to any serious size, it has already produced the heads of most of its subdivisions, even to the second degree, and they are all evidently closely related to one another, and to the leader of all, of which the first follower certainly, and later ones with rapidly decreasing probability, are direct descendants (*cf.* also *Evol.*, App. III, p. 199).

In our list of these 61 families, it will be noticed that the larger a family is, the greater number of tribes does it seem to show, a fact which at first seems contradictory to our theories. But in a large family, as compared with a small, the leading genera are older, and will consequently have more descendants, and as all or most of these will agree in showing some of the characters of their leader, we shall thus get a group marked out by its possession of these characters, and *so numerous* that we shall give it tribal rank. This of course will not show nearly so well in smaller families, so that it is only when their leading genera show some well marked divergence, especially when that divergence has been elsewhere admitted as of tribal rank, that we shall recognise them as the heads of tribes. Thus in *Sarraceniaceae*, in spite of the very great divergences shown by *Heliamphora* as against *Sarracenia* and *Darlingtonia*, such as raceme (solitary fls.), perianth simple (double), G 3-locular (5-loc.), we do not give it any rank beyond a section of the family, numbered, not named. But if it had a number of descendants more or less closely akin to itself, it would doubtless head a sub-family or tribe. In the *Basellaceae* with five genera, the well marked sectional characters, which mark tribes in larger families like *Urticaceae* or *Chenopodiaceae*, simply divide it into two sections. It is simply because of these tendencies that the proportion of leading genera that head sub-families or tribes is greater in a large family than in a small, and that they are not so clearly marked off from one another.

For the last eighty years we have been so much in the habit of expecting any structural feature to have been developed from something that was closely like itself, allowing of transition stages towards itself, that a serious change in the viewpoint is not easily assimilated. Divergence of variation, so constantly shown, was always one of DARWIN's principal difficulties (*cf.* GUPPY in *AA*, pp. 103-5, especially the latter part about DARWIN). This divergence is not only frequent, but general, in fact one of the general laws by which evolution is working itself out in nature. It is very strikingly shown in the way in which the taxonomic divisions of families, tribes, genera, &c, are made by divergence at the earliest possible opportunities that offer themselves after the birth of the species (or genus if one prefer, for they are the same thing at the start) that was the first head of any family. Thus for example some species of *Senecio* was probably the first head of the *Compositae*. Had all descendants been closely like their predecessors in every respect, it would not have been possible to group them by the endless variety in structure which they actually show. The supporter of selection is compelled to use that popular refuge, the destruction of the intermediate or transitional types that might have filled the gaps, whether structural or geographical. But, as we have seen, there is little evidence for this, especially now that fossils have been shown somewhat incapable of bearing the weight that has been placed upon them, and when one thinks of the almost fabulous destruction that would be required, and which has left practically no trace, fossil or other.

Destruction of intermediate or transitional forms. To go over the whole question of destruction, and of relicdom, which is involved with it, upon both of which we have written so much, would take up too much space, but it is so important in the present connection that a brief review may be permitted. In accepting divergent mutation, with development in the order family-genus-species, as opposed to the Darwinian conception, the writer took up a new position. But he felt strongly confirmed in his opinions when he found that he could make so many deductions, every one of which proved correct when tested upon the facts. It was one of these that showed, as we have seen in recent chapters, that the heads of the sub-families and other groups into which a family was divided would be the nearest possible of relatives, and not widely separated, as Darwinism, or the result of structural investigation, would make them.

Chap. XIV in *Evol.*, p. 164, gives a general discussion of the pre-war situation (the writer has since been cut off from most literature and correspondence). The weakness of the selection theory, and the many assumptions upon which it rests, and of which a list of 33 is given, were pointed out. The writer realised the illogicality of the theory in his early days in CEYLON, and from 1902 onwards continually attacked it when his work provided an opportunity. One line of attack, based upon the study of endemism, is described in *Evol.* pp. 27-32. The main point that is insisted upon is that in the flowering plants of the present day the local species or genera, and the small genera, are nearly always young beginners, and not relics. There *are* many relics, especially within range of the ice of the glacial period, but they are few and far between compared to the great numbers of local species and small genera. The figures of genera on p. 185, *AA*, give 4853 of one species and 1632 of two, out of a grand total of 12,571 genera. Even *Ranunculus*, admittedly a very old genus, with over 300 species, has only about 25 of very large range, most of its species being much more local (*cf*. map of New Zealand on p. 65), while in smaller genera, except in water plants, whose range is usually larger with fewer species, the species of large range are still less common.

Most of *Ranunculus* consists of species of medium or small area, the last being relics upon the older conceptions, though their percentage is greater in a large genus like *Ranunculus* than in a smaller one, which latter comes nearer to one's conception of a relic. If the two genera are reasonably closely related, so as to be not unlike in their reaction to external conditions, the difference is that in the smaller there are few, if any, of the species of very large area of dispersal that occur in such a large genus as *Ranunculus*, even though rarely. This occurrence of age size and area, all connected by the laws of ASA, is fatal to the idea of *general* relicdom for species of small area. And this is further emphasised by the fact that the so-called relics do not occupy broken areas, as one might surely expect, nor are any fossils to be found (and especially so in *Araceae*), except in a few very rare cases, like *Cercidiphyllum*. Real relics are simply rare exceptions to the general rules. Many difficulties, to which no reply has been given, are pointed out for the theory of relicdom in a list of queries upon p. 90 of *AA*, and we may also refer to *AA*, pp. 58-9, 86, 88, 93, 165, 186, 199, 216, 229-34, and *Evol.*, pp. 17, 26, 30-1, 61, 79, 93, 113, 128, 132-3, 160, 173.

The matter is also discussed in a general way under the head of structural discontinuity on p. 90 above, and another general review is in Chap. XXII, *AA*, p. 228, especially from the foot of p. 231, where the arithmetical and other difficulties that we have brought into the question with the laws of ASA are considered. There is also a chapter by de Vries on p. 222, that is well worth consideration, especially p. 226, where he says " the conclusion obviously is, that specific characters have evolved without any relation to their possible significance in the struggle for life. The facts are contrary to the main principle of the selection theory of DARWIN. Moreover, intermediate steps between the endemic species and their parents, in the midst of which they are ordinarily still living, are wanting, and therefore must be assumed never to have existed. Endemic species must have appeared at once; by means of one or a few distinct steps, which embrace their whole differentiation from the parent type... their origin is in full accord with the principles of the mutation theory... one of the best proofs of its applicability to evolution in general. "

DE VRIES also points out that mutation is really a support to the main evolutionary theory of DARWIN. The writer's contentions are largely aimed at getting rid of the illogical appendages, to which, on account of their popular appeal (and without which the theory of evolution might not easily have become firmly rooted), the name of "Darwinism" was given, and which, illogical though they were, have been so much invoked in an attempt to justify the breaking out of the great war.

In the theory of divergent mutation, the writer has gone beyond this standpoint, but that is the result of separate scientific discoveries, and he is also largely concerned with getting the immortal theory of evolution properly established upon a completely scientific basis. If one destroy any previously accepted belief, one should try to find something to put in its place, and for this he has adopted the theory of dichotomous divergent mutation, working downwards towards the species, not upwards as selection demands, and with survival of the parent. For this the evidence is very strong, and continually becoming stronger, and he ventures to hope that it will be found a satisfactory substitute. The way in which the "man in the street" regarded the theory of natural selection has been very well put by Mrs. ARBER (*Evol.*, p. 6), and perhaps that individual may regard the substitution with less disfavour when he realises how well it too agrees with the ordinary observation of everyday life.

In *AA*, chap. XIV, p. 137, Mrs. REID considers the matter from a palaeobotanical standpoint, pointing out that fossil botanists are looking more for the exceptional cases, while the writer is seeking the general laws that underlie them, hence the differences between the two. There are two lines of attack upon a biological question, and so many laws are interacting in any case, and many of them probably unknown to us as yet, that it is difficult or impossible to obtain a direct and unequivocal answer. Facts are collected from below upwards, in the endeavour to ascertain by induction some law that has governed their appearance. In this way the laws of ASA were discovered, but it must be clearly understood that the finding of an exceptional case does not necessarily disprove the law, any more than the ascent of a balloon disproves the law of gravity. The best proof of a law that is usually available is its use to make predictions that can be verified, under which head may be placed the bulk of the new facts that are brought forward in this book, such as those given on pp. 24, 26, 40, 51, 52, 69, 70-73, 81, and so on. But there are so many exceptions that it is always easy to bring up objections to any laws proposed. But here the exceptions are always much less numerous than the cases that go as the law directs, and some of the most troublesome exceptions, such as those which fossils were supposed to provide, have been shown to rest upon incorrect interpretation.

Mrs. Reid goes on to point out the chief and undisputed facts of plant migration, extinct floras, &c, and on p. 141 she says, with perfect truth, that the palaeobotanist must stand for endemics being, in many instances, survivors from races that once, though now no longer, flourished widely, like *Sequoia* which, belonging to a very old family, is now an undoubted relic; but it is only one among many, where it makes no difference to the figures. The whole number of relics forms but a small proportion to that of the local species and the small genera that are so numerous. The great majority of the flowering plants, and *especially the smallest genera*, which are the youngest, as the laws of ASA show, and as is confirmed by their great preponderance in number at the tail ends of the hollow curves, closely follow the laws of ASA in their development and distribution about the world. Speculation comes in much more when we have to deal with the older and larger genera, that have undergone greater vicissitudes in their much greater span of generic life, and that show much better the broken distribution which on the whole is conspicuously missing in the young ones.

Local, or endemic, species and genera, so fiercely defended as relics, belong to the older genera and families to a very great extent indeed, and are but few in number in the small or young ones, which is not what one would expect upon any theory of relicdom, and indeed cannot be explained upon such a theory. They occur in large numbers in places where there are many widely distributed species. Cf. the Spanish and Balkan endemics on pp. 70-73.

We have pointed out in places above, that the further back that we go into the past, the more do we reach a field in which so many things may have happened, geological, climatic, and other, that the resources of several sciences have to be called upon, whilst the results must be largely a matter of speculation, which is a somewhat fascinating pursuit. Genera found fossil in the Pliocene are practically all genera of the present day, when they are of course usually large. In connection with fossils, we must also remember that comparatively local ones, as are so many of those of flowering plants, have been regarded as ancestral to existing things. The laws of ASA, however, indicate that a descendant will in general occupy less area than its ancestor, and that usually largely within the area of the latter. Fossils of small area, as so many are, are therefore probably completely extinct offshoots of the evolutionary tree, with no living descendants, while even fossils found very far back in time show little or no sign of intermediate or transition characters between one form and another, though they may show different *mixtures* (*cf.* SCOTT, p. 169) of characters — facts that are very difficult to fit into any theory of selection. Upon our theories, however, there is no special reason to expect the death of any transitions, and perhaps there never were any, or only rarely. *" Success ", under natural selection, means the destruction and death of the less bountifully equipped species* (nature red in tooth and claw, to use HUXLEY's phrase), *but under divergent mutation this is not necessarily so at all.* We must realise that the operation of selection, in plants at any rate, and during their first evolution, is individual, and rarely specific, if indeed it is ever so when once the species has become established upon some area other than very small. With the more careful and detailed splitting and definition of characters that is always going on, this question of intermediates becomes steadily more important, for close *structural* relationship is continually being shown among things that have no geographical connection, even by overriding genera in their own family, and often across barriers so ancient that they must be older than the plants concerned.

Most of the facts of distribution call for a simple mechanical explanation, which has been provided by the laws of ASA. Selection is individual and does not pick out one species as against another, though it is one of the laws of life. Agricultural work also goes to show that its result is to pick out, not the best *types*, but the best *populations*, which are usually composed of a mixture of types. In the case of man, the competition between really valuable qualities is commonly soon replaced by war, which depends more upon the resources available, and can be prepared for in advance.

Relics or supposed relics should receive proper study in each individual case. What caused them to be taken up with such energy in a collective way was partly Darwin's surrender to the incisive criticism of Fleeming Jenkin (*Evol.* pp. 5, 13, 25, and especially 165), which compelled him to stipulate for origin of species on large areas. Examples of actual areas upon which species occur are given in *AA*, pp. 150-168, *Evol.*, pp. 24-32, 34, 50, 62, and above, pp. 66, 107, and map of *Ranunculus* at p. 65. This stipulation of course implied that plants occupying small areas had once occupied larger, and therefore must be relics. But we have shown that one of the laws of evolution is divergent mutation. This in turn means that parent and child will most often, perhaps almost always, be mutually sterile, so that even a solitary divergent child may grow into a new species, without fear of parental crossing. Both will simply follow the laws of ASA, and any competition will be as chance may direct.

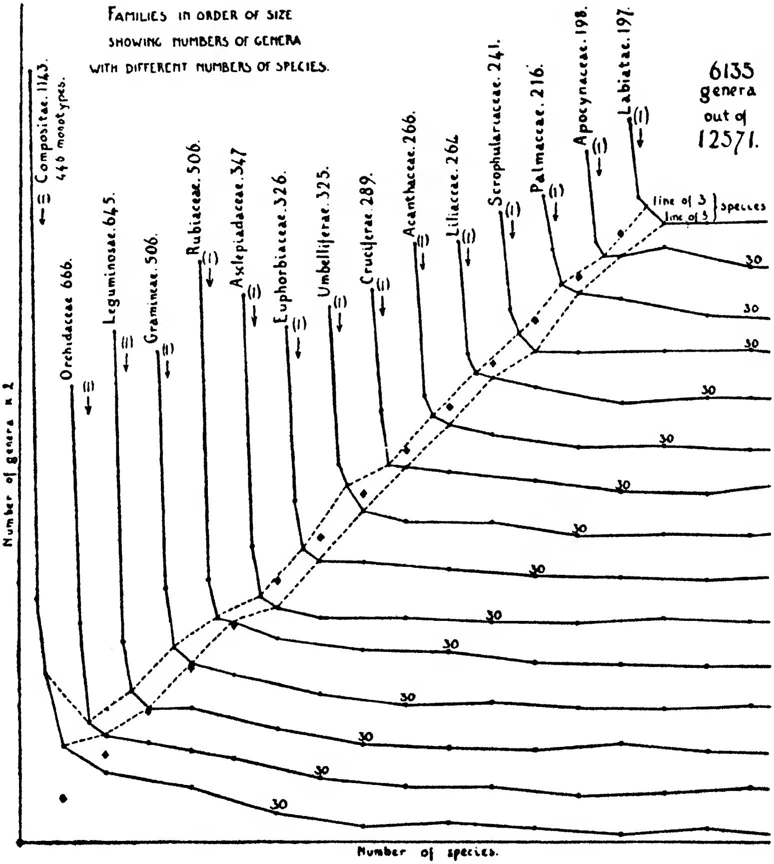
One great difficulty for the theory of relicdom, which we pointed out many years ago (*AA*, *cf.* index), is the fact that in all families there are very few large genera at the top, but a crowd of small at the bottom, and those especially " ones ". To this the only answer made, but one often repeated with different illustrations, is that the curves thus made are " accidental ". If they were really so, it is very remarkable indeed that the same accident should happen in hundreds of cases, and suggests markedly inferior workmanship in some part of the mechanism. It is evident that there is some law at work, which is evidently the law that differences occur more frequently the smaller that they are, or the younger in the case of plants. At the top of a family we find the oldest genera with divergences that on the whole (as usual) mark their descendants right down through the family, thus dividing it into tribes, while later divergences split these into subtribes, and so on downwards. *Divergence is the mark of evolution.*

Another difficulty lies in the query, why should there be so many genera just at the point of disappearance, followed by little more than one third as many, on the average, that are two points from disappearance, and so on upwards, in a hollow curve giving a logarithmic straight line?

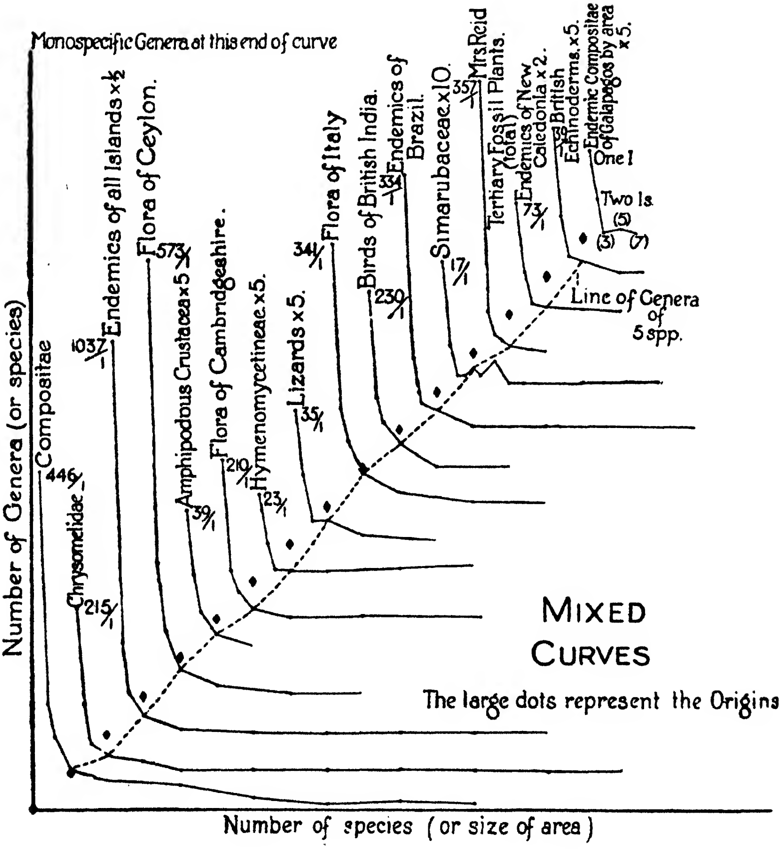
The universal hollow curve was a great blow to any theory that small genera or local species were of relic nature; hence the fierceness of the defence of relicdom as general, and not as only occasional, which seems to be the real state of affairs. The further discovery made by YULE, that for a family of reasonable size the hollow curve plotted as a straight line by logarithms, showed that the growth of genera followed the formula 1-2-4-8-&c, and did not involve the death of the parent that was stipulated for under Darwinism, but never proved. See pp. 260, 262 (log. curve).

There is no reason to suppose that competition is between entire species rather than individuals. Once the species has established itself as a few individuals at some distance apart, the competition continually diminishes *for the species, but not for the individual.* This is a principle that should be of some importance in the work of organising the world, once the general minimum necessities of food, clothing, and housing have been attended to.

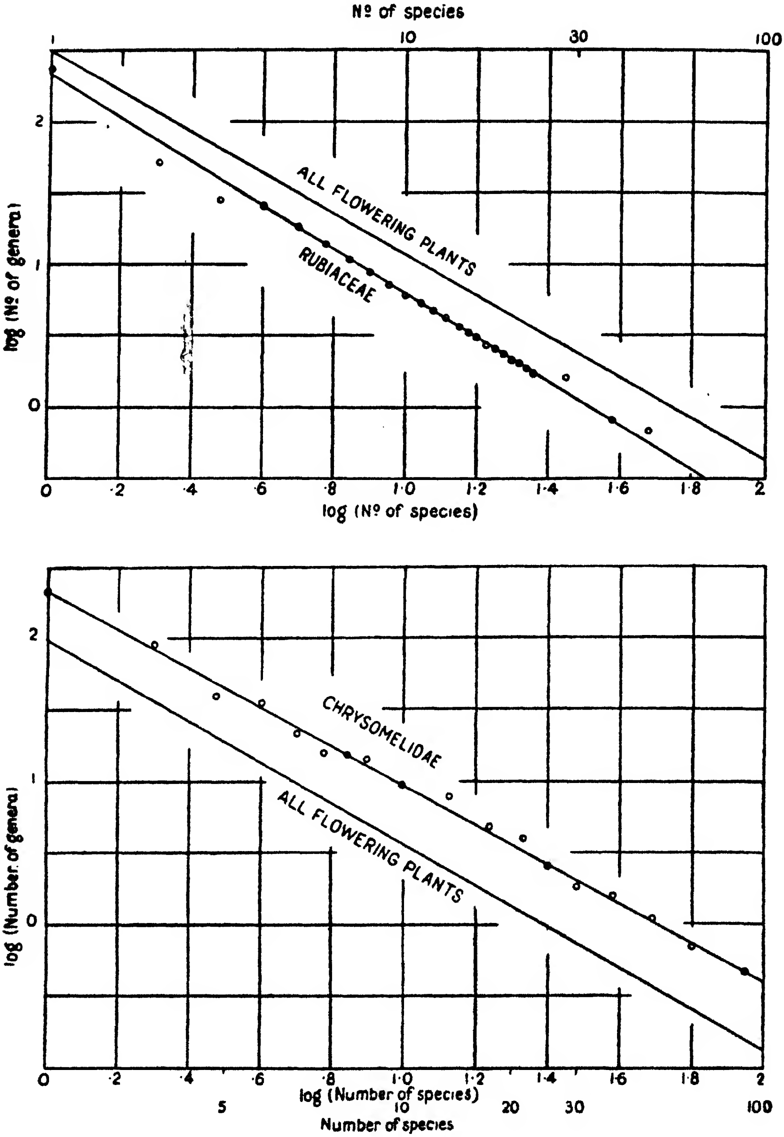
Proof of the theories brought forward here, and in the two preceding books, involves the destruction of the older theory known by the name of Darwinism, but should help still further to establish DARWIN's immortal work upon evolution, which will be freed of some of its encumbrances. The writer has been able, especially by the aid of the subconscious mind, to make a great many predictions founded upon the work described in the first two volumes of this trilogy. He has thus been able, finding them all to be



HOLLOW CURVES FOR 15 LARGEST FAMILIES



MIXED CURVES : PLANTS, ANIMALS



Logarithmic curves for flowering plants, for Rubiaceae, and for Chrysomelid beetles (by courtesy of the Editor of *Nature*) verified by the facts, to write the present connected account of the whole subject. As it all seems to hang together well, it thus makes a strong argument in favour of the line that he has adopted and followed.

It is thus becoming clear that the great variety that we see in species was not caused by the continual acquirement of new characters in a casual way by selection, but that the new characters were due to genetic acquirement from above, according to laws as yet unknown. In fact we need some kind of extension of the laws of Mendelism to cover their application to the question of specific heredity as different from, and more comprehensive than, individual. Such a law might ordain, so to express it, that "this simple leaf must become compound at this mutation, because of (some unknown but definite) reason", and the leaf becomes compound. In this connection, the physiological principle of compensation is probably of great importance; "what is lost on the swings is made up on the roundabouts", or the reverse.

The outstanding fact, proved almost automatically by the differences that we have seen to exist between the earliest (largest) genera of a family, which show among them all the breaking up of that family into its principal sub-families, tribes, sub-tribes, large genera, sub-genera, &c, is that *divergence is the first feature to show itself in the evolution of a family.* This may be seen right down to the families of two genera only, as is clearly shown in the table on p. 199 of *Evol.* The same thing occurs within the genus, and we have seen that the species, and even the sub-species (as in *Rubus* or *Hieracium*) divide upon the same principles, the most widely distributed (the oldest) belonging in most cases to different groups (cf. pp. 182-3, and many later). What seems most to matter is the period at which any mutation appeared in a family, for the same mutation may appear at an early stage, marking the division into tribes, or only at a late one, marking division into species. But on the whole one may say, that divergence becomes less as one comes downwards towards the species, and that the divergence is of the same kind throughout, but involving more characters as one goes upward from genus to class. But there is no difference between even one class and another that could not be crossed by a single mutation. It is not improbable that the comparative "width" of the differences may be due to the fact that the possible variety of difference is small at the beginning of life, but tends continually to increase as time goes on, for each new variation may bring other possibilities in its train. As soon as the changes had produced a real leaf for the first time, the road to all kinds of variations in form and structure and arrangement of leaves would begin to open, and so on.

The writer has observed several things that make him think that perhaps it may be possible that very small mutations may be frequent at any time or place, such mutations as will make differences too small to be noticed among the differences obviously due to fluctuating variation, but the evidence is at present so vague that he does not propose to give it, but simply to note the fact.

At the period when a new family is being divided up into sub-families, tribes, and other divisions, all its genera will obviously be quite young and very small, and at that time they will all, with equal obviousness, be as closely related as is possible. It necessarily follows that our classifications, which must, being based upon divergences, put these early genera (*at any rate when they grow large and important*) into separate groups, do not exactly follow the genetic lines of evolution. Consequently they are not " natural " in the sense in which we have hitherto used that word, taking for granted that beings that are closely allied *structurally* will necessarily also be closely allied genetically. This idea is nearest to exact truth, probably, in such things as the small sub-sub-species of *Rubus* or *Hieracium*, departing from it more and more as one goes upward to sub-genus, genus, and family, class. If a classification is to be useful in practice, therefore, it cannot be otherwise than artificial in great part, though such a family as the *Cruciferae*, clearly marked off by its tetradynamous stamens, showed clearly enough in the very artificial system designed by LINNAEUS for practical purposes, and would probably be equally well defined in any other artificial system. From the point of view of the average enquirer, therefore, it would seem better frankly to acknowledge the artificiality of our present system, and to design a simpler one for general use.

The species or genus A gives rise to B, and so on, and the question at once comes up why A should be the head of a family and not also B in turn. It is fairly clear that B and its descendants must follow the same rules as A, which is only one generation further back. At each upward step, the divergences tend to become more clearly defined, though not necessarily larger. They are *older*. The result is that at each step upwards it tends to become more difficult to connect to the next step again, so that at last we come to B and A. We can connect B to A as its parent, but the next step above that is often very difficult to take, and so we agree to regard the group headed by A as a family. At each step upwards, too, the number of genera of sufficient size to be the parent of the one that we are considering becomes smaller. All this seems to indicate that "larger" mutations, whatever that may mean, are commoner the higher we go. But whether a mutation from Di- to Mono-cot, though rare, is really a larger one than usual, we do not know.

The first mutation in Compositae from *Senecio* probably gave rise to *Hieracium*, thus beginning the two great sub-families *Tubuli-* and *Liguli-florae*. But as yet we have no means of knowing for a certainty that all the former are descended from *Senecio*, or the latter from *Hieracium*, for the divergence between them may have been repeated, or reversed, at some other mutation. This is rendered almost a certainty by the much greater number of the *Tubuliflorae*. *Hieracium*, again, is not only the child of *Senecio*, but is the parent of the heads of the two great sub-tribes of *Liguliflorae*, the *Crepidinae* and the *Leontodontinae*, whether directly or not. The same kind of behaviour is seen all through a family, right down to the heads of the sub-genera, and even down to the heads of the sub-species of such things as *Hieracium* or *Rubus*.

This new outlook, after all, agrees better with what has been so clearly made out in the physical sciences during the last twenty years, and as biology has necessarily a physical basis, it need be no surprise to see mathematical order appear in it also. If once established, and the evidence in its favour is already very great, it may have important bearings upon the various sciences of life, such as ethics, politics, or government. Since our early publications of 43 years ago, we have now spent our leisure for 26 years, and the entire time of about 17, in collecting and marshalling facts, in making deductions by the methods described above on p. 249, and in writing them up in a trilogy of books, and in many papers. But there remains a great assemblage of papers upon statistical facts, and other work, which should be very useful to other workers upon these lines, and which we hope to be able to put in order. The possibilities of new directions of research that are opened out by an acceptance of the views that are here being put forward are very considerable. We venture to hope that in future geographical distribution will be less despised and rejected than in the past. To it, we think, may be applied a quotation from TYNDALL, *The Glaciers of the Alps,* p. 13 of the Everyman edition. Describing a glacier, he says "At first the ice presented an appearance of utter confusion, but we soon reached a position where the mechanical conditions of the glacier revealed themselves, and where we might learn, had we not known it before, that confusion is merely the unknown intermixture of laws, and becomes order and beauty when we rise to their comprehension ".

Having now given, as usual, the necessary connection to the series of predictions and deductions from the facts, of which we are constructing this book, let us go on with the illustration of our theme by individual families, taking the *Araceae*, which incidentally shows that Monocots behave like Dicots. It has been worked up (in *PR*) by a firstrate taxonomist, my friend the late Prof. ENGLER. It shows the usual splitting at the top of the family into the heads of the subdivisions of the family, and also shows some other interesting features that require consideration. Of its eight sub-families, the last two are very small, and the last of all, *Pistioideae*, contains only the pantropical water-plant *Pistia Stratiotes*.

Any family, other than very small, is usually found to be composed of a few larger genera at the top, well separated by structural characters and by numbers of species, and a larger number of " ones " at the bottom, while between there are genera increasing in size, with less and less overlap in size the higher that one goes. As we have seen, it is the larger genera that give their characters to the sub-groups, each of these beginning with one of them. Thus any grouping necessarily tends to be more or less of a hollow curve, and it is this fact which has specially impressed many of my opponents who wish to prove that these curves are " accidental ", but neglect to explain why each of them is usually headed by one of the large genera at the top. The more that we break up the family into smaller units of classification, the less do the divisions, though each usually begins with a large genus and ends with increasing numbers of small, approach to the true logarithmic curve, which shows well in the larger families (fig. on p. 262). Their curves are often so irregular that one is surprised when one finds them adding up to a normal curve. This irregularity fits very well with that of their geographical distribution, which is very well shown indeed in the *Araceae*. Let us therefore begin with the usual list.

The Araceae, in order of world size (PR)

1.	Anthurium	489	Heading	*Pothoideae*	Trop. Am., W. I.
2.	Philodendron	222	Heading	*Philodendroid.*	Trop. Am., W. I.
3.	Arisaema	101	Heading	*Aroideae*	Warm As. Afr. E.N.
4.	Amorphophallus	90	Heading	*Lasioideae*	Palaeotrop.[2] Am.[1]
5.	Homalomena	81	2nd	Philod.	Malaya, trop. Am.[3]
6.	Schismatoglottis	75	3rd	Philod.	Malaya
7.	Alocasia	63	Heading	*Colocasioid.*	Indomal., Phils.
8.	Raphidophora	61	Heading	*Monsteroideae*	Indomal., Phils.
9.	Pothos	48	2nd	Pothoid.	Indomal., Madag.[4]
10.	Aglaonema	41	4th	Philod.	E. Indomal., Phils.
11.	Cryptocoryne	38	2nd	Aroid.	Indomal., Phils.
12.	Xanthosoma	38	2nd	Colocas.	Trop. Am., W. I.
13.	Dieffenbachia	27	5th	Philod.	Trop. Am., W. I.
14.	Monstera	27	2nd	Monster.	Trop. Am., W. I.
15.	Spathiphyllum	27	3rd	Monster.	Trop. Am., W. I.[5]
16.	Typhonium	23	3rd	Aroid	Indomal., Austr. 5.
17.	Stylochiton	22	4th	Aroid.	Trop. and S. Afr.
18.	Stenospermation	21	4th	Monster.	Warm S. and C. Am.
19.	Scindapsus	20	5th	Monster.	Indomal.
20.	Caladium	16	3rd	Colocas.	Trop. S. Am., W. I.
21.	Epipremnum	16	6th	Monster.	E. Indomal., Phils.
22.	Culcasia	15	3rd	Pothoid.	Trop. Afr.

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[1] Nearly all in MONSOONIA; 4 in ATL. N. AM., MEX.

[2] 34 spp. in AFRICA, mainly west and central.

[3] Six spp. (sub-genus *Curmeria*, probably an independent genus) COLOMBIA and VENEZUELA to COSTA RICA.

[4] One in MADAG.; none east of PHILS. [5] One in CELEBES and PHILS.

Cyrtosperma (11-12 spp.) has two in AMAZONAS and GUIANA, one in AFR. *Sauromatum* (4 spp.) is found from E. As. to AFR. (*cf. PR*).

23. Syngonium	15	4th	Colocas.	W. I., warm Am.
24. Anubias	12	6th	Philod.	W. Afr.
25. Arum	12	5th	Aroid.	Medit., Europe
26. Urospatha	12	2nd	Lasioid.	Trop. Am.
27. Biarum	11 or 12	6th	Aroid.	Medit.

and 2/11, 2/10, 1/9, 4/8, 1/7, 4/6, 2/5, 7/4, 3/3, 16/2, and 40/1, of which one (*Calla*, 1 N. Temp.) is head of *Calloideae*, and another (*Pistia*, 1 pantrop., a common water plant) head of *Pistioideae*, which contains no other genus or species, while *Calloideae* has three other monotypic genera, one, *Symplocarpus*, the skunk-cabbage, showing the same distribution in E. ASIA and E. N. AM. that is seen in some *Berberidaceae*, in *Epigaea*, &c (p. 89).

Very little study is enough to show that the distribution of the genera is peculiar. Some are confined to AMERICA, some to the old world, and there is little, if any, overlap. Being at a region where the PACIFIC is 6000 miles wide, the gap is serious. In each six of which the list is composed, there are some from both sides. The family was evidently started by the largest genus, *Anthurium*, with its first offspring, *Philodendron*, in S. AMERICA, the two, as is most usual, being in separate sub-families. But it is hard to imagine *Anthurium* crossing the Pacific in time to give rise on the other side to so large a genus as *Arisaema*, especially when one remembers how this is so largely north temperate. *Pothos*, which is tropical, and smaller, and was united with *Anthurium* by LINNAEUS, might be a part of that genus, on the other hand, but there are others between. One must also explain how the great gap, now filled with salt water, came, at so early a period, to be covered with the dense tropical forest in which these genera grow.

AFRICA evidently received its *Araceae* from the Asiatic side, and not in an eastward direction from the American, as is the more usual course. The size of the genera alone shows the course, or order, of formation. The two largest American genera have 489/222, Asiatic 75/63, African 22/15, and the average sizes of all the local genera are 28, 12, 5. If the family was monophyletic, the dispersal was evidently east to west, an unusual direction that at once raises the question as to whether it is not really polyphyletic, from two sources at any rate, even if *Pothos* belongs to the American line. Let us therefore begin with tables of the sub-families :

Pothoideae arranged by size and dispersal

1. Anthurium	489	Heading *Anthurieae*	Trop. Am., W. I.
2. Pothos	48	Heading *Pothoeae*	Indomal., Madagascar (1 sp.)
3. Culcasia	15	Heading *Culcasieae*	Trop. Afr.
4. Heteropsis	6	Heading *Heteropsideae*	Trop. S. Am.
5. Anadendrum	6	2nd Pothoeae	Indomalaya
6. Acorus	2	Heading *Acoreae*	N. temp., E. As.
7. Gonatopus	2	Heading *Zamioculcasieae*	E. Africa

and 2, 1, 1, 1, all Old World.

The dispersal of 1 and 4 should especially be noted; also of 3. The parent of *Culcasia* must have belonged to another tribe, or more probably sub-family.

Philodendroideae

1. Philodendron	222	Heading *Philodendreae-Philodendrinae*	Trop. Am., W. I.
2. Homalomena	81	Heading *Philodendreae-Homalomeninae*	Malaya; trop. Am.[1]
3. Schismatoglottis	75	Heading *Philodendreae-Schism'glottidinae*	Malaya
4. Aglaonema	41	Heading *Aglaonemateae*	E. Indomalaya
5. Dieffenbachia	27	Heading *Dieffenbachieae*	Trop. Am., W. I.
6. Anubias	12	Heading *Anubiadeae*	W. trop. Afr.
7. Zantedeschia	8	Heading *Zantedeschieae*	Southern Africa
8. Piptospatha	8	2nd Schismatogl.	Mal. Penin., Borneo
9. Peltandra	2	Heading *Peltandreae*	Atl. N. Am.
10. Microcasia	2	3rd Schismatogl.	Borneo

and 1, 1 *(Schism.)* Borneo; 1 *(Homalom.)* New Guinea; 1 *(Philod.)* Amazon valley; 1 S. Nigeria *(Anubiadeae)*; 1 Malaya *(Aglaonemateae)*; and 1 Zanzibar, Madagascar (Heading *Typhonodoreae*).

The dispersal of each genus of this remarkable list should be noted, for example the contrasts between 1 and 2; 3, 4, and 5, 6; all previous genera and 9; and even the contrasts in the last few.

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[1] Includes six species of *Curmeria* in the lower Andes from Colombia and Venezuela to Costa Rica, treated as a sub-genus by Engler, but more probably an independent genus with considerable resemblance; it is widely separated geographically, and there is no evidence of any fossils or transitions.

Lasioideae

1.	Amorphophallus	92	Heading	*Amorphophalleae*	Palaeotrop.
2.	Urospatha	12	Heading	*Lasieae*	C. Am., Brazil
3.	Cyrtosperma	11-12	2nd	Lasieae	Trop. As.[1]
4.	Dracontium	10	3rd	Lasieae	Trop. Am.
5.	Cercestis	9	Heading	*Nephthytideae*	W. Afr.
6.	Anchomanes	4	2nd	Amorphoph.	Trop. Afr.
7.	Nephthydis	4	2nd	Nephthytid.	W. Afr.
8.	Pseudodracontium	3	3rd	Amorphoph.	Siam, Indo-China
9.	Echidnium	2	4th	Lasieae	Hylaea, Guiana
10.	Montrichardia	2	Heading	*Montrichardieae*	Trop. Am., W. I.

and 1 Bengal, 1. W. Afr., 1 Himal. Assam, in *Amorphoph.* 2 trop. As., 2 S. Ind., 1 Mal. Pen. Borneo, 1 S. Braz., in *Lasieae,* 1 W. Afr. in *Nephthytideae* (a definitely West African group).

Colocasioideae

1.	Alocasia	63	Heading	*Colocasieae-Alocasiinae*	E. As.
2.	Xanthosoma	38	Heading	*Colocasieae-Caladiinae*	Trop. Am., W. I.
3.	Caladium	16	2nd	*Colocasieae-Caladiinae*	Trop. Am., W. I.
4.	Syngonium	14	Heading	*Syngonieae*	W. I., warm Am.
5.	Steudnera	8	Heading	*Colocasieae-Steudnerin.*	Himal., SE. As.
6.	Colocasia	7	Heading	*Colocasieae-Colocasiin.*	Trop As. Medit.
7.	Schizocasia	4	2nd	Colocas.-Alocasiin.	E. Indomal.

and 2,2 trop. As., Afr. *(Steudn.)*; 1,1, Colombia, 1 Matto Gr. *(Calad.)*; 2 Costa Rica, Colombia, *(Syngon.)*; and *Hapaline,* heading *Colocas-Hapalininae,* 2 Burma, Mal. Pen.; and *Ariopsis,* heading *Ariopsideae,* 1 Assam to *Travancore.* Here we have two very small leaders, due to the need for splitting involved in the structural divergence.

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[1] 2 spp. S. Am., 1 W. Afr. The whole list is geographically wrong.

Monsteroideae

1. Raphidophora	61	Heading *Monsterieae*	E. Indomal., Cey.
2. Monstera	27	2nd Monsterieae	Rio to Mex., W. I.
3. Spathiphyllum	27	Heading *Spathiphylleae*	Mex., trop. Am., 1 sp. in Celebes Phils.
4. Scindapsus	21	3rd Monsterieae	E. Indomalaya
5. Stenospermation	21	4th Monsterieae	Andes, Peru-Costarica
6. Epipremnum	16	5th Monsterieae	E. Indomalaya

The rest are, in *Monsterieae*, 11 trop. AM., 2 W. AFR., 1 VENEZUELA, 1 AMAZONAS, 1 MAL. PEN.; and in *Spathiphylleae*, 2 NEW GUINEA. Note the species of *Spathiphyllum* in CELEBES and PHILS.; also the contrasts of generic localities.

Aroideae

1. Arisaema	101	Heading *Areae Arisaematinae*	Warm Old World Atlantic N. Am.
2. Cryptocoryne	38	Heading *Areae Cryptocorynin.*	Indomal., Phils.
3. Typhonium	23	Heading *Areae Arinae*	Indomal., Austr.
4. Stylochiton	20	Heading *Stylochitoneae*	Trop. and S. Afr.
5. Arum	12	2nd Areae Arinae	Medit., Europe
6. Biarum	11 or 12	3rd Areae Arinae	Medit.

Here again are geographical puzzles, shelved by placing them in separate groups; let us take the detailed classification.

Tribe	N° in *PR*. Genera		
1. Stylochitoneae	76. Stylochiton	20	Sudan to S. Afr.
2. Asterostigmateae	85. Spathicarpa	6	S. Braz., Parag. A.
	79. Taccarum	4	trop. S. Am.
	80. Asterostigma	5	Braz. Parag. Boliv.
	82. Spathantheum	2	Bolivia
	83. Gorgonidium	1	Malay Archipel.
	and 1, 1, 1, 1, Cuba, Andes, Goyaz, and S. Braz. Uruguay		
3. Protareae	86. Protarum	1	Seychelles
4. Callopsideae	87. Callopsis	1	E. and S. Afr.

Tribe	Nº in *PR.*	Genera		
5. Zomicarpeae	90.	Zomicarpa	3	Bahia (Brazil)
and 1, 1, 1, Colombia, Hylaea, Bolivia				
	89.	Xenophya	1	New Guinea
6. Areae Arinae	97.	Typhonium	22	Indomalaya
	96.	Theriophonum	5	Ceylon to Ganges
	98.	Sauromatum	4	E. As. to Afr.
	93.	Arum	12	Medit. Eur. C. As.
	100.	Biarum	11 or 12	Medit.
and 4, 2, 1, Medit. to C. As.				
Arisarinae	101.	Arisarum	3	Medit.
Arisaematinae	102.	Arisaema	101	Monsoonia, temp. E. As., Atl. N. Am.
Pinelliinae	103.	Pinellia	6	E. Asia
Ambrosiniinae	104.	Ambrosinia	1	Medit.
Cryptocorynin.	106.	Cryptocoryne	38	Indomalaya
	105.	Lagenandra	5	Ceylon, S. India

Finally, there are two very small sub-families, *Calloideae* with four monotypic genera, *Calla*, widely spread over N. temperate regions, and found fossil, with three others in E. Asia and N. America; and *Pistioideae*, composed only of the pantropical water-plant *Pistia Stratiotes*.

In the *Aroideae*, in spite of all the splitting, no harmony can be made between the structural and the geographical classification, so that destruction of the most inconceivable extent and selective efficiency has to be called in, while at the same time not only have the intermediates to be killed out, but the surviving genera themselves have to undergo vast destruction to reduce them to their present small size in so many cases. Look, for example, at any of the structural groups that have not been reduced to a solitary genus, and note that even then there are geographical discontinuities. For example, in the *Asterostigmateae*, we find only such small genera as 6, 4, 4, 2, and 5/1, one of these five being the very discontinuous *Gorgonidium* in New Guinea, the rest of the group being American. Or again, look at the *Zomicarpeae*, with only a 3 and 4/1 (again a very great number of ones for so small a parent), three of them and those widely separated in South America, the fourth in New Guinea. Again fabulous destruction is required, fully efficient, and in very small, probably young, genera. And finally the tribe *Areae* in this sub-family is split into six sub-tribes, but even then structure and geography are not well harmonised, though the pressing problems are less immediately obvious. Even in groups reduced to one genus only, we shall see that there may be disharmony within the genus. Most of the largest group, *Arinae*, are in the Mediterranean-Central-Asiatic region, yet the leader *Typhonium* and a follower *Theriophonum* are Indomalayan, and are not followed by any ones there.

Looking in a general way at all these lists, one cannot but be struck by the peculiar disconnected distribution that they show, with many genera in AMERICA and ASIA, though with little or no real overlap, while there are fewer in AFRICA, or in the Mediterranean region. In five of the eight sub-families, the first genus is divided from the second by the widest part of the PACIFIC. In *Pothoideae* and *Philodendroideae* the leader is American, in *Lasioideae*, *Colocasioideae*, and *Monsteroideae* it is Asiatic, while in *Aroideae* there is discontinuity between ATLANTIC NORTH AMERICA and the other regions where they are found. If the grouping be genetic, the crossing of the PACIFIC must have been in both directions, and by smaller and smaller genera, for the pairs are 489/48, 232/81, 92/12, 63/38, and 61/27.

These phenomena evidently suggest that the family arose from at least two separate heads, or is polyphyletic. It is very difficult to conceive of *Anthurium* crossing the PACIFIC in such early days, when, as it is mainly composed of species of forest undergrowth, it must almost certainly have needed the shade of forest for the whole 6000 miles journey, and finally reaching MALAYA in time to give rise to so large a progeny, in which it does not itself appear. And the difficulty is much increased when we remember that similar relationships occur in five sub-families, with continually younger and smaller genera, to say nothing of other pairs that seem to have behaved like this also. And if one take up the idea that the family is polyphyletic, one has to explain why the same sub-family characters appear independently on both sides of the Pacific in so many cases, though it is true that the cases of a few species in *Cyrtosperma* and in *Spathiphyllum* on both sides seem to point to the possibility that even a genus may be repeated. And it is also true that the sub-family characters are largely vegetative, not involving serious floral differences, so that it is possible that similar conditions might produce similar results here too, and we may leave it at that.

It would lead too far to go into further detail, but we have said enough to draw attention to the hopeless geographical-taxonomical incongruity, which cannot be explained upon the old idea of destruction of intermediates. The destruction must be so efficient as to leave no traces, though there is nothing even to suggest that there was ever any selection. The confusion is only increased by the splitting. To get an idea of it in another way, we have only to look at the genera that are confined to Africa :

The purely African genera of Araceae

Genus	Spp.	Sub-family	Tribe	Dispersal in Africa
1. Stylochiton	20	Aroideae	Stylochitoneae	Trop. Afr., Na.
2. Culcasia	15	Pothoideae	Culcasieae	Trop. Afr.
3. Anubias	12	Philodendr.	Anubiadeae	West Afr.
4. Cercestis	9	Lasioideae	Nephthytideae	West a. C. Afr.
5. Zantedeschia	8	Philodendr.	Zantedeschieae	Southern Afr.
6. Anchomanes	4	Lasioideae	Amorphophalleae	Trop. Afr.
7. Nephthytis	4	Lasioideae	Nephthytideae	West Afr.
8. Gonatopus	2	Pothoideae	Zamioculcasieae	East trop. Afr.
9. Afroraphidophora	2	Monsteroid	Monstereae	West Afr.
10. Zamioculcas	1	Pothoideae	Zamioculcasieae	E. Afr. Bourb.
11. Amauriella	1	Philodendr.	Anubiadeae	Nigeria
12. Typhonodorum	1	Philodendr.	Typhonodoreae	Zanz., Mad. &c
13. Pseudohydrosme	1	Lasioideae	Amorphophalleae	West Afr.
14. Rhektophyllum	1	Lasioideae	Nephthytideae	West Afr.
15. Protarum	1	Aroideae	Protareae	Seychelles
16. Callopsis	1	Aroideae	Callopsideae	East a. S. Afr.

Thus, confined to AFRICA, we have members of

Sub-family	Tribes	
Pothoideae	Culcasieae (all)	Zamioculcasieae (all)
Philodendroideae	Anubiadeae (all) Typhonodoreae (all)	Zantedeschieae (all)
Lasioideae	Amorphophalleae	Nephthytideae (all)
Monsteroideae	Monstereae	
Aroideae	Stylochitoneae (all) Callopsideae (all)	Protareae (all)

But there must have been, or more probably, must be, in AFRICA some parental genera for all these, especially as all the nine that are marked (all) are purely African tribes, which would mean " large " mutations from some other groups. Only the *Amorphophalleae* and the *Monstereae* have any members outside of AFRICA. AFRICA is, as we have seen, evidently the westernmost limit of the dispersal of the « *Araceae* ", and we have seen that the rule in such cases is, that the original leading genera of the family should be well represented—exactly that which is not the case here. Comparing this list with that of the leaders of the *Araceae* given on p. 267, the only outside genera represented at all are

3. Arisaema	101 spp.	Aroideae - Areae - Arisaematinae
4. Amorphophallus	92	Lasioideae - Amorphophalleae
9. Pothos	48	Pothoideae - Pothoeae

Only *Amorphophalleae*, be it noted, was represented in the list of African tribes given just above. *Arisaema* has only a couple of montane species in ABYSSINIA, *Pothos* a solitary one in Madagascar. *Amorphophallus* is the only possible outside parent for the African *Araceae*, *unless there has been vast selective destruction*, for which we have seen that little or no evidence can be produced. *Amorphophallus* is the fourth genus of *Araceae*, and the only leader really represented in AFRICA, with 34 species there, against about 82 actual local species, mostly in small areas. The tribe *Nephthytideae*, and the couple of small *Amorphophalleae*, are normal enough descendants in its own sub-family. *Aroideae*, on the other hand, though *Arisaema* is actually their head, only have a couple of species of this genus in the mountains of ABYSSINIA, which could hardly be parents to the three *purely African* tribes (one in the SEYCHELLES only) actually shown as the only representatives of *Aroideae* other than the two *Arisaemas*. In the same way, the one stray *Pothos* in MADAGASCAR could not be the parent of the two tribes of *Pothoideae* actually found in AFRICA.

The more we look into the geographical distribution, and compare it with the taxonomy, the more hopeless does the incongruity seem to become. And the old refuge resort of wholesale destruction of transitions or intermediates no longer offers any security now that we have shown that divergence is the marked feature of evolution, and that selection hardly comes into the matter at all.

The production of one form—be it species or genus, or of tribal or family rank—from another, was long supposed to be a gradual process, the most lately born individuals being better adapted to the local conditions than their predecessors, and replacing them by virtue of that superiority. Now that we have seen that it is not gradual, but sudden, there are various modifications that have to be made in our ways of regarding the process of evolution. In the first place, its immediate direction is reversed. In place of the former idea that small varieties were the first to be formed, and that these gradually separated by the destruction of the inferior transitional forms, into species, and later into genera, &c, we now have to regard it as moving the other way.

With the gradual formation of structures in the upward direction, by which they gradually increased in complication and in efficiency, adaptation and structure went hand in hand, but now that quite important structural changes may come about at a single mutation, the two things become independent. The essential feature of evolution is now the divergent mutation by which it goes on, producing a new species or other form at one operation. Adaptation thus takes an entirely different place; anything that has not inherited sufficient adaptation to survive and to reproduce will simply die out as a result of the continual competition that is always going on; and that will be the end of it. Success will be determined by inheritance of enough adaptation, but there is no longer any necessity for actual improvement in adaptation, though any improvement that may appear as the result of any mutation, and that does not cost too much in material or otherwise, will probably be retained as a matter of course, so that slowly the general standard of efficiency may be raised, though we do not know that an improvement will survive the next mutation.

When evolution is going on under the definite influence of some outward conditions, as for example in the *Podostemaceae* it is always going on (129,136) under the influence of the maximum possible plagiotropism, the mutations that take place under that influence will tend to show its effects, as the *Podostemaceae* show it in increasing dorsiventrality. There is evidently far more to work upon, and also greater variety possible, in the vegetative organs than in the floral, and the effect shows more there. As the parents will differ a little, the offspring will also tend to differ.

Under my working hypothesis (p. 96), at certain times a mutation of at least specific rank will happen in any line of descent. It will probably be conditioned more or less by some state of stress, perhaps temporarily increased by some more or less local happening. In the *Podostemaceae* we have even suggested that it may be possible that after a certain time such a mutation must take place, while the evidence of ordinary water plants, which live under very uniform conditions, without much strain, and show comparatively few species in a genus of very wide dispersal, seems to indicate that in them the rate of change is usually very slow, corresponding with the small and slow variation in conditions.

If the stress be definitely and always in a particular direction, like that in the *Podostemaceae* that urges them in the direction of dorsiventrality, or like that which in many regions that are or have been growing slowly drier urges the plants in the direction of reduction or protection of the transpiring surfaces, the mutations that subsequently occur may be in directions that give indication of the forces that have been at work. In the *Podostemaceae* one sees increasing dorsiventrality of structure, chiefly in the vegetative organs, and in the *Cactaceae* one sees increasing reduction of transpiring surface and increasing storage of water, the perfection of both of which would be theoretically reached in a spherical body, as full of water as possible, with the least permeable skin possible, a condition almost reached by some *Mammillarias*.

Thus on the whole, the outside conditions are still the determining force in evolution, but instead of working by selection of casual variations in directions that may be favourable, they work rather by actual compulsion of transitions in a favourable direction. If, as is usually the case, they are all working more or less parallel, and with more or less equal force, the mutation will not show any recognisable adaptational effect, but when one of them works much more strongly than the rest, as plagiotropism in the *Podostemaceae* is continually working with its maximum efficiency, there will tend to be a corresponding effect shown, as that family shows a continually increasing dorsiventrality in its vegetative organs, and even at times in the flowers.

Here one must not forget, as some writers upon adaptation seem to have done, the distinction between climate and weather. In any short period the weather in A or B may vary very much between wet and dry, warm and less or more warm, and so on, but on long periods this averages out, and we may say that the rainfall averages so and so, the heat so and so, and so on, and see clearly the difference of *climate* between A and B. A plant may be adapted to the climate of A, but will need a good deal of adaptability to stand the continual variation that is going on in warmth, moisture, &c. But the same plant would not also be adapted to B, unless the difference between the two were so small that it came well within the range of immediate adaptability.

So long as the averages of the climate of a place remain constant, so long will the adaptation of any plant that is suited to it remain also constant. But the conditions are not absolutely uniform over any region of uniform climate, and selection will pick out some species as best suited to such or such an association of plants, others as best suited to some other association. But if the conditions are definitely changing in new directions, especially in one definite direction (like that of greater dryness), then the whole or most of the plants will tend to show greater or less alteration in the direction of better adaptation to those conditions. The adaptation will not be gradually picked up by selection of those best suited, but at each mutation a definite step will be made, which will sometimes, or perhaps always, show some improvement in the reactions to the local conditions.

But under ordinary mesophytic conditions, more especially, or over any short period, any mutational changes that may take place will be dictated largely by purely internal conditions in the plant itself, and from an adaptational point of view will be quite indifferent, with no effect worth mention upon the life of the species. A good illustration is the specific difference between the two common *Chrysosplenia*. The flower is much the same in both, but one has alternate, the other opposite leaves. Both live together, covering much the same areas in the north palaeotemperate region, but *alternifolium* also goes beyond this into NORTH AMERICA, so was probably the parent species of the two.

In the local ecological grouping of the plants of the British or other flora into plant associations of many kinds, the plants found in one association are not plants that have mutated into new species to suit the conditions, or even simply to relieve any strain upon their make-up caused by those conditions. They are those plants that with the least strain can best live in those conditions, being picked out as such by ordinary natural selection. But if those conditions remained constant (which is exactly what they do not do) for long ages, mutations to suit them better might ultimately take place, as xerophytic structure, whether newly formed, or whether an advance upon previous similar structure, tends to appear in most young species (those confined to small areas) in SOUTH AFRICA for example (*cf. Penaeaceae*, p. 301).

Between plants that descend from different parents, the result of a change of climate may be *a general similarity of the vegetative body*, which is evidently the portion most likely to be affected by external climatic conditions. The change is unlikely to appear also in the flowers, that are much more likely to retain their general family features, which there is no reason to change, as they have nothing to do with climatic conditions, while in the vegetative organs no change that does not suit the changing conditions is likely to survive at all. In the cases where many plants, originally descended from the same ancestral genus (or closely related genera) are living together in the same conditions, the same floral structure and the same vegetative structure are likely to appear throughout that group, and to be greater than any vegetative likeness that there may be with some other group.

The taxonomic classification of the Araceae is given in the table which follows, but only sizes (taken from ENGLER's monograph), and not names, of the genera. The general tendency of taxonomy is to "split" continually, making new genera from parts of old, and so on. This makes the difficulties less conspicuous, but does not solve them. ENGLER has here carried it a long way towards its logical conclusion of a group for each genus, but not even all this splitting, into 42 groups for 109 genera, has laid to rest the geographical-structural discrepancy everywhere seen.

Subfam. I. *Pothoideae*			
Tribe	Pothoeae		48, 6, 2, 1
	Heteropsideae		6
	Anthurieae		489
	Culcasieae		15
	Zamioculcasieae		2, 1
	Acoreae		2, 1
II. *Monsteroideae*			
	Monstereae		61, 27, 21, 20, 14, 11, 2, 1, 1, 1
	Spathiphylleae		27, 2
III. *Calloideae*			
	Symplocarpeae		1, 1, 1
	Calleae		1
IV. *Lasioideae*			
	Lasieae		12, 11, 10, 2, 2, 2, 1, 1
	Amorphophalleae		92, 4, 3, 1, 1, 1
	Nephthytideae		9, 4, 1
	Montrichardieae		2
V. *Philodendroideae*			
	Philodendreae		
		Subtribe Homalomeninae	81, 1
		Schismatoglotidinae	75, 8,
		Philodendrinae	232,1,2 1, 1
	Anubiadeae		12, 1
	Aglaonemateae		41, 1
	Dieffenbachieae		27
	Zantedeschieae		8
	Typhonodoreae		1
	Peltandreae		2
VI. *Colocasioideae*			
	Colocasieae		
		Subtribe Steudnerinae	8, 2, 2
		Hapalininae	2
		Caladiinae	38, 16,
		Colocasiinae	7, 1, 1, 1
		Alocasiinae	63, 4
	Syngonieae		14, 2
	Ariopsideae		1

Sub-family VII. Aroideae		
Tribe	Stylochitoneae	20
	Asterostigmateae	6, 4, 4, 2, 1, 1, 1, 1, 1
	Protareae	1
	Callopsideae	1
	Zomicarpeae	3, 1, 1, 1, 1
	Areae	
	Sub-tribe Arinae	22, 12, 12, 5, [4, 4, 2, 1
	Arisarinae	3
	Arisaematinae	101
	Pinelliinae	6
	Ambrosiniinae	1
	Cryptocoryninae	38,5
VIII. Pistioideae		
	Pistieae	1

The way in which the larger genera give the characters to most, if not to all, the groups is well enough shown by the fact that the average size of the leaders of all these groups is 38, and that of their next followers only 5. Direct inheritance of characteristic features of the leading genera does not seem very pronounced when one finds the first three, *Anthurium*, *Philodendron*, and *Arisaema*, each with a tribe to itself (or practically so), while 17 others also have each a tribe.

Most of these groupings, in spite of the enormous splitting, do not even yet show complete congruity between structure and geography, nor do most of them show proper arithmetical arrangement, such as should come by dichotomous growth, and such as commonly shows in most families. A few small groups, like *Zamioculcasieae* with a 2 and a 1 in the same region of EAST AFRICA, or *Anubiadeae* with a 12 and a 1 in WEST AFRICA, are passable, but most show a good deal of incongruity, in spite of the fact that 109 genera have been placed in 31 tribes, and that three of these have been divided into 14 sub-tribes, making 42 divisions in all for the 109. No amount of taxonomic splitting seems to make any difference, for it does not (cannot) follow the lines of divergent mutation upon which all families have been formed.

The genera of the Araceae. Even to leave the family for the genera does not get us out of our difficulties. We have seen that it is improbable that *Homalomena* is really represented in AMERICA by the half dozen species of *Curmeria* which are at a higher level, and largely on the further side of the ANDES, in spite of the structural resemblance, and the same may be said of the two species of *Cyrtosperma* in SOUTH AMERICA and the one in AFRICA, and of the one very isolated *Spathiphyllum* in CELEBES and the PHILIPPINES. There is no evidence in favour of relicdom in any of these cases, other than structural, and we have seen how large are the divergences that may appear in that at a single mutation. If the writer's suggestion of kaleidoscopic mutation, already brought forward in several places, and discussed in the next chapter, be adopted, and it be realised that *all* the characters of *Araceae* are being handed down to them out of a kind of Pandora's box carried by their ancestors, the matter is made more simple, and one may begin to collect evidence in its favour by inductive methods.

Even within one genus as defined by structural characters only, one may at times find great geographical discontinuity, for which there seems no reason whatever. And owing to its being within the genus rather than the tribe, to imagine that the intermediates have been completely killed out over such enormous distances becomes even more difficult to accept, without definite evidence, which does not seem to be forthcoming.

We have seen, *e.g.* in *Evol.*, pp. 18, 59-60, 107, that adaptation must be generic to account for the wide area reached by so many genera that are large and therefore old, when the great bulk of their species are comparatively local, even in such an old and "successful" genus as *Ranunculus*. Even there only about 25 species cover very large areas, and one cannot imagine the other 250-odd to be provided with adaptational outfit in such a way as to make their areas form a hollow curve. There is no evidence to show that species compete seriously as units among themselves, as we have seen in *Evol.*, Testcase I, p. 90, and pp. 107, 142, 144, 166, 179, &c. The competition described in (28) is quite a different affair. It is between those portions of two already established species which happen to find themselves suiting the same conditions at one particular place, and resembles that between two individuals that is always going on. Why then should there be serious discontinuity among the members of a genus, unless we can show that a barrier has been interposed in an originally continuous area. But if we look at a monograph of any large genus, we are liable to find special structural discontinuity among species that are in close geographical relations, and great structural resemblance between species far apart (Cf. *Evol.* p. 155).

Let us look at *Cyrtosperma*, divided by ENGLER as follows :

Leaves sagittate
1. Lasiomorpha (mainly marked by several ovules); 1, West and Central Africa; 2, New Guinea.
2. Eu-cyrtosperma (2 ovules); 3, Polynesia, New Guinea; 4, Perak; 5, Solomon Is.?; 6, Sumatra, Java, Borneo, New Guinea, Phil. Is.
3. Uniovulatae (1 ovule); 7, Borneo; 8, Sumatra; 9, New Guinea.

Leaves tripartite, portions pinnatisect
4. Polytomophyllum (ovules 1-2); 10, French Guiana; 11, N. W. Central S. America (S. Gabriel).

There is a great gap between NEW GUINEA and AFRICA in § 1; and between AMERICA and ASIA between § 4 and the rest. The simplest explanation is to suppose that the characters were independently given to the sub-genera in question. In this small genus, §§ 2-3, or more than half the genus, is centred in the MALAY ARCHIPELAGO, evidently its original home. Finally § 4, of two species only, is separated from the rest by the whole width of the PACIFIC, and the ANDES, so must have arisen independently.

No reason whatever can be brought up for the discontinuity in this genus, upon the old conception that structural closeness involved geographical nearness, or destruction of the intermediate forms, and there also seems little possibility of our solution of an overriding genus (**151**, p. 165). The most probable solution seems to us to be that similar characters were being handed down on both sides of the gaps, and just happened to be combined in a fairly similar way in different places.

Something the same solution is suggested for *Spathiphyllum* which has 26 American species, and a solitary one in CELEBES and the PHILIPPINES (implying considerable age). The species is not even given a separate group in the classification of the genus, the main characteristic being that the petiole is vaginate to the knee, not to the middle, and the simplest explanation is again that of polyphyletic origin.

Or suppose we take a large genus like *Arisaema*, it is not possible, with the small detail available, to place the species in exact order by area as one places genera by size, but the most widely dispersed seem to belong to nine of 15 of Engler's divisions, which contain 92 species out of the 101 all told, so that it is clear that the earliest or oldest species show the greatest divergences, and tend to head the subdivisions of the genus, just as the oldest genera behave in a family, or the most widely dispersed sub-species of *Hieracium* or *Rubus* in the divisions of the species. Everywhere it is the same result; the earlier mutations of the leaders of families, of sub-families, of tribes, of sub-tribes, of genera, of sub-genera, of species, and of sub-species, in general show the largest divergences, and are the most numerous, or cover the largest areas. This fact, which seems ever to appear more distinctly, practically excludes the action of selection as we usually think of it, and gives little reason to suppose that advantage is seriously concerned in evolution, though of course any real advantage that does not cost too much will probably be retained, even if not inherited by the next generation.

We have called these divergences the largest, but as the same one may appear sometimes at the top, sometimes in the middle or lower, this is evidently not a correct description, and we must wait for further work to elucidate the position more completely. As the earliest in any single case, they will be likely to gain much in importance by having more descendants that are liable to exhibit them, and these descendants increasing more and more rapidly with the passage of time. One can hardly put down evolution to mere chance, when one sees how beautifully and simply all its laws work out in their operation, gradually making things more and more complex, and possibly bringing the greatest good to the greatest number, but with slow action. When we learn what these laws are, and can control them, so as to bring out the results that are desired, great changes may take place.

Most of the larger of the 15 groups of *Arisaema* show one or more species that are isolated from the rest by considerable geographical gaps, *e.g.* § 1 has an endemic species in Hong-kong, which is usually put down as a relic, but now that we have seen how little evidence there is for any destruction of the necessary intermediates, is much more simply explained as a probable case of polyphyletic origin. The largest group, § 5, has several widely separated species in SOUTH INDIA and CEYLON. Here probably the expansion of the large section in that direction was normal enough, and as this is a pattern of discontinuity common to many genera in different families, was probably caused by a change of climate which made the intermediate lower hills unsuitable to many things. §§ 7 and 11 show species in Atlantic NORTH AMERICA, again a common type of distribution (*cf. Epigaea* p. 89), with an explanation required that is common to all. The groups that are confined to comparatively small regions are small groups, as usual in such cases, with few species, showing smaller range, whether in structure or in geography. The regions where they are found are usually near the centre of the country occupied by the genus, where its species are most numerous. In this case, it is evidently the country of south east ASIA, from the HIMALAYA to CHINA on the one side, and to INDO-CHINA on the other.

Amorphophallus and other large genera show similar phenomena to those we have just seen, but with the total range gradually contracting as the species become less numerous (law of size and space). There are eleven sections, and as usual the structural arrangement mixes up species that are widely separated geographically, without always an overrider. Thus 17, 18 are in the MALAY islands, 19-23 in tropical AFRICA, 23-9 in SE. ASIA, 30 on the GOLD COAST, and so on.

Wherever one looks, one finds this great difficulty of taxonomic-geographic incongruity. It is manifested in a simple way in the great variety of taxonomic relationships that show everywhere, for example in the flora of BRITAIN, where so great a proportion of the taxonomic groupings are to be found, even in quite small families, and one finds the same kind of thing even in genera and species, and we have also seen that it is due to the early breaking up of the leaders by divergent mutation, and is quite independent of selection, adaptation, or relicdom.

If then we are searching, as we always profess that we are, for genetic relationships, it is clear that they are not to be found simply from the taxonomic facts (mainly of structure), or the geographical facts, but that these must be combined with genuinely genetic investigations, and the combined results used. We have no right to call upon selective destruction in the light-hearted way in which we at present do, to explain the structural relationship between species 1 of *Amorphophallus* in FORMOSA, and species 2 in SIERRA LEONE, for example. There is no evidence for such colossal selective destruction. Now that we have shown that structural divergence is a characteristic feature of evolution, the old explanation, it seems to us, is no longer valid. The destruction that has so often occurred was usually not selective destruction at all, but indiscriminate, due to changes of conditions that were so rapid and so complete that they killed off many species together, before these could acclimatise themselves to the new conditions. If one add together all the localities of any one genus, for example those of *Amorphophallus*, one will often find, as we saw in *Rhamnus* (p. 107) all the geographical regions covered whose conditions are suitable, while the gaps are reduced mainly to those which are common to many species that have all been exterminated by the same cause, such as the incoming of the sea, or a great change of conditions. There is no evidence for *selective* destruction upon the scale so often demanded. And now that we know what great changes a single mutation can bring about, there is no longer any need to call it in, nor would it be reliable as a proof were it feasible. We no longer require evidence of gradual intermediates between extremes.

It is very clear that, as we indicated in Chap. IV p. 89, we must draw a very distinct line between what we there distinguished as real, and structural, discontinuity. The former is due to the interposition of some serious barrier in what was once a continuous area of distribution. Upon the country occupied by this barrier, be it a stretch of sea, a mountain chain, a desert, or something else, the conditions would ultimately no longer allow any species of the previously present genera to exist, unless perhaps a few survivors, or some local endemics better suited to the local conditions, that might occur, especially at the higher levels. The discontinuity thus affects a considerable number of genera *alike*, as we may see in the great number common to both old and new worlds, in all of which a gap has been made by the ocean; or again, in the plants on both sides of a mountain chain or a desert, or those common to EAST ASIA and EAST NORTH AMERICA (p. 89).

The ease with which this explanation gets over the difficulty of real discontinuity, which usually involves large genera, has led to its almost universal employment to explain structural discontinuity, which is more commonly shown by small genera, and is shown in almost every conceivable direction, the different directions rarely coinciding. The result has been rather to bring the explanation into disrepute. The structural likenesses between species or genera that are far apart are much more probably due to polyphyletic appearances of the character that is in question as showing structural affinity.

Suggested origin of Araceae. In making suggestions like those that follow, for as yet there is little to go upon, the author fully realises that he is going beyond the present bounds of inductive reasoning and knowledge, into the land of speculation, hitherto the great hunting ground of many would-be students of distribution. But he wishes to show that with the now reduced value and importance of mere structural resemblance, other speculative possibilities are open, that are just as probable as those put forward in the past. The work described in this book opens up new directions in which direct inductive work may be done, and new directions in which such subjects as genetics may be brought into play in the study of the problems of distribution, which in their earlier stages we have now seen to be governed by simple and definite laws.

The two questions that mainly come up in the present connection are (1) if the *Araceae* are polyphyletic, what was, or what were, the American and the Asiatic ancestors, to say nothing of AFRICA for the present; and (2) what determines the productions of the similar results that may frequently be observed under the influence of similar conditions, results which we often call adaptation to those conditions, and have often put down to simple selection of casual alterations in the direction of greater efficiency?

The first question at once splits into two : was the ancestor a member of the *Araceae* at all, or was it (as in any case the original ancestor of *Anthurium* must have been) of some other family, and if so, what? There is little evidence of direct genetic relationship between the American and the Asiatic *Araceae*, unless perhaps *Anthurium* and *Pothos* are parent and child. But there are larger genera than *Pothos* in ASIA, and to have the relationships that are hinted at by the sizes of genera would require a return journey to AMERICA by younger genera. With no evidence for any transitions or intermediate links, between the American and the Asiatic genera, it is going beyond the bounds of reasonable speculation or probability to drown the supposed transitions in five different cases, in anything up to 12,000 feet of water; whilst to join these genera by way of AFRICA is even more impossible. It would seem not improbable that the American genera on the one side and the Asiatic on the other were independent descendants of some genus or genera that did not belong to the *Araceae*. What genus best fulfils the necessary requirements has then to be found. ENGLER says that *Pothoideae* are evidently the oldest group, and are only distinguished from *Liliaceae* by the fleshy outer integument of the seed. But there is no genus in *Liliaceae* as large as *Anthurium*, nor do they affect similar habit of life. In general, it must be a larger genus than *Anthurium*, at least on the American side, for we have seen that destruction, hitherto so much and so lightheartedly invoked, is a broken reed upon which to lean. In the Monocots themselves, the only genera that seem large enough, and widely dispersed enough in more or less similar conditions to have been in both western and eastern tropics in time to be the ancestral genus in both, are perhaps *Carex* and *Dioscorea*, while in the Dicots there are rather more, especially *Begonia* (800 spp.), *Miconia* (600), and perhaps the most probable of all, *Piper* (750) with its follower *Peperomia* (500). *Miconia* is confined to AMERICA, and does not grow in quite the same conditions, nor does *Carex*. The choice perhaps lies between *Dioscorea*, *Begonia*, and *Piper*, with the probabilities in favour of the last, though it involves a mutation from Dicot to Monocot. It is noteworthy that in the families of these three, there is a distribution of sizes not unlike that which we have seen in *Senecioneae* (p. 177) and in *Siparuneae*, with a great gap below the leader :

Dioscoreaceae : Dioscorea (600), and 20, 5, 4, 3, 5/1
Begoniaceae : Begonia (800), and 10, 3, 2, 1
Piperaceae : Piper (750), Peperomia (500), and 8, 6, 5, 2/2, 2/1.

One can imagine that this gap is possibly filled in reality by members of some other family altogether, and now that we have seen the divergent way in which evolution works, it is not completely improbable that some of the missing genera were *Araceae* in two or more distinct regions. It is at least as probable an explanation as the old one, and shows the way to investigation that might produce interesting and perhaps unexpected results. If *Piperaceae* should prove to be the ancestral family, it will be a step on the way to proving the frequently suspected polyphyletic origin of Monocots.

Similar conditions, similar results. In the *Podostemaceae*, we have seen similar conditions producing similar results, but not identical, in different regions of the world. When once the family started to live always upon naked rock in flowing water, it was committed to very definite and strongly marked conditions. The plants were usually forced to lie down, and the rock prevented the roots from taking their normal downward course, so that the plants came under the maximum possible influence of plagiotropism, from which there was no escape. The most widely dispersed genus, *Podostemon*, shows comparatively little dorsiventrality, but the younger and more localised genera tend to show more and more of it. As this is a family which by its plasticity lends itself rather well to experimental work, it may be worth noting that in the opinion of the writer the best taxonomic work that has been done is, by much, that of Tulasne among the general workers. Most writers have used only herbarium material, where the peculiar mode of life makes it impossible to get proper specimens, even if the rock, to which the *Podostemaceae* cling like limpets when alive, though the free parts fall away when dried, be removed also, and so have much confused species with one another. Even Trimen's descriptions of the Ceylon species, though they are to be found in the river a mile from the herbarium, were done from herbarium specimens, and he has drawn a pencil through the leaves in a (correct) drawing by the Peradeniya draughtsman, W. de Alwis, with a note " obviously algae ".

I can remember finding several species mixed up on a sheet in the great herbarium at Kew. Examination of the living plants *in situ* is required for really satisfactory results. Just before leaving Rio we found that seed could be cultivated in the little mountain streams in the gardens.

The effects of this strenuous urge towards dorsiventrality working upon the plasticity of the material due to its subaqueous life, have been to produce a general likeness throughout, though one must point out at once that the changes that have gone on to produce that likeness are changes in the vegetative organs; the flowers were much alike to start with, and have remained so. It is of special interest to note that there is a marked difference between the *Podostemaceae* of America and those of Asia, so much so that one can usually say offhand from which continent a specimen comes. Those of Africa again are sometimes different from either. In America the dorsiventrality shows chiefly, but not exclusively, in the production of large leaves, while in Asia a thallus is more usually produced, commonly a flattening and virescence of adventitious roots. Differences between parents result in differences between offspring, as one would expect. But the differences show mainly in the vegetative organs, though there is a marked difference in the flower of *Podostemaceae* and that of *Tristichaceae*, the former being markedly dorsiventral, though it stands very erect; this dorsiventrality becomes more and more marked, up to its extreme in the very local *Farmeria* of Ceylon and S. India (**129**). Illustrations of the amazing variety shown by the vegetative organs in this family will be found in (**148**).

Another example of this production of similar results by similar causes is shown by those plants which have gradually become subject during their dispersal to drier and drier conditions, till at length they have been forced, in their mutations, to adopt storage of water, and we see a general resemblance in such things as *Cactaceae*, S. African *Euphorbias*, and other xerophytes, including the bulbs of tropophytic bulbous plants, of epiphytic orchids, &c. In these the ultimate tendency seems to be toward the spherical form, which is the most economical of all. In other places the tendency has been, probably owing to some peculiarity of the parents, to a production of phylloclades or of phyllodes; in others again to the reduction of the transpiring surface to a minimum by the production of small leaves, twiggy green shoots, and so on.

A troublesome and at present inexplicable question is why there are so many morphological likenesses, in both vegetative and floral organs, between *Araceae* on both sides of the PACIFIC, for the sub-families, as we have seen, seem almost to make a point of appearing upon both sides, though we have seen what difficulties there are in the way. But if their ancestry was from an overriding genus, *Araceae* or not, there is a very fair chance that the similarity is due to that fact, for after all it only means going one generation farther back.

Whether similar conditions would produce likeness in floral organs that were unlike to start with is rather doubtful, but we have little or nothing to go upon at present, for want of proper inductive investigation. The question really is, whether *Araceae*, and especially their sub-families and tribes, could arise independently on both sides of the PACIFIC. If the ancestor belonged to the same genus, it might quite well be possible for the family itself, but if this were not so, would be more unlikely. The question of the sub-families is a more difficult one, but it is worth notice that non-floral characters are a good deal used in their determination, for example presence or absence of latex, parallel or net veining of the leaves, tuberous, climbing, or other stems, &c. The whole question must evidently be shelved until more inductive work has been done, but has been brought up here in order to show that all possibilities of speculation are not yet used up, but that as reasonable an explanation of the facts is still possible as any previous one, and one which suggests feasible inductive work for its solution.

It is clear how in many cases, and especially in the *Araceae*, polyphyly may supply a solution to various problems that confront us. If characters are always, as we know to be the case with most, handed down in a complete condition from an ancestor, *whether that ancestor showed the characters or not*, it will explain many problems that have hitherto been somewhat puzzling, for example the problem of complexes. We have suggested above that the reason that they appear so much more in large genera, and therefore especially in the leaders of large families, is because only these have existed long enough to allow single characters of other genera of the family, and perhaps even small groups of characters, to have appeared in them, and to have been transmitted to so many descendants that they became " important ". If in a genus of say 500 species, some 50 were to show some character that was considered to be a marked character of some other genus in the family, there would be disputes as to whether this group of 50 should be kept among the 500, transferred to the other genus that showed it, or even made into a special genus with its own particular combination of characters. It is not difficult to find examples of the head of a family showing one or more of the special characters of other genera in the family, and we may instance *Hibiscus*, the head of the *Malvaceae*, where it occurs.

Conclusions. The *Araceae*, and the same is true of other families when studied in the light of the laws of ASA, of divergent dichotomous mutation, and of other principles that we have indicated, are anomalous in several respects, bringing up various problems difficult of solution. We have seen that they look normal enough at first glance, but really form a rather marked exception to the rule of monophyletic families, and in dealing with them I have in one place departed from my rule of induction-deduction, with definite purpose. To explain the distribution upon the old lines would require fabulous destruction of intermediates, in all directions, at all possible times, and disregarding such obstacles as the Pacific at its widest.

The whole evolution, if monophyletic, seems so incredible that I have suggested that *Araceae* are at least di-phyletic, with one parent for America, one for Asia, and perhaps even a third for Africa. These might belong to some overriding genus which would give a similar stamp to its offspring at great distances apart, and while if there were a more suitable Liliaceous genus, that would be the most likely, I have suggested *Piper* as a possible suitable candidate for the post, as it is apparently older, is more widely distributed, has many points of resemblance, and occupies somewhat similar localities to *Anthurium*. Mutation to monocot structure is probably simple, and the difficulty is largely to explain why the same mutation occurred at such widely separated places. No reason can be suggested till we know something about the laws of incidence of character, of which at present we are ignorant. An interesting point turns up with regard to *Piper* itself in the fact that there is a great gap (in sizes) between *Piper* (and its follower *Peperomia*) before one comes to the few and small other followers, just as we saw in *Senecio* and *Siparuna*.

There is a great improbability of immediate genetic connection in the family, though the various groups tend very much to appear on both sides of the PACIFIC, to cross which would probably require that the whole route be covered with heavy tropical forest at a very early period. It is much more probable that there has been much polyphyly involved, and that similar conditions, probably acting on things that were not too distantly related and that were living under similar conditions, have produced similar results.

Polyphyly, which the writer has specially brought forward, is a great help towards the solution of many puzzling problems, such as the instances of character-discontinuity that we put forward in Chap. IV, and which find a good illustration in the *Araceae*. The reversal of the immediate direction of evolution to family-genus-species, for which we have given so many and so conclusive proofs, both in *Evol.* and above, involves an appreciable change of outlook in work upon many problems of biology.

Admittedly the whole problem is one of great complication and difficulty, but if any other theory than that which has so long held the field, and which has been shown to be so improbable and unsatisfactory, can be brought up, it deserves at least a proper trial, with inductive study of its premises. The writer is unfortunately now too old for this work, and has been reduced to bringing up a new theory, which seems at least as probable as the old, and one more easily tested by inductive work.

The new views bring simplification into the whole question, and bring evolution into line with the other sciences that are being placed upon a mathematical basis. To suppose that nature advances simply by a casual method of trial and error does not give her credit for the exactness of method that she is now being shown to possess in the physical sciences. Whether any mutation represents an advance is open to argument, but sometimes it must be so, and there will consequently be improvement in the long run, slow though it may be. At present we do not even know that an advantage may not again disappear in the same way as it came, by simple mutation.

It is more probable than any other explanation that all the characters shown by all the genera were handed down by ancestors in a dominant *or recessive* condition, and that their appearances were frequently polyphyletic, so that a character might often be shown that was not present at all in the immediate ancestor, and the latter might even have belonged to some other family. Such ideas will no doubt be unwelcome to many, but we have shown the great weakness of the old position and the probabilities in favour of the new, probabilities which seem to be converging with others in other branches of biology. We have also shown the great likelihood that our present system of classification is far from being genetic — as indeed is now being taught at Geneva and probably other Universities, on other grounds than those that we have here brought up.

It is clear that the species in regard to the areas that they occupy are governed by the rules of ASA, like the genera in their relative sizes. The whole scheme of evolution, as it is being developed here, has followed by deductions from the original discovery of age-area. It is thus assuming a much greater likeness to the growth, development, and dispersal of a single human family. There too, however well we may know the characters, featural, mental, or other, we cannot predict what the offspring of any marriage will be like. Both in animals and in plants, it would seem as if Galton's law, that about half the characters come from the two parents, a quarter from the grandparents, and so on, seems to be operative, but we must fit this into the law of divergent mutation in some way. It is not in the least clear what determines, at any birth, which if any characters shall be changed; probably there is some law that connects the two, for all the characters seem to exist as potentialities among the ancestors. One is familiar with the popular commentaries upon offspring, which in general only apply for one or two generations back; "he has got his mother's eyes", "she's the living image of her aunt as she was at her age", "he is taking to his grand-uncle's line of work", and so on, remarks for which there is usually much justification. The writer has taken, quite independently, to the lines of his grand-uncle, William Swainson, F. R. S., an authority upon geographical distribution a hundred years ago, and a great traveller, whose father was one of the seven original founders of the Linnean Society (*cf.* GAGE's history); a niece is just like her aunt was about the time of our marriage; his grandson is very like himself in feature, of course at the same age. Such remarks are very frequent in taxonomic works; we may refer to such a family as *Annonaceae* in (BH), where many genera are described as having the stamens of some other, the carpels of some other again, and so on.

This work thus opens up new avenues for speculation, and provided that these lead to inductive work, this is to the good as it may lead to progress. The most important feature about the writer's own inductive work seems to be that, as a reviewer of *Evol.* said: the confusing mass of facts making up plant geography begins to make sense... If mutation does proceed in some uniform and regular manner, Nature through evolution is unfolding as some vast stream of change more challenging to the imagination than the random variations of DARWIN.

CHAPTER XII

General Considerations

Evolution by divergence, downwards; classification; incidence of character; chemical analogies; permutations and combinations; kaleidoscopic mutation

In this chapter we have attempted to draw together some of the threads that run through the whole of this work, and it may be well to give an index of them.

Index

1. *Introductory.* So many changes in outlook are suggested that a further review seems advisable. We have seen how age and area led to size and space, with the complementary

law of size and age. By way of the hollow curve discoveries, these led in turn to dichotomous divergent mutation, with its corollary that evolution went towards the species, not conversely, and this led to further deductions, which are continually increasing. We have also seen how large and how divergent a mutation can be, not only in single species, but in the large families, tribes, genera, and other divisions. We have given many examples of these, showing how the descendants tend to go into other divisions than does the parent, and that automatically. The phenomenon, in fact, is completely general, and is a law of evolution. The turning of the evolutionary process back to front clears up at one stroke many difficulties that have long beset us, and makes the whole process much simpler and clearer.

Evidently species and genera began as very local endemics, gradually increasing in number, and spreading further afield, and that with increasing rapidity (" to him that hath ") as time went on (*AA*, p. 34), so long as not interfered with by other agencies or barriers. Evolution worked downwards towards the species, not away from it (*cf. Evol.*), in discontinuous mutation that covered a varying number of characters; and according to the size, number, and " importance " of the divergences, we have been accustomed to judge the rank of the newcomer, which has, however, not usually been recognised as such.

Perhaps the greatest difficulty that has always troubled the theory of evolution by selection of advantageous variations first presented in a very rudimentary condition, has been the considerable and discontinuous, often incompatible variation between one species and another. Many of the characters in common use show such incompatibility that one cannot trace them back to a common source, even in such simple cases as leaf glabrous/hairy, or ovule erect/pendulous. In nearly all cases, there is divergence somewhere, that cannot be made gradually to merge in some ancestor, selection or no selection. Such union, which must occur somewhere, is only possible if the joint ancestor was carrying the potentialities of both characters, but could only display one. Some kind of super-Mendelism is evidently at work. The first plant of the family, of course, was not necessarily carrying all the characters, afterwards displayed, in a ready-made condition. The possibilities were there if certain things were put together in certain ways. Each new divergence makes other ones possible, as the formation of a new compound in organic chemistry makes further combinations possible.

The mere fact that however far back one may trace angiosperms, one finds no sign of new families, goes to show that the upward direction of evolution from species, demanded by the older school, cannot be upheld. And the final proof that it must have been the other way seems to be given by the table on p. 173, which cannot be explained except by downward evolution, and the tables of leaders (cf. Index).

We have shown that mutation covers the whole divergence between two species at one operation, and selection is not valid in dealing with such. At most a choice may be made between the two *faits accomplis* of parent and child. As the latter must, when it survives, have inherited enough of adaptation to do so, and this, unlike that of the parent, centred upon the local conditions, the child will probably be at no disadvantage, unless by its small numbers. Its divergence will isolate it from loss by crossing with the parent.

Selection being thus eliminated as a leading urge in evolution, we no longer need to find the supposed great numbers of intermediates, whether as relics or as fossils. Many years ago, HOOKER said (*AA*, p. 205) " the advocate of creation by variation may have to stretch his imagination to account for such gaps in a homogeneous system as will resolve its members into genera, classes, and orders... ". For a long time we have been accustomed to believe that this could be done upon a system of gradual progressive development, though the thought of the discontinuities was always disturbing, and this was more clearly realised with the work of BATESON, DE VRIES, WENT, and others. The difficulty disappears with the acceptance of divergent mutation, which turns some of the evolutionary process back to front (not upside down), taking away the need for destruction of intermediates. There is now no reason for the death of the parent, so that the number of species and genera tends to increase upon the principle of compound interest, the logarithmic straight line. In this connection, one may look at DARWIN's diagram of evolution in the *Origin*, p. 91, with an actual decrease at first, followed by an increase at a far future date.

Characters, it would seem, are not usually acquired for adaptational value by selection along the road, but by some much more definite method, with a law behind it, which, as WENT said in 1907, had no adaptational aim, that indeed seems almost impossible under divergent mutation. Development of characters seems to be by the action of conditions, probably mainly external, upon certain internal characters. As none of them is likely to repeat itself exactly, the way is thus open for an enormous variety in evolution, as the number of characters increases, from which permutations and combinations can be formed. Upon the whole, the selection of the best individuals that is always going on will keep things always near the highest possible pitch of efficiency for the conditions met with at any particular place and time. But there will be no further progress in efficiency till possibly, though not necessarily, a new mutation may bring in a more efficient variety or species. And we must never forget that a plant depends upon the total efficiency of all its characters, any improvement probably costing material which will have to be made up elsewhere. Any mutation that lessens the total efficiency will be punished, probably by extermination.

Though the possibility of occasional acquisition of a character by selection cannot be excluded, it is probably rare. In the writer's early days, desperate efforts, in which he took a small part, were made to find adaptation in everything, with the result of almost complete failure. A much more probable view is that potentialities of all or nearly all characters are handed down from above by heredity, so that at any time, as far as we can see, any character found in a family, or more rarely outside of it, like the superior ovary in a few *Rubiaceae*, may appear. In the changes or divergences that this is liable to bring about at any mutation, it reminds us of the behaviour seen in inheritance by the laws of Mendelism. This does not in any way mean that in an early protophyte there *are* the characters of say the *Labiatae*, but that there are certain potentialities that if they go through certain changes in the future may result in *Labiatae*, but if they do not, no *Labiatae* will appear, or a family *Dubitaceae* may appear in their stead. The characters of *Labiatae*, or any other family, are, it would seem, a kind of chance lot that happened to come together in a way dictated by previous changes in the first ancestor of the family, and with no mutual correlation that we can yet perceive except that they generally cover all parts of the plant. For some reason unknown, they remained very constant in the heredity, and formed the family characters. But a very small change anywhere in the processes that went on would have produced a different result after a few mutations more, and would perhaps have given us a new family or families now quite unknown. These suggestions seem to get over the former difficulties about divergence and transitions, to a very fair extent.

One must not forget the possibilities in HARLAND's suggestion (*Evol.*, p. 62) of selection of slight genic changes. These might be added up till the strain upon the nucleus produced a divergent mutation, probably electrically controlled (*Evol.*, pp. 182, 47). But we do not know that such changes are actually adaptive, so that selection can hardly be expected to do much, and in a case like the pollen patterns of *Acanthaceae*, it would seem powerless. If two species meet with close similarity of stress, there seems no reason why they may not mutate upon more or less parallel lines, but that is about as far as we can go at present.

Without doubt, selection has proved itself an unsatisfactory explanation. Even without much other contradictory evidence, it is helpless to explain all the arithmetical results brought up in the establishment of the laws of ASA, the hollow curves, the dichotomous divergent mutation, the early production by the leader of the leaders of tribes, subtribes, and so on. The whole process of evolution and dispersal seems to be following arithmetical rules, and bearing out what YULE and the writer said in 1922, that evolution is unfolding itself by mathematical law, while the vital and other factors only cause temporary deviations from the dominant plan (and *cf.* summary in *Evol.*, p. 191). Beyond this statement the writer's lack of mathematical training will not allow him to go, but YULE (158) worked out a mathematical theory of evolution based upon our joint discoveries.

Under the conceptions that we have brought up, evolution seems to run with comparative simplicity and smoothness, and we have given above, and have in reserve, a formidable mass of favourable evidence. The kaleidoscope, which we have used as an illustration for 40 years, gives fair suggestions of what seems to be happening. The theories here put forward seem to explain with simplicity the difficulties whose pressure has long been increasing, such as the apparently casual and purposeless nature of the differences between species &c, the wide structural discontinuities so often seen between species of the same genus living near together, and the narrow ones sometimes seen when they are far apart. Destruction of transitions has been too much called upon, especially when it is often impossible to have a transition. Some may be explained by the writer's conception of an overriding genus or species (147).

One may see this impossibility of transition by looking at the list of CEYLON WEs on p. 111, and there is evidently no conceivable use-value in such divergences. They are evidently incidental results of the mutation, which readjusted the equilibrium of the nucleus, and may be compared to the chemical changes that so often occur when one brings together two bodies like chalk and an acid. The substances after the reaction are quite different from those before it; their atomic content is the same, but put together in a different way. There has been no destruction, but only a permutation to a new combination of the units. Sometimes the pressure of the surrounding conditions exercises a definite pressure in one direction, and there seems a tendency to produce mutations that show movement also in that direction, which one may, if one please, regard as "adaptation". Like causes tend to produce like results upon material that is not too dissimilar. Many xerophytes show such phenomena, which we may see in a small family like the *Penaeaceae*, which are localised in CAPE COLONY with five genera, *Penaea* (12 spp.) *Brachysiphon*, 5, *Sarcocolla* 4, *Endonema* 2, and *Glischrocolla* 1. Yet, as so commonly occurs, there are two tribes, showing once more that the direction of evolution must have been downwards.

All show ericoid habit with crowded evergreen opposite leaves, xerophytic characters which must have appeared in the first species of *Penaea*, probably *P. mucronata* the most widely dispersed. Their appearance was in some kind of response to the dryness of the country. The characters of this first species have been handed down, and as the family is evidently recent, it has not yet had time or opportunity for much variety. But young and small as it is, there is already an indication of the behaviour which in larger genera produces complexes, where the same character may appear unexpectedly in more than one place, and in different genera, for *Sarcocolla* has sometimes one, and *Glischrocolla* with its solitary species always one ovule, so that there are signs of intermingling. This kind of thing, upon a large scale, is frequent in large genera.

Even in so small a family as this, we have to use such words as usually, or sometimes, for the characters tend to alter, even the family characters, to some extent at every mutation. Larger size offers more opportunity for change, as one may see in *Violaceae*, where *Rinorea* with 260 species in the *Violeae* has sometimes an appendage at the back of the stamen, but shares the useless character with *Gloeospermum* in its own tribe, and *Amphirrhox* in *Paypayroleae*; sometimes it has not the appendage, and shares that divergence with *Melicytus* and *Hymenanthera* in its own tribe, and *Paypayrola* and *Isodendrion* in *Paypayroleae.* A still more complicated phenomenon of this kind is described in *Evol.*, p. 139, where the same divergence occurs in three separate but related families. It is in something of the same kind of way, rather than the trial and error once so much appealed to, that what we usually call adaptation has been brought about.

Evolution must apparently go on, though but slowly in such cases of uniform conditions as *Hippuris.* It is more rapid in *Podostemaceae*, though the conditions are perhaps even more uniform, for there is a constant pressure of plagiotropism, and a whole lot of useless modifications seem to have been brought about in response to that. Even in such plants as the more or less internal fungi, like the *Puccinias* (700 spp.) or the *Polypori* (500) there are many species, in spite of the apparent uniformity of the conditions. This may be due to the greater plasticity of the body of the plant, or more probably perhaps to the variety in chemical composition of different hosts.

As yet we cannot say whether outside pressure *compels* mutation in any given direction, *encourages* it by the gain that may result, or perhaps most probably *kills off* those mutations that go too far in any other direction. The known facts show that under the normal conditions of mesophytic life on land, for example, the mutations may affect any of the features of the plant, but especially, as is well known, those of the vegetative rather than the reproductive organs. It is even possible that some of the changes in the latter are correlated with those of the former.

But to the results of these periodical mutations, it is usually quite impossible to attach any adaptational value. In practically the whole list of divergences in CEYLON endemics on p. 111, the characters are neutral or indifferent. As we said in 1907 (**131**), one of these endemics, *Acrotrema lyratum*, " only occurs on the summit of Nillowekanda, an isolated precipitous rock in the Hinidum pattu. Is it to be supposed that the long peduncles that characterise this species are a special adaptation to the conditions on the very small area of the top of the rock? "

It was also pointed out in that paper how much simpler the tracing of descent becomes upon the theory of mutation with large divergences, and that unless these are actually harmful in the struggle for existence, there is no reason why " the whole tree of a family should not actually exist upon the earth at the present moment ". In a following paper, suggestions (very crude, for lack of more detailed knowledge) were made for a tree of *Dilleniaceae*, and many suggestions are made in this book.

2. *The laws of ASA*. We have already said so much about these, for example upon pp. 16-23, and in the two preceding books of this trilogy, that there is little to add. Age and area, the law from which all the rest of my work has logically followed, is described on pp. 16-19, and was the main subject of the first book, in which the law itself is dealt with on pp. 54-83, answers to objections on pp. 84-100, and a review by Dr GUPPY, the coauthor of much that is here brought up, upon p. 101. The law of size and space, deduced from age and area, is dealt with on pp. 113-8. In this book it is described on pp. 19-22, and illustrations are given. The third law, of age and size, necessarily follows from these two, and the laws of ASA (p. 23) are complete. They have proved to be universal in distribution, and by their application, apart from subsequent deduction, a good deal of the incoherent mass of facts that have so far constituted the subject of geographical distribution, may be reduced to order. Special instances of their applicability will be found, not only in the latter half of *Age and Area*, but also in *Evol.*,

pp. 27-32, where there is a brief summary of the whole position, in Testcase III, p. 69, and several other testcases, especially XXV, p. 140, and XXVI, p. 146. In this book, besides the description on pp. 16-23, there are references on pp. 26, 30-34, 38, 45, 50-58, and so on nearly all through.

3. *Competition individual, not specific.* In 1867 FLEEMING JENKIN made what DARWIN considered the best criticism made of his·ideas, changing them to suit it. JENKIN showed that evolution could only work with very small variations if the competition was between considerable areas of the new and the old, or any improvement would soon be lost by crossing. This, by making a new species begin upon a considerable area, caused the growth of the ideas of relicdom for species or genera of very small area. For many years we have been trying to show that there is no reason to suspect relicdom, except near the coming of the ice, or in other exceptional places, and indeed a glance at the map of the New Zealand *Ranunculi* on p. 65, or the S. American *Siparunas* on p. 224, makes the idea seem somewhat absurd. Even in *Ranunculus* itself, a bare 25 of its 300 species are really widely distributed. The distribution of the genera in BRITAIN goes largely with their size in the world, much more so than with any vital factor.

Part of the legacy involved in these conceptions of DARWIN and JENKIN was the idea that species competed as units, and that the competition reduced the older one to a relic, or killed it completely out. But with what we have now seen of the operation of the laws of ASA and of dichotomous divergent mutation, it is very evident that that idea must be discarded. Competition is a law of life, but it is not the controlling force of evolution.

We have referred to this matter at various places, notably on pp. 27-8, 88-9, 208-9, and many others. If competition is specific, or in other words if relicdom be the general rule, then we are on the way, as the writer has often pointed out, to a wholesale extinction of genera and species, so that ultimately only a very few will be the survivors, even in *Ranunculus*, old and large genus though it is. But there is nothing whatever to show any superiority of one species over another; the larger area occupied by some species is simply the result of their greater age, as has now been abundantly proved.

It is also, perhaps, not fully recognised that the competition that is really going on is much more complicated than a mere struggle between two species as to which shall win when one, for example, has ten stamens, the other only five, or one a superior, the other an inferior ovary. It depends in any single case upon the efficiency of the whole outfit of the one individual as against the other, and also upon whatever may happen to be, at that particular time and place, the whole pressure of the local external conditions upon the two competitors, which may and usually will differ at every time and place, and may even differ for the two competitors themselves, whose surroundings will be different. It is a competition restricted almost entirely to individuals; very rarely indeed, if ever, will a whole species take part in it, unless in the case of a new species beginning as a few individuals at a definite place.

Such competition as that described by CROMBIE in (28) is quite a different matter, for there it is a competition of two species of different genera, in one particular locality and set of conditions, but not over the whole range of these already established species. A comparison of the divergences given in the tables on pp. 111, 132, 165, &c above will show this clearly. All Smiths are not competing with all Browns, though John Smith and William Brown may be desperate rivals. Thomas Smith will win in one place, in one set of conditions, James Brown in another.

4. *The hollow curve.* Our work upon this subject has aroused even greater opposition than that upon age and area. Opponents have insisted that it is accidental, not realising, perhaps, that an accidental, but regular, occurrence is one that must have behind it some law or laws. Besides a good deal in *AA* (especially Chap. XVIII, p. 195) and in *Evol.* (especially Chap. IV, p. 33, pp. 96-7, Testcase V, p. 99, and on pp. 164 and 173), there are many references in the present book, of which we may just mention those on pp. 18-19, 30-35, 67, 124, 170, 185, 190-93, 204, 219, 258-9 (and curves).

YULE showed that the curve was just the *necessary* result of dichotomous mutation with survival of the parent. Some people think that the law of compound interest, which we have followed here, and which certainly gives a very close approximation, is too simple. It is for example, not improbable that the formation of new species does not exactly follow this law. But in dealing with such matters one must remember that nature was not out to create new species and genera, which are more or less artificial conceptions that deal with nature's divergences by making them into groups, which we regard as greater in standing (genera), or less (species). One cannot define these, but only describe them, and largely by mutual comparison. Not being a mathematician, the writer can only refer the makers of such objections to the paper by YULE, formerly President of the Statistical Society (**158**), and to our joint paper in (**159**). When a family is young, it follows very closely, as we have seen, the chief laws that we have brought out, those of ASA, of the hollow curve, and of dichotomous divergent mutation. But as it grows older, and especially as its leading genera begin to exceed about 20 species, other factors, whose gradual results only show themselves after long periods of action, begin to make their effects visible. Such factors are changes of climate, the effects of irruptions of the sea, of the formation or disappearance of mountains and other barriers, and so on.

There can be no doubt that the formation of the hollow curve is due to the action of a general law, and we owe this discovery to YULE, who showed that what the writer had suspected was due to the continual operation of dichotomous mutation with survival of the parent. In this connection, the first 12 pages of YULE's paper, which require no mathematical knowledge, should be read, as well as our joint paper in (**159**).

The 15 largest families of all show beautiful parallel hollow curves (fig. at p. 260) which by logarithms plot out into sloping straight lines (p. 262). Down to families of say 100 genera, the curves are good, but lower down, below say 20, they begin to become very irregular, so much so in many cases that one does not feel sure that they are really the early stages of the good curves shown higher up. Yet there cannot be one law for large and another for small, and the suggestion obviously is that some of the very small families, of which great numbers have been made in recent years (p. 341) upon structural considerations only, are not strictly genetic, as under the circumstances one might expect. But as we have shown that this is inevitable, it does not matter (now) from the taxonomic point of view, and the breaking up into separate families will probably be better for identification purposes. Now that we have seen that as one goes upward in a family from the small genera to the large, genetic relationship increases in closeness, while the divergences become more distinct, we can no longer take structural resemblance as the only, if even the chief, test of genetic relationship. Size of a genus, or area covered by a species, is of equal or greater importance. The largest genera in a family are the most closely related that is possible, though of course all over the family there are groups of genera that are equally closely related, formed in the same way by the descendants of a single mutation at the top, like the mutation that formed the head of the family.

One must not forget that the great bulk of genera and species are contained in the larger families at the top. Those with more than 100 genera are (*cf.* p. 173) only 28 in number out of 309, but they contain 8005 genera out of 12,516, or nearly 64% of the grand total. That the rule of " to him that hath shall be given " holds here as everywhere may easily be seen by noting that new genera are added in greater proportion to the large families. In the last issue of the Supplements to the *Index Kewensis*, there were 406 genera added to the 28 large families, and only 370 to the small 281.

The great irregularities shown by the smaller families, *e. g. Aceraceae* (*Sapindaceae*, genera of 110, 1), *Achariaceae* (*Passifloraceae*, 1, 1, 1), *Actinidiaceae* (*Dilleniaceae*, 250, 25, 12, 1), *Alangiaceae* (*Cornaceae*, 30, 20), *Aquifoliaceae* (180, 12, 3, 2, 1), and so on, show that there are probably several disturbing causes at work. But the grand total of all these very irregular families is so small that it is clear that if they were genetic they would be obeying the same laws as the large. Their formation has much in common with that of such a group as the sub-family *Thunbergioideae* in *Acanthaceae* (details on p. 216), which is founded on structural characters only, showing the somewhat marked divergence of papilla- rather than hook-shaped retinacula. This is shown in the large and widely dispersed *Thunbergia* itself with its 150 palaeotropical species, mostly African, but outside this genus is only shown in *Pseudocalyx* with one species in MADAGASCAR, and *Meyenia* with one in the EAST INDIES (these two evidently originating from different species of

Thunbergia at different places). It is evident therefore that the two or three intermediate genera, if there were any, must have mutated back to the group that contained the original parent of *Thunbergia* itself.

The divergence producing *Thunbergia* could evidently only be a mutation, and the genus has no genetic right to a special sub-family on that account. Probably the same thing may be said of many of the little families, especially those made during this century (the name of the family from which they were split off is given in the first four above). They are very convenient for purposes of systematic classification, but probably often have no right to be considered permanent genetic groups. We may almost look upon some of them as what we may perhaps call temporary extrusions from some other sub-group. They have been given their rank for structural reasons only, and we have now seen that the rules of taxonomy are necessarily different from those of genetic descent. We have not fully understood that incidence of character seems always to be determined by law, and have therefore had to work by " valuation ", which is well known to differ in almost every case, the real and only connecting link being that of age. Probably some of the direct descendants that ought to fill in the unexpected gaps, such as are found in *Thunbergioideae* or *Aquifoliaceae*, have reversed or altered the particular mutation that gave rise to their group.

Having regard to the rule of dichotomous divergent mutation, it is not easy to believe, for instance, that *Piper* and *Peperomia* (*cf.* p. 289), or such genera from small families as *Acer*, *Begonia*, *Canna*, *Dichapetalum*, *Dioscorea*, *Erythroxylum*, *Nepenthes*, *Oxalis*, *Plantago*, *Salix*, *Sauraujia*, or *Xyris*, have a real right to their positions as supposed heads of genetic families.

On the theories that we have adopted here, it is clear that on any one continent, the members of a family should be fairly closely related, arising as they do from one or more of the now large genera that have led the family or its subgroups from the commencement, and that in a large family tend to occur in many, or even all, of the continents. For example, taking the first five families by size from p. 173, and looking at their leaders, we find *Senecio* and *Panicum* in all five large areas in the world, *Astragalus* and *Psychotria* in four each, and *Dendrobium* only in two, though all the families occur in all five. In the single case of the *Compositae* we find the leaders down to 150 all more or less cosmopolitan, while the smaller leaders of the last four, none larger than 80 species, are all confined to one continent each. In such cases one must not forget the law of " to him that hath ".

If the laws that we have suggested hold, therefore, we shall expect that upon each continent each genus that reaches it, of over say ten species, will form a hollow curve in proportion to its size. The result of all this should be the formation of a combined hollow curve for each large division of the world. We have seen how this is the case in *Acanthaceae*, and in large divisions on pp. 180-1 in *AA*.

The hollow curve is a regularly recurring feature of the growth of a family, and may be added to the very many simple arithmetical demonstrations that show how mechanically followed out are the processes concerned in evolution and in geographical distribution, though they are interfered with in their regularity by the intervention of barriers, and other factors that cannot be easily foreseen, or discovered to have been intervening in the past, such as changes of climate, and other things. See diagrams at pp. 260-2.

5. *Divergent mutation.* We have already said much about this in Chap. V, especially on pp. 99, 100, and the description of teratology on pp. 100-105, and again in Chapter VIII, but there are still points of interest that must be clearly brought out. HITCHCOCK (**63**, pp. 4-5) says that " the generally accepted classification in use... is based upon genetic relationships. The theory of organic evolution assumes that the organisms of to-day are descended from similar, though slightly different organisms of the past, and that all organisms are genetically related... The modern classification of animals and plants is an attempt to arrange the groups of individuals in a system which shall represent their genetic relationships. "

It would seem that a somewhat different point of view will now have to be taken, as nature seems to lay great stress upon creating marked differences, to a greater or less extent, at every mutation, and we have been accustomed to lay too much stress upon close structural relationship in as many details as possible. We have considered as awkward difficulties those divergences, such as ovary superior/inferior, which appear to be part of nature's scheme. What the writer proposes in place of the older conceptions is what he has called dichotomous divergent mutation, whose essential features are pointed out upon p. 99. They include dichotomous mutation, survival of the parent, automatic isolation of the new form, well marked divergence in one or more characters, less in others, acquisition of the needful local adaptation by simple heredity, and no necessary improvement, though any deterioration is at once punished by natural selection, usually with prompt death. A new form is thus produced at one operation, ready to begin to spread with no risk of loss by crossing, if it can survive to the stage of reproduction.

The great tendency seems to be for the earliest mutations, whatever the character of the differences, to head the taxonomic divisions into which we split the family. These earliest mutations will be the most obvious, distinct, and " important in that family " because they are the oldest there, appearing before so many other mutational changes have come to (perhaps) obscure the first, though as a matter of fact they usually show clearly enough; and still more because, being the oldest, they can pass on some at least of their peculiarities to a great many descendants if the family be of any size. Though all these will probably inherit most of their peculiarities, there is no guarantee, nor indeed upon our theories any expectation, that they will inherit all, or nearly all, inasmuch as every mutation seems to change, more or less, more than one single character, in a divergent way. At present we know no laws governing the matter of the changes, which seem to come by mere chance.

The exhibition first of all of the leaders of tribes, subtribes, &c, working downwards to genera in these groups, and only rarely with a further break into something markedly divergent and new, shows that the greatest divergence of character is at the top, and that it diminishes downwards, though at times we may get a more " important " divergence than usual, producing even the head of a new genus, subtribe, or other group. At present we are quite in the dark as to why, when, where, and how these things happen, and it is one of the many new tasks brought up by all this work, to find answers to these questions. There seems no appreciable difference in divergence between the first two genera in a large, and the first two in a small family, but there is a fairly definite one between the divergences which on the whole are near to the head of a family, and those which are near to the foot. This difference, easily seen, but not so easily defined, though appearing on the whole to be marked by divergence in more characters, seems to the writer one of the most important points needing consideration in connection with the incidence of characters.

There is, as we have said, probably some systematic and perhaps arithmetical distribution of characters going on, upon what we have called super-Mendelian lines, which may need some work to elucidate. The characters are evidently handed down in such a way that every organ that existed in the parent is again provided with some character in its offspring, sometimes by a definitely divergent mutation, sometimes by a change of size which is more like a fluctuation, except that it has a new mean. At other times, and especially in the case of flower or fruit characters, the change is less noticeable, and the ovary may remain inferior, for example, changing only in minor features, which make no difference to its essential character.

As HITCHCOCK says on p. 5, " fundamental or inherent characters are inherited with certainty (the writer would add a proviso that any one might change at any time)... superficial are easily modified... inherited in a less certain or less definite manner. " This is largely the problem that lies before us. Why are there these differences in inheritance? Why do the family characters remain almost unaltered through a series of mutations? What selects certain characters for " inherence " in one group, while in another they may be rare, or variable? That at any one mutation any one character should remain unaltered is not surprising, but that two should do so, and remain in the same mutual relation is much less common, and that several, like the family characters, should do so, even though only to a great extent, is much rarer.

The larger the family, the greater the probability of exceptions among the smaller members, and of complexes among the larger. If all the unexpected characters that may appear in a large genus were to do so *together*, we might get a completely new family or genus, as we illustrated in (146). Or let us take *Psychotria*, the head of *Rubiaceae*, and put together all its unusual or " abnormal " characters, when we should get an almost herbaceous undershrub, 50 cm. high, with large dark-coloured four-pointed stipules united into a cup, heads of 4-merous flowers, 2-3 cm. long with very small bract and bracteoles; calyx oblique at mouth, corolla with circle of hairs at base, teeth horned as in *Rudgea*; ovary 5-locular, fruit with broad wings. All taken together, these characters would fully justify a new genus, but that they should all happen together is practically excluded by the ordinary laws of chance.

The heads of tribes are mostly in the largest (oldest) genera of a family, and tend to be the first to reach a given country, as we have seen in BRITAIN, so that as a rule a family with only two British genera shows a marked divergence between them. A genus A heads a family, and splits off B, which in three cases out of four heads a new tribe. It is by no means unlikely that the next two or three mutations may all be from A, which has a long start while B is getting established. A careful study of the genetics of the large genera might be profitable. For example *Begonia*, which has a very large series of chromosome numbers, has but very few and very small descendants that show its own main characters; most of the even numbers of the grasses occur in *Carex*, and so on.

The species behave in the same way as the genera, taking space rather than size. The British genera in A with only two species each, but with these accepted by all workers, show :

Achillea	L. linear, serrate; heads few, hemispherical L. much divided; heads many, small, ovoid	
Althaea	Perenn., with velvety down	Annual, with long hair
Anemone	L. ternate	L. bipinnate
Anthriscus	Umbels terminal	Umbels lateral
Arctostaphylos	L. evergreen, shining, box-like L. strongly veined, withering at end of year	
Asperula	L. about 8 in whorl	Opp., or 4 in whorl
Aster	Invol. bracts few, oblong	Many, narrow-linear

This bears out what we predicted above.

At the beginning of a family, the child is three quarters sure of being in a different group from the parent, but this rapidly diminishes in later stages. It is clear that rank goes mainly with the comparative age of the parent. This, in fact, is the principle which GUPPY named rank and range (*cf. Evol.*, p. 100). The effect of mere age has been quite ignored in taxonomy, to say nothing of the geometrical increase of numbers.

More than one character seems to change at each mutation, some more than others, while they are practically all unsuited to selection, and many to transitions. Some of the smaller changes may probably be attributed to the principle of compensation, a loss in one place being made good by a saving in another. This may be the reason why, for example, some species of *Krascheninikovia* (*Stellaria* p. p.) show dimorphic flowers, the sterile with petals, the fertile without. There are many such cases.

Divergences may occur in any character, and each new one may open the way to the possibility of yet others, so that on the whole, though some may be lost, the available total will increase, like the numbers of chimes that can be rung upon larger and larger sets of bells, so well described in *The Nine Tailors* of Miss Dorothy Sayers. We have seen how large and how divergent a mutation may be, in endemics in Chap. V, small genera on pp. 130-31, small families in *Evol.*, p. 199, genera that head tribes on p. 173 *et seq.*, and in species on pp. 182-3. In the early division of a family or genus, *no matter what the characters of divergence may be*, the offspring show a strong tendency to go into a different group from the parent.

As soon as it has become reasonably established, B tends to repeat the procedure of A, its early descendants including most of the heads of sub-tribes, and so on downwards, upon what we must regard as a diminishing scale of operation, from family through tribe to genus, species, and sub-species, where we have to use area of occupation as an index of age. If one follow the mutations of A, or B, and not those of their offspring, we seem to keep to " larger " mutations. But there seems little or no difference in rank of the first mutation shown by a large, or by a small family. The whole subject needs much intensive study.

What are often called transitions to other families or genera are in my conception simply appearances by divergent mutation of characters that more distinctly mark other families or genera. Such are, for example in *Rubiaceae*, the whorled leaves of some *Argostemmas*, *Limnosipaneas*, &c, the sometimes winged seeds in *Anotis*, *Kadua*, or *Sickingia*, no endosperm in *Henriquezia*, and so on. The last named, with its zygomorphic flowers and other peculiarities (for *Rubiaceae*) is often called a transition to *Bignoniaceae*, but now that we know that the whole step may probably be accomplished at one operation, it is no longer necessary to look for transitions. There are no transitions in single characters, except very rarely. What such things as *Henriquezia* represent is really a mixture of characters, of the one side or the other, but just as finished as usual.

In the case of large families, it is necessary for reasons of convenience to break them up into more subheads than in the case of small ones, where two lines in the key will often suffice. The larger number of subgroups in a big family (*cf*. table, p. 173) is thus partly due to such needs, and they are not always so well distinguished as in small.

We have dealt with evolution in many places above, in the whole book *Evol.*, and in places in *AA*, and we shall carry it further in the section upon the Orders, upon p. 323. Selection and adaptation being now excluded as important agents in urging it on, though they cause "deviations this way and that from the dominant plan", the latter becomes a good deal more mechanical. The size of a divergence matters less than its age, and the isolation that age gives to it. The principle of "to him that hath shall be given" thus assumes very great importance as a law of distribution. Even in the details of ecological distribution, as we have seen on pp. 24-8, 38-9, and 42, the most widely dispersed species of a country include most of the dominant species of its associations, which were simply among the first to arrive there, so that they have become specially well adapted to the local conditions, and that in a variety of places.

Under "Darwinism" such things as the innumerable sub-species of *Rubus* or *Hieracium* had to be regarded as incipient species, but, as we have pointed out on p. 184, this is no longer necessary. They are later ripples of the evolutionary wave which is dying out, and not the first ripples that come with the onset of the wind, and gradually unite and develope into larger waves.

In the lifetime of the flowering plants, with which we are mainly concerned, it is not yet possible to say with certainty that mutation is decreasing in emphasis from above downwards, so long as one keeps to the line of the families, for one can see no difference between bi-generic (*Evol.*, p. 199) and large. But in an individual family, it seems to diminish from family through genus to species and variety, and the divergences are better marked and in more characters, perhaps, at the top. In any case, the taxonomic scheme which will be employed in dealing with any group soon reveals itself, and this is a very important law which seems to run throughout. In this connection, we may refer especially to pp. 168-77, 181-84, 188, 206-10.

When life first appeared, perhaps in the form of something like a schizophytic alga, there would be so little complication of structure that possible divergences would be few and simple in most cases. A hydrophytic alga might modify for life on land, probably in different places, and a few changes of form would occur, each one perhaps making others open to its descendants, while with increasing possibilities, the time between changes might be lessened, so that the next big change, to a moss or a pteridophyte, might not need so long a wait, and so on.

In fact, we would suggest that the list of heads of these great groups might be like that of the leading genera of a family, chiefly formed among the earlier mutations, even though these were few and far between. Further possibilities would tend to open out upon an increasing (hollow curve) scale. This description fits better with the line of attack upon the whole question that was taken by my friend Dr GUPPY, and which caused him to give to the whole theory the title of Evolution by Differentiation, which seems to the writer less descriptive than Divergent Mutation.

The acceptance of the laws of ASA and of dichotomous divergent mutation thus brings comparative order out of what has hitherto been rather chaotic, the understanding of distribution. The laws of ASA are evidently of supreme importance in this respect, and age, size, and area are among the characters that are of most importance. But we are still almost ignorant of the laws that govern the incidence of characters, and when we begin to gain an insight into that problem, we shall be upon the way, with the help of Mendelism and of that insight, to obtaining some control of evolution. One must be careful not to suggest that the structural result of any evolution might be predicted. The plan upon which it works appears to be always the same, but a very trifling difference in the earliest stages might ultimately lead to totally different final results, so that instead of getting *Compositae*, for example, we might get some family quite unknown, by some other combination of characters than any that exists, or has existed.

6. *Isolation*. In our two earlier books we have said a good deal about this subject, whose increasing importance we have long realised. When we adopted the theory of mutation in the early years of the century, it was clear that its logical conclusion was that it must very probably produce a new species at a single operation, not, as was so frequently supposed, by a series of small mutations that gradually added up to a specific distinction. The supposed driving force of selection was necessarily abandoned if one took up mutation, and what was to ensure that one small mutation should be followed by another which would help towards the formation of a new species? Where and when, for instance, was the boundary that commonly exists, that of mutual sterility, crossed? It was much simpler, as we gradually left behind us, with the new century, the period of the boom in adaptation, to imagine the new form, specific or generic, formed at a single mutation. This, incidentally, would make it quite possible for the new species, now really isolated, to commence its existence, and to begin to spread, among a number of individuals of the parent species, without any risk of loss by crossing. Had this been earlier thought of, there need not have been so great a boom in relicdom as occurred. This isolation, which would not in any way involve the death of the parent form, thus becomes a very important factor in evolution.

The writer's working hypothesis (p. 96), used since 1907, of sudden specific or generic mutation under a strain of outside conditions, has of course always included the notion of the isolation thus brought about, and the subject has been brought up in many places. We may refer especially to *AA*, chaps. XV, XVI, to *Evol.* pp. 57, 92, 24-30, and the chapter there on isolation on p. 61, and to various references above, in the present book.

HARLAND's work, referred to in *Evol.*, p. 62, adds considerable importance to this matter, by suggesting that long continued gene separation may lead to gene change, and this in turn might cause the necessary pressure to ensure specific or varietal mutation. The work of STEBBINS may also be referred to (**121**). There is a fair chance, especially when the land is not too closely occupied, that a seed may be carried further than usual, and start life in a geographically isolated position, when, if some gene change had occurred, it might even be able to commence a new form. The gradual succession of forms that we have described in some *Podostemaceae* (**129**) at different cataracts in the same river goes to indicate that the outfit of potentialities of character may differ between two individuals. The seeds having no adaptation for clinging to the rock (except in *Farmeria*) are usually washed away and lost, so that it is not an easy matter to colonise a new cataract.

If the individual possessor of some gene difference remain isolated, its later mutations will tend to differ from those of a normal plant, but there would be no reason to look upon it as a relic, as would formerly have tended to be the case. The process of formation of new forms seems to have considerable resemblance to the formation of new individuals in man, with the generations at great distances apart.

The writer's observations over many years, with those of HARLAND added, have suggested that it is not impossible that no two individuals of any species may be exactly alike in the make-up of the genes, chromosomes, and other features, to say nothing of any possible effect that might be due to simple fluctuation in the characters. If this be so, isolation may automatically tend towards increasing difference, followed by sudden mutation when the pressure reaches a certain point. The fact is evident, that isolation and its effects are worth much more of careful study.

7. *Adaptation, advantage, and selection.* The writer spent some years in the arcana of natural selection, in the palmy days of that theory, and began his investigations at the period when all efforts were devoted to finding adaptation

in everything structural. This was clearly necessary if advantage in the struggle for existence was to be kept upon its pinnacle as the moving force in the evolution and distribution of living things. It was taken for granted at that time that as evolution was only visibly shown by structural differences, it was these same differences which represented the advantages that had led to the survival and to the relative success and wider distribution of the species that showed the most efficient of them.

Thanks largely to the criticism of FLEEMING JENKIN (74) it was assumed that a new species must begin upon a comparatively large area in order to have any chance of survival and success. This of course meant that the great numbers of species occurring only on very small areas, as do, for example, about a couple of hundred CEYLON endemics, must be relics of previously existing vegetation that were slowly diminishing their areas of occupation. The writer has devoted a great deal of work to combating this strongly held opinion. For example he showed that on RITIGALA summit in CEYLON (**130**) the local endemic *Coleus*, confined to that summit, was accompanied by the most widely spread species of the genus, but showed no sign whatever of any inferiority, or of dying out, and the same proved to be the case with practically all endemics, wherever they were found. Not only so, but the endemics existed in great numbers, especially those of the smallest areas of occupation. For example, dividing them into five groups from small areas to large, they showed in

Ceylon	233	192	136	139	90	
New Zealand	296	190	184	120	112	(*AA*, pp. 60-4)

A state of relicdom caused by selection could not graduate the numbers like this, and this discovery, borne out by similar ones in many other places, was a blow to the conception of relicdom. A long list of queries made to its supporters, which seem in general to have been found unanswerable, and have been entirely ignored, is given in *AA*, pp. 90-92, and to them we may just add a few others :

(1) The larger (more "successful") genera are marked by close genetic relationship, which seems to the writer the only possible explanation of all the tables that we have given

of the genera at the heads of many families. As the " relics " among the small genera show the same tribal characters as some of these large ones, and in a general way form groups of satellites round the latter, we have now to support relicdom explaining how all this came about with inheritance *from above*. Surely if the relics were older than the successful genera, they would not show the tribal characters of the latter, in a family where the latter were formed by divergence from the head of the family.

(2) How did epiphytic things like *Rhipsalis*, in what must be a lesser competition for lack of numbers of individuals upon a given space, come to evolve so many local, endemic, species?

(3) Why do the endemics of New Zealand, which is much older as an island than Ceylon, occupy in general so much larger a space than those of Ceylon?

(4) Why do the wides and endemics of New Zealand appear in the different zones of 100 miles in length, from north to south of New Zealand, in the following numbers?

Zones	0-100	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
Wides	208	207	235	234	234	239	233	224	213	202	110
Endemics	234	280	330	368	386	537	532	527	516	414	137
					Cook's	Strait				Foveaux	Strait

The wides take no notice whatever of Cook's Strait at the middle of New Zealand, and a smaller one than the endemics of Foveaux Strait at the south end, where 54% of them cross, as against 33% of the latter. The endemics suddenly increase from 386 to 537 at Cook's Strait. This seems a practically conclusive proof of the writer's theory of the greater youth of the endemics, which are beginners, not relics. As we saw with *Ranunculus* at p. 65, many of the endemics tend to begin in the south, and this is enough to account for their comparatively good showing at Foveaux Strait. But it is clear in any case that the wides are much older than the endemics, and therefore that the latter are not relics.

The writer's work upon age and area and the hollow curve led to a very long series of deductions, in number about a thousand, mostly by aid of the sub-conscious (p. 249), which have proved correct when tested by the facts, and have provided the material for *Evol.* and for the present book. It is this testing which has involved the great amount of labour spent upon this work in the last fifty years. Its uniformly successful result has made him believe strongly in its premises, the probable general truth of the laws of ASA and of dichotomous divergent mutation, working downwards.

It further proved to be the case that the larger, *i. e.* upon the old conceptions the more successful, and the more widely distributed that a genus was, the more " relics " did it show, upon the average. Even in so old and so large a genus as *Ranunculus* only about 25 of its 325 species are really very widely distributed, *i. e.* found in the whole north temperate, or at least the north palaeotemperate zone, and very few other genera can rival this.

Almost everywhere one may find a few wides, one or other or more of them usually going to the extreme edge of the distribution of the genus, at least if the locality were not so geographically isolated as to prevent this. Except in cases like this, the endemics did not generally reach the edge, and in a long isolated island like NEW ZEALAND, where the time had been available, they often formed the characteristic pattern of distribution that one may see in the species of *Ranunculus* in that island (p. 65). The map shows the local dispersal of the genus as proceeding from the southern half of the SOUTH ISLAND, while three of the four wides cover the whole of both islands, as well as the CHATHAMS, 375 miles to the east, thus showing how much older the wides are than the endemics.

Endemics, in fact, are evidently the offspring of the wides among which they usually occur. There are exceptions to which we shall refer in the next chapter, but in *Ranunculus*, for example, they are not very numerous. The older theories of relicdom cannot hold their ground against such arithmetical methods of distribution, especially since the many proofs that have been given (*cf. Evol.*, especially Testcases, and the tables in this book, especially that on p. 173) that evolution has proceeded by dichotomous divergent mutation, *downwards* towards species, not upwards as hitherto supposed.

It is now becoming fairly certain that this was the course of evolution, and if this be the case, it is also clear that adaptation and advantage can have but little influence upon that course, as YULE and the writer said in 1922 (**159**).

There is little for selection to act upon, and the great structural divergences everywhere shown seem almost never to have adaptational value. The simple and automatic way in which evolution and distribution seem to proceed makes a great obstacle to any belief in the efficacy of selection when one has to deal with large spaces (larger than those occupied by single plant societies) and long time (longer than the life of a society or two). General conditions may favour growth of forest rather than prairie, but our work seems to show that it is in general rather the earliest arrivals of the species of the preferred kind that will become the leaders. The first arrivals will get a good start in becoming well adapted in detail to local conditions, which will always be changing a little.

The former conception that large groups, whether families, genera, or species, were the " successful " ones, is true enough if one look at number, or great dispersal, as signs of success, but they go, as we have now abundantly shown, principally with age, and progress is largely operated by the somewhat cynical law of " first come first served ", or " to him that hath shall be given ". Age is everywhere proving to be a factor of very great importance. The writer has been preaching this doctrine ever since the publication of *Age and Area* in 1922.

The *Anemoneae* (pp. 30-1) are evidently not demonstrably superior to the *Helleboreae*, both showing similar curves, and being distributed side by side. But the uppermost *Anemoneae* like *Ranunculus*, *i. e.* the oldest, are older than any *Helleboreae*, and show both greater numbers of species and greater dispersal. Even in a little country like BRITAIN, the difference can be seen, the local distribution of the top four being

of all *Anemoneae*	112 (a)	109	76	49	Total	346
of all *Helleboreae*	112 (b)	66	65	33		276
of *Anemoneae* without *Ranunculus*	109	76	49	46		280

a) reached by six *Ranunculi*, *b)* reached by one *Caltha*.

Even without *Ranunculus* the *Anemoneae* are equal to *Helleboreae*.

On p. 278 we have given an instance of specific distribution in *Chrysosplenium*, and on p. 11 have shown that there is nothing to choose between large and small families. There is no inferiority in the latter but greater youth.

8. *Classification of plants*, like any other, depends for its keys upon finding characters that exist in many, in few, in two, or in one only, of the objects to be grouped. Evolution seems to be a great series of divergent dichotomies, and while nature is evolving the plants, and probably the animals too, she is also providing a system upon which they can be grouped. This is evidently largely dependent upon their mere age. But without perhaps realising this fully, we are continually trying to make our classifications more " natural ", by which we mean following more closely the genetic lines of development. We have not fully realised that genetic and structural resemblances do not necessarily go together in detail, and that things with the closest genetic affinity may structurally be widely separated, and be placed in different tribes &c. This procedure especially characterises the genera at the top of a family, where they are the most closely related that is possible. *The first dozen or so of genera have already traced out the taxonomic lines of descent of the family, the tribes, the genera and the species.*

Our present classification depends entirely upon structural resemblances, which we call affinities, taking notice of divergences only to use them for keys, for their proper explanation has escaped notice. Taxonomy and genetic development, therefore, are not capable of the agreement into which we try to force them, and time and labour might be saved by a frank recognition of this fact, while at the same time the actual classifications might be simplified. It is generally recognised that since the fashion for attempted reconciliation has come in, our groupings have become more complicated and more difficult to use for their primary purposes, while people are tending to go back to the earlier system of BENTHAM and HOOKER.

A classification that follows nature's divergences is as natural as any other, but the term is not used in the same exact sense everywhere. However we classify plants by structural characters, the largest genera are so divergent that they must be at the tops of any divisions that we make.

This is for the simple reason that they were first formed in the genetic descent from the head of the family, and that this divergence is greatest among the oldest genera, whose descendants therefore form the great divisions of the family, though they themselves belong to a small and closely related group. To make a really correct genetic classification will probably prove to be as difficult and complicated a process as to make a chromosome map, another very desirable thing, and it should not be allowed to interfere with the making of a taxonomic classification, by structural characters only, unless some helpful feature can be brought in from elsewhere. Such a classification should be in international use, and should be adopted at a botanical congress, and only altered by the vote of subsequent congresses, for which long notice should be given.

9. *Classification contd. The orders or cohorts.* In families and genera there are many characters with which one can work that are common to many of them, while the divergences are seldom so great or so numerous as to make one feel uncertain about broad genetic connections. But as we go upward towards their origin, whether it be from one or from many points, the divergences become more numerous, and at times perhaps greater, making it more difficult to trace probable relationship, as one will soon find in dealing with orders, next above families. Among other things, this is shown by the great shuffling and rearrangement that is made in each new system. It is here that our classification is most unsatisfactory, especially when we try to make it genetic. As we have seen at a lower stage in the *Araceae*, there is a tendency to put the most difficult families, singly or in small groups, into orders of their own, thus temporarily shelving the difficulty. It is also shown by the increasing number of orders, and by the various ways in which the families in BENTHAM and HOOKER's *Incompletae* are dealt with. The same difficulties were evidently felt by these authors long ago, when they placed most of the difficult families there.

Looking closely at these difficult families, it seems fairly evident that much of the trouble arises from the fact that in the formation of the various combinations of characters that mark what we call families more of those characters usually considered "important" have been changed than usual, and importance largely rests upon mere age. In a large family, as we have seen in (**146**), or on pp. 311, 312, all kinds of changes may occur, but usually the most marked happen at different mutations, while if all occurred at once, the result might be impossible to place in any present family (cf. p. 312). Fortunately this kind of thing rarely happens, but it is not improbably to occurrences like this that we owe the existence of the *Incompletae* (see below).

The list on p. 173, supported by subsequent lists, indicates that the genera at the top of any family show, in about three quarters of the cases, such structural divergences from the immediate parent, which must usually be close above, that we have to place them in different sub-families or tribes. This of course is partly due to the fact that coming as they do so near the very top of a family, they have the best possible chance of leaving a large number of descendants visibly carrying their own chief characters, and thus forming a tribe of some importance. The same tendencies are shown in their own proper descendants, which tend to break up into heads of sub-tribes, and so on right down to what we have seen with species and sub-species upon pp. 182-4. As there are but few genera in the family at this period, any divergence tends to assume importance, which is continually made more and more valid as the descendants that show it increase in number. We know so little as yet about the possible electro-chemical syntheses and changes that may go on in living beings, that it is usually impossible to make any predictions, and everything tends to look as if it were simply a matter of chance. There are certain cases where the same chemical compound appears to be made in unrelated plants that might perhaps afford a path of approach to this question.

The phenomena seen again suggest forcibly that the mutation that is going on is, to a greater or less extent, a matter of what appears usually to be a casual choice of characters in which divergence is to be effected. And when this choice happens to include two or three characters that were of great importance in the parent, the result may be so different that we find it very difficult to place the family in its proper genetic position. This kind of difficulty, however, need not affect our classification, as we have pointed out. Discussions as to genetic position should be kept separate from taxonomy, until results commonly accepted are reached, and those such as may be inserted in taxonomic works without making them more cumbrous and difficult to use.

Leguminosae or *Orchidaceae*, for example, are well defined groups of plants. If we take the former, and begin with the monotypes we find (figures some years old) 240/1, that we may in general regard as beginners as *Leguminosae.* They form well over a third of the whole family's 675 genera, though their species are a mere 240. Being the youngest, they had the largest possible number of potential parents available, but beginning in a very small way, they will require a very long period of time to reach the stage of two species, after which they will expand with increasing rapidity (*AA*, p. 34). There is rapid decrease in number of larger genera, there being only 70/2, 42/3, 33/4, and 22/5. These are older genera, or most of them are, born when the family was smaller. After 5 we get the genera separating more and more rapidly from one another by size (pp. 30-33), and the hollow curve shows clearly, plotting logarithmically into a close approach to a straight line p. 262.

Leguminosae by sizes of genera in the World

Genus	Spp. (world)	Sub-family		Tribe
1. Astragalus	1600	Heading	*Papilionatae*	*Galegeae*
2. Acacia	550	Heading	*Mimosoideae*	*Acacieae*
3. Cassia	450	Heading	*Caesalpinioideae*	*Cassieae*
4. Mimosa	400	2nd	Mimosoid.	*Eumimoseae*
5. Crotalaria	350	2nd	Papil.	*Genisteae*
6. Indigofera	350	3rd	Papil.	2nd Galeg.
7. Trifolium	300	4th	Papil.	*Trifolieae*
8. Bauhinia	250	2nd	Caesalpin.	*Bauhinieae*
9. Desmodium	180	5th	Papil.	*Hedysareae*
10. Aspalathus	175	6th	Papil.	2nd Genist.
11. Lupinus	175	7th	Papil.	3rd Genist.
12. Phaseolus	160	8th	Papil.	*Phaseoleae*
13. Vicia	160	9th	Papil.	*Vicieae*
14. Dalea	150	10th	Papil.	3rd Galeg.
15. Inga	150	3rd	Mimosoid.	*Ingeae*
16. Tephrosia	150	11th	Papil.	4th Galeg.

The figures of size of genera given in Engler-Diels, 11th ed., though slightly different from mine and often a trifle lesss ,how the first seven in exactly the same order, and in the others, *Lupinus*, *Dalea*, and *Vicia* are displaced by *Oxytropis*, *Psoralea*, and *Rhynchosia*, with a result hardly different. This is the rule for every family. *Compositae* is the first in matter of size, and we have given a table of its leaders on p. 176; *Leguminosae* is the third (in genera, but second in species), and as we have had few Monocots, it will be well to give a table for the *Orchidaceae*, the second family.

Orchidaceae by world sizes of genera (tribes from NP/1)

1.	Dendrobium	750	Heading	*Dendrobieae*
2.	Pleurothallis	550	Heading	*Pleurothallideae*
3.	Bulbophyllum	450	Heading	*Bulbophylleae*
4.	Epidendrum	425	Heading	*Laelieae*
5.	Habenaria	400	Heading	*Ophrydeae*
6.	Oncidium	350	Heading	*Oncidieae*
7.	Eria	325	2nd	Dendrob.
8.	Eulophia	200	Heading	*Cyrtopodieae*
9.	Stelis	175	2nd	Pleurothallid.
10.	Microstylis	150	Heading	*Liparideae*
11.	Angraecum	120	Heading	*Sarcantheae*
12.	Calanthe	120	Heading	*Phajeae*
13.	Coelogyne	120	Heading	*Coelogyneae*
14.	Liparis	120	2nd	Liparid.
15.	Masdevallia	120	3rd	Pleurothallid.
16.	Maxillaria	120	Heading	*Maxillarieae*
17.	Cyrtochilum	115	2nd	Oncid.
18.	Disa	110	2nd	Ophryd.
19.	Chloraea	100	Heading	*Neottieae*
20.	Oberonia	100	3rd	Liparid.
21.	Odontoglossum	100	3rd	Oncid.
22.	Polystachya	100	Heading	*Polystachyeae*.

Thus in the first sixteen, there are 12 heads of tribes, but all in the sub-family *Monandrae*. It is clear that here, as in the other two very large families, there is a great deal of well marked divergence at the top. In Engler-Diels the classification of Mansfeld is used, but there are only small differences, the chief being that the tribes of PFITZER are reduced to sub-tribes, so that *Dendrobieae* becomes *Dendrobiinae*, and so on.

Thus these first three families, heading all the rest by a large margin, are not only as divergent from one another as it is possible to be in the flowering plants (*Gamopetalae-Inferae*, *Monocotyledones*, *Archichlamydeae*), but show, among their largest genera, the heads of six out of seven sub-families, and of 32 tribes out of 60, including nearly all the most important.

Taking the tribes headed by any of the genera in the first sixteen of each family there are

in the first three tribes of each, together, about 280 genera
second 560
third 800

This tendency to increase in size from the very early tribes is well marked at the top of many families, and we are not yet clear as to its meaning; more work is needed, and time is insufficient. Two other features that we have mentioned are evidently associated with it in some way; (1) the way in which the offspring of the leader of a family tend to go automatically into other tribes (pp. 173-8) and (2) the great differences that show between the upper and the lower tribes in some large families (figures for *Compositae* on pp. 187-8).

It is not of course impossible, or even improbable, that some flowering plants were in existence before any of these big families. The earliest families of all might be things like *Magnoliaceae*, which are woody, would probably be of slow growth, while the divergences open to them would probably be but few. The family is usually looked upon now as one of the oldest of all, and if we remember that in any case its early members would belong to the period of marked divergence, it is probable that such a group as *Schizandraceae*, often regarded as a separate family, should really be considered as a sub-family only. Cf. also notes about *Magnoliaceae* on pp. 338-9.

The same rules of behaviour apply to all families of moderate or large size, and as we said in *Evol.*, p. 76, " the first mutation, in a family newly formed by a large change from some ancestral form, may be in turn large ". *Evol.* is really a first volume to the present one, and the whole chapter may be read in the present connection, especially the letter from HOOKER to HUXLEY on p. 74, and p. 85, where we have said " It is clear that if we suppose the big genera of a family to be the first formed, and that by the most divergent mutation that on the whole occurs in the family, whilst the intermediate and smaller genera are younger, we can get a satisfactory picture of what seems to have gone on. "

We have now added greatly to the proof that this is in general correct. The convincing evidence given by the table on p. 173, and the following tables of the leading genera of families, had not been fully collected in 1940. But while this theory of evolution that we are now putting forward diverges from that previously held, there is no doubt that the evidence in its favour is very strong. Evolution and distribution seem to proceed in a simple and arithmetical way as if directed by simple law like other scientific disciplines, and this seems to fit on naturally to such sciences as chemistry and physics (*cf. Evol.*, p. 175, noting also the paragraph about Dr GUPPY at the top of the page). Later in this chapter we shall point out the chemical analogy.

Of course, going so far back into the past as we are now doing, we cannot be sure that the three gigantic families mentioned above are really the oldest of all. It is quite likely that *Rubiaceae*, which is largely a forest family of damp and warm conditions, was really earlier than *Compositae*. This is more suited to drier and more open situations, where, incidentally, evolution and distribution might be much more rapid. Somewhat similar objections might be urged against *Orchidaceae*. But in the list of the 45 largest families just below, there can be little doubt that most of the oldest are included. It is clear that they are well and divergently separated, none of them giving any suggestion of relicdom, and they are well scattered in the lists of orders given by different writers.

It is by no means improbable that the general rule of increasing size does not hold indefinitely far back, even if only for the reason that there are very few genera that come up in size to the standard of the largest of the flowering plants. At the real top of the list, when it is finally made up by age only, there may be a shrinkage in size by reason simply of lack of material upon which to work, and such families as *Magnoliaceae* may come in near the very top.

The first 45 families of Angiosperms, by world size

Family	Gen.	Leader	Spp.	«Ones»	Gen. Pl.	Position in	
						NP/1	Hutchinson
1. Comp.	1179	Senecio	2000	446	B2	B10	B67
2. Orchid.	726	Dendrobium	750	231	M1	M11	M
3. Legum.	675	Astragalus	1600	240	A11 (1)	A21 (1)	A41
4. Gramin.	548	Panicum	500	221	M7 (1)	M4 (1)	M
5. Rubi	496	Psychotria	500	232	B1	B8	B66
6. Asclep.	352	Cynanchum	200	189	B7 (1)	B5 (1)	B65 (1)
7. Crucif.	344	Draba	270	143	A2 (1)	A19	A11
8. Umbell.	334	Eryngium	220	138	A15 (1)	A30 (1)	A59 (1)
9. Acanth.	273	Justicia	325	117	B9 (1)	B6 (1)	B75 (1)
10. Lili.	269	Asparagus	300	95	M3	M9	M
11. Scroph.	259	Pedicularis	275	93	B9 (2)	B6 (2)	B75 (2)
12. Euphorb.	251	Euphorbia	750	93	Inc7 (1)	A23 (1)	A38
13. Palmac.	219	Calamus	325	73	M4	M5	M
14. Apocyn.	202	Tabernaem.	110	75	B7 (2)	B5 (2)	B65 (2)
15. Labiat.	200	Salvia	550	63	B10 (1)	B6 (3)	B76 (1)
16. Melast.	193	Miconia	600	50	A12 (1)	A29 (1)	A33 (1)
17. Sapind.	160	Serjania	175	70	A10 (1)	A24 (1)	A57 (1)
18. Rutac.	153	Fagara	200	58	A7 (1)	A23 (2)	A55
19. Rosac.	142	Potentilla	300	45	A11 (2)	A21 (2)	A40
20. Gesner.	129	Cyrtandra	250	49	B9 (3)	B6 (4)	B75 (3)
21. Eric.	122	Rhododendr.	700	48	B4	B1	B60
22. Bignon.	121	Arrabidaea	100	50	B9 (4)	B6 (5)	B75 (4)
23. Borrag.	119	Cordia	280	42	B8 (1)	B6 (6)	B73
24. Annon.	114	Uvaria	100	45	A1 (1)	A18 (1)	A2
25. Cyper.	111	Carex	900	36	M7 (2)	M4 (2)	M
26. Arac.	108	Anthurium	500	41	M5	M7	M
27. Flacourt	104	Homalium	160	47	A2 (2)	A27	A27
28. Chenop.	102	Atriplex	250	41	Inc. 1	A17 (1)	A19
29. Solan.	99	Solanum	1350	37	B8 (2)	B6 (7)	B74
30. Verben.	93	Clerodend.	175	38	B10 (2)	B6 (8)	B76 (2)
31. Myrt.	92	Eugenia	750	26	A12 (2)	A29 (2)	A33 (2)
32. Menisperm.	91	Stephania	40	45	A1 (2)	A18 (2)	A5
33. Sapot.	90	Sideroxylon	100	43	B6	B4	B61
34. Anacard.	89	Rhus	140	31	A10 (2)	A24 (2)	A57 (2)
35. Malv.	87	Hibiscus	180	30	A6 (1)	A26 (1)	A36
36. Gentian.	86	Gentiana	400	25	B7 (3)	B5 (3)	B68
37. Aral.	83	Schefflera	150	37	A15 (2)	A30 (2)	A59 (2)
38. Amaryll.	81	Agave	275	21	M2	M9 (2)	M
39. Saxifrag.	80	Saxifraga	325	47	A11 (3)	A21 (3)	A14
40. Caryoph.	79	Silene	400	30	A4	A17 (2)	A17
41. Campanul.	78	Campanula	300	25	B3	B10	B71
42. Morac.	78	Ficus	800	32	In.7 (2)	A12	A50
43. Malpigh.	73	Byrsonima	120	13	A17 (2)	A23 (3)	A37
44. Cucurb.	70	Melothria	85	24	A13	B9	A30
45. Stercul.	70	Hermannia	150	26	A6 (2)	A26 (2)	A35

A = Polypetalae or Archichlamydeae, B = Gamo- or Sym-petalae, Inc. = Incompletae, M = Monocots.

If we now sort these families into the orders wherein they are distributed, we find them well and widely scattered there. They are not, as might upon the older views have been expected, closely structurally related at all. The first three are *Compositae* (placed in *Gamopetalae-Inferae*), *Orchidaceae* (*Monocotyledones*), and *Leguminosae* (*Archichlamydeae*), as widely separated as it is possible for flowering plants to be. If we sort the first 40 into the 40 orders (cohorts) of Bentham and Hooker, we find them in

	Polypetalae	Gamopetalae	Incompletae	Monocotyledones
First ten	11, 2, 15	2, 1, 7, 9	—	1, 7, 3
Second	12, 10, 7, 11	9, 7, 10, 9	7 (Euph.)	4
Third	1, 2	4, 9, 8, 8, 10	1 (Chenop.)	7, 5
Fourth	12, 1, 10, 6, 15, 11, 4	6, 7	—	2

(Numbers of orders as in my *Dict.*, pp. 1-liv at end.)

The families cover the field in very fair proportional numbers, with widest gaps, and no duplication, in the first ten. These ten families contain 5196 genera, or about 40% of all genera known (12, 571); of these 2300 are *Gamopetalae*, 1543 *Monocotyledones*, and only 1353 are *Archichlamydeae*. There are no *Incompletae* in the first ten, and only *Euphorbiaceae* and *Chenopodiaceae* in the rest. These are facts which throw some doubt upon currently received opinions as to *Archichlamydeae* and *Incompletae*, and their position in the history of the development of the flowering plants. But in any case it is clear that even if we had to deal with the whole 40 families, there would be little difficulty in placing a plant belonging to one of them in its proper family. It is only when we add the great crowd of younger and smaller families that there begins to be serious difficulty.

If we compare the various groupings into orders made by the various authors, we can see at once the great shuffling that has gone on, and that takes no notice of age, size, or area, the three great factors that have been so controlling in importance and in distribution. Like a family, an order that contains no large family or genus should probably take a lower rank, as being younger, unless it be an evidently very ancient group like the *Magnoliaceae*, that go back to the very first days of the angiosperms (*cf.* p. 338-9).

Why are there such wide gaps between families at the top unless it is that in the early days when they were being formed, the divergences, which must have been matters of indifference to selection in most cases, tended to be large? In early days, too, there was probably less material for divergence to work upon; the possible variety has probably been increasing all the time, each new one opening the way to yet more.

It would be absurd to try to show which family was actually the first; we cannot be sure that the flowering plants are even monophyletic. But everything connected with times so far back in geological history, when conditions were probably so different, is still almost entirely a matter for speculation, and one in which other sciences are involved. Much further inductive work is needed; as yet we do not even know the relative rates at which families increase and become dispersed. For example, probably neither *Compositae* nor *Dipterocarpaceae* should justly, by actual age, occupy the positions that their numbers assign to them.

It is of interest to see how soon such characters as one cotyledon, inferior ovary, tetradynamy, and a number of others, appear in these families at the top of the list, and though we cannot place them accurately in order of age, there is little doubt that on the whole these are very old families.

When one sees the regularity with which every family in turn gives the same kind of picture with its leading genera, one realises that one has come upon a general rule, or in fact a law, that is followed by a family in the course of its development. The figures are so consistent that there can be comparatively little doubt about their interpretation.

It is clear that the growth has been by divergence at every mutation. This in turn means that the evolution is working downwards towards the smaller forms, not upwards as we used to think. As GUPPY and the writer independently realised long ago, people were trying to make evolution work backwards (*cf.* *Evol.*, pp. 22, 32, 65-8, 88, 98, 175, especially 68, 175). The final evidence required to support our views, which really date back to GEOFFROY ST. HILAIRE, OWEN, and MIVART, seems to be provided by the many tables here given, especially that on p. 173 and the many of leaders of families, notes on genera like *Galium* on p. 182

and below, and on sub-species on pp. 182-83. This behaviour seems universal, and no other explanation of such consistent figures seems possible to the writer at the present time. All must be due to the operation of the same law, and neither adaptation nor selection, nor " upward " evolution, can even begin to explain why the taxonomic classification that we use should begin with the widest possible divergence in the oldest genera, which now possess the most numerous species and the widest dispersal. Had evolution been " upwards " and casual, it would not be possible to find this phenomenon shown as it is. The behaviour of the species, especially those of the earliest and largest genera, also goes to show that this is the more correct view to take. Like the families and the genera, especially the older ones, they too begin at once to break up into their taxonomic divisions.

Up to the genus which as the largest or oldest is the head of a family, we can still feel fairly sure that we are dealing with one family, even in the *Leguminosae*, where the top three genera are sometimes given a family each. But above this point it is clear that divergence has affected more characters at once. This tends to be more the case the larger (older) the family, so that it becomes very difficult to place a big family in its proper relationship to other big families, by structural methods of comparison. It is probable that all the top families are really closely related to one another (perhaps, if they be polyphyletic, in groups), but genetically, not taxonomically. Their divergences are more marked, affecting more of their " important " characters. These we have seen to be the oldest, upon the whole, so that they would be available for divergences at a very early period. But as time went on, they would probably become mixed with other and younger (less " important ") characters, so that their chance of being affected at any individual mutation would become less.

It is clear that size simply follows from age, and that wide taxonomic divergence largely does the same thing in any one line of descent, while on the other hand the higher one goes, the closer tends to be the relationship of the genera. Neither selection nor adaptation will account for the fact that the large genera at the top tend to show such clear and well marked distinctions, nor can one call in such destruction of transitions as will account for such separation of incongruous types, with such marked divergences, between which transitions can but rarely be conceived.

The principle at work seems to be first of all a division of the first parental genus of a family by a divergent mutation, followed by the same happening to each new genus in turn. The earliest divergences are the largest or the most numerous, or both, and there is a gradual diminution as time goes on, so that the rank of a genus is largely determined by its age. We cannot as yet tell what the relative rank of a single mutation of one character is, and a comparison of the early mutations in small families, as given in the table on p. 199 in *Evol.*, with those in the big families seems to show little or no difference; but there seem to be more of well marked ones in the larger families. It may therefore be worth while to look at a list of the largest genera of the flowering plants, and to note how they diverge from one another, almost all belonging at least to separate tribes, and often to separate sub-families also, whilst it is not common for them even to occupy the same family, unless that family be very large.

The 30 largest genera of the flowering plants

Genus	Size	Fam.	Sub-family	Tribe
1. Senecio	2000	Comp.	Tubuliflorae	Senecioneae
2. Astragalus	1600	Legum.	Papilionatae	Galegeae
3. Solanum	1350	Solan.		Solaneae
4. Carex	900	Cyper.	Caricoideae	Cariceae
5. Begonia	800	Begon.		
6. Ficus	800	Morac.	Artocarpoideae	Ficeae
7. Hieracium	800	Comp. 2	Liguliflorae	Cichorieae
8. Mesembryanth.	800	Aizo.		Mesembryanth.
9. Oxalis	800	Oxal.		
10. Dendrobium	800	Orch.	Monandreae	Epidendreae
11. Eugenia	750	Myrt.	Myrtoideae	Myrteae
12. Euphorbia	750	Euph.	Crotonoideae	Euphorbieae
13. Piper	750	Piper.		
14. Rhododendron	700	Eric.	Rhododendroideae	Rhododendreae
15. Centaurea	650	Comp. 3	Tubuliflorae (2)	Cynareae
16. Vernonia	650	Comp. 4	Tubuliflorae (3)	Vernonieae
17. Croton	600	Euph. 2	Crotonoideae (2)	Crotoneae
18. Dioscorea	600	Diosc.		Dioscoreae

Genus	Size	Fam.	Sub-family	Tribe
19. Miconia	600	Melast.	Melastomatoideae	Tamoneae
20. Acacia	550	Leg. 2	Mimosoideae	Acacieae
21. Peperomia	550	Piper. 2		
22. Pleurothallis	550	Orch. 2	Monandrae (2)	Pleurothallideae
23. Salvia	550	Labi.	Stachyoideae	Salvieae
24. Anthurium	500	Arac.	Pothoideae	Anthurieae
25. Aster	500	Comp. 5	Tubuliflorae (4)	Astereae
26. Erica	500	Eric. 2	Ericoideae	Ericeae
27. Myrcia	500	Myrt. 2	Myrtoideae (2)	Myrteae
28. Panicum	500	Gram.		Paniceae
29. Psychotria	500	Rubi	Coffaeoideae	Psychotrieae
30. Sedum	500	Crass.		

Myrcia is often regarded as part of *Eugenia*, *Mesembryanthemum* often broken up into many smaller genera. *Piper*, *Peperomia*, *Begonia*, *Dioscorea*, and *Oxalis* are all much too large for their small followings, and we have given a possible explanation on pp. 288-9.

These 30 genera, which must include at any rate many of the oldest, thus belong to 20 families; five are in *Compositae*, and two each in *Eric.*, *Euph.*, *Legum.*, *Myrt.*, *Orchid.* and *Piper*. The orders to which the Dicot genera here belong are (68).

7. Piperales (2 gen.)
14. Saxifragales (1)
17. Caryophyllales (1)
20. Geraniales (1)
30. Cucurbitales (1)
33. Myrtales (3)
38. Euphorbiales (2)
41. Leguminosae (2)
50. Urticales (1)
60. Ericales (2)
66. Rubiales (1)
67. Asterales (5)
74. Solanales (1)
76. Lamiales (1).

Going upwards from species to families, the differences increase in complication and emphasis. A very little more of divergence than such as marks the difference between two sub-families, such as *Caesalpinioideae* and *Papilionatae*, would make it absolutely necessary to treat them as separate families, while now most people include both in *Leguminosae*. In reaching so nearly back to the beginning of the Angiosperms as we are doing here, we have come to a region of emphatic differences. On the other hand, in working downwards, the differences become less strongly marked, and are not so liable to cause difficulty. We have long divided the *Papilionatae* into *Galegeae*, *Genisteae*, *Trifolieae*, and the rest of the ten tribes. The difficulty in placing a thing in its proper *structural* connection diminishes as we come downwards, though we have no longer any right to assume that there is a gradual passage of one structural form into another. We have now seen the effects of the divergences that separate species and genera at the mutations that give rise to new ones. They cannot be passed over by gradual stages, in such cases as flower x-merous/y-merous, ovule erect/pendulous, raphe dorsal/ventral, fruit loculicidal/septicidal, capsule/berry, anther opening by pores/slits, extrorse/introrse, pollen powdery/in pollinia, pollen-sac septate/not so, pollen of different patterns, as in *Acanthaceae*, corolla hypogynous/epigynous, poly-/gamo-petalous, and so on, all of them changes which must come by sudden mutation. They could not be due to gradual acquirement by selection, even if there were any reason to suppose that it could act upon such characters. It must act upon total, not individual, value, and could not bring them to the state of perfection in which we commonly find all of them, with a clean-cut differentiation like that shown in the examples just given. And while selection becomes less and less important as one goes upwards, differentiation increases (*cf. Evol.*, Testcase XXII, p. 137), and the closest relationship of all is shown by the topmost genera of a family.

Another upwards stage, offering still less opportunity to selection with the always increasing divergence, takes us to the very top of the largest families, where we always find the family ending (upwards) with a single genus that shows a wide gap in number of species between it and the next largest, it being in general almost exactly twice the size of the second. The 45 largest families in the table just given show the following result :

Spp. in Genus	1	2	Difference	Av.	% of second to first
First 15 fams.	8650	4610	4040	269	53,3%
Second	6030	2855	3175	211	47,3%
Third	4210	2105	2105	140	50,0%
Total 45 fams.	18890	9570	9320	207	50,1%

There is great variety among these families, which in general go back to very early days indeed, when the number of characters had not yet been increased by later mutations, so that there was comparatively little to draw upon, and what we now consider the most important characters were liable in consequence to frequent and often well marked change. We have tried to make it clear in various places in this and previous books that age is one of the most important factors in the evolution and distribution of plants, because it *allows time* for the changes made by other and more active factors. Importance of a character in taxonomy depends upon age, as we have frequently pointed out, and it is their first mutations, therefore, that produce the most important characters of all.

We shall therefore, with this increasing divergence, find great difficulty in tracing structural features back into preangiospermous days. For some way back into the fossil period, say at least as far as the Eocene, we can trace a number of our present families back but we find no new ones, so far as I am aware. But there is no evidence to show that the first Angiosperm or Angiosperms did not arise directly by mutation from some Gymnosperm or Pteridophyte, remembering that we are back at a period of large mutation. In fact, probability is much in favour of this suggestion. The mutation need not be much larger than those that separated the earliest Angiosperms.

Things with some of the characters of one group, and some of another must be regarded in general not as actual transitions, but as things that have received an unusual mixture of the characters that the immediate ancestor was carrying. They may perhaps have bad luck in meeting with some catastrophe, or may have proved in some way unsuited to the local conditions.

10. *The Incompletae* of BENTHAM and HOOKER, containing families that they were not able to place among their *Poly-* and *Gamopetalae*, have long been a very difficult problem. ENGLER made the first great change, by throwing them boldly among his *Archichlamydeae*, but they are usually so divergent from most of these that it is no easy matter to place them. In fact, it is as difficult as to place a family in its proper order, and the tendency is, as usual, to put each

one or few in a different group, temporarily shelving the difficulty. Of the 33 orders given in ENGLER-DIELS (11th ed.), a number, and especially those near the start, contain *Incompletae* only. The actual figures are

Position of Incompletae in Engler-Diels

Orders	Fams. contained	Fams. of Incomplt.	Gen.	Spp.	Percentage of Fams
1 to 15	21	19	286	4,516	90%
16 20	22	16	404	5,526	68%
21 25	47	8	119	2,042	15%
26 30	84	3	255	4,402	3.5
31 33	27	4	56	612	14%
33	201	50	1,120	17,098	24%

Of the last 18 orders, families of *Incompletae* are found in 12.

In the later grouping of HUTCHINSON, the Englerian view, that the *Incompletae* were earlier stages, is abandoned. This seems supported completely by the work that we have described here. *Magnoliaceae* and *Ranunculaceae* are put in their place. Upon the writer's views no living family can be accepted as a relic without detailed individual proof, nor can any fossil be taken as ancestral unless frequent and widespread.

Some of the *Incompletae*, like *Euphorbiaceae*, though as incomplete as most, are important and flourishing families, but marked by divergences that happen to cover characters usually considered as important, mainly because they have usually been found so in other families. One must not forget that importance is mainly due to age, and its occurrence in one family does not guarantee any importance whatever in another one. *Euphorbiaceae* is particularly marked by the unisexual flowers, the perianth of one whorl or none, the stamens one to many, free or variously united. It is a large family, the twelfth of all, and we have seen that variety of character is sure to occur in a large family, while this one is old enough to go far back into the earlier period when divergence tended to be greater. *Scrophulariaceae* and *Palmaceae*, on either side of it, both show wide variations, and had they not agreed rather well among themselves in vegetative habit &c, might have been split into smaller families.

As we have had no examples of any *Incompletae* in our tables, we give the first eight *Euphorbiaceae* below :

Euphorbiaceae in order of world size

	No. in world	Subfamily		Tribe
Euphorbia	750	Heading	*Crotonoideae*	*Euphorbieae*
Croton	600	2nd	Crot.	*Crotoneae*
Phyllanthus	500	Heading	*Phyllanthoideae*	*Phyllantheae*
Acalypha	400	3rd	Crot.	*Acalypheae*
Macaranga	200	4th	Crot.	2nd Acal.
Glochidion	175	2nd	Phyllan.	2nd Phyllan.
Jatropha	175	5th	Crot.	*Jatropheae*
Manihot	175	6th	Crot.	*Adrianeae*

There are only these two sub-families in the great mass of the family, but two more with leaders of 18 and 7, separated by the simple mutational character of ovules one or two per loc., a character more " important " when older in the family.

The differences in *Incompletae* are in general such as can only be passed by sudden mutation, being usually incapable of intermediate stages. This is especially important as there is no conceivable use for intermediate stages, and still more for such upon a graduated scale of usefulness. One has only to think of the many embryo-sacs of *Casuarina*, of the scaly emergences on the leaves of *Hydrostachys*, of the distinctive characters of *Garrya*, *Myrica*, *Balanops*, *Leitneria*, and so on, to realise how widely these genera diverge from anything that one might imagine to be related, whether living or fossil.

The families of *Incompletae*, where it is even just possible to suppose them relics dying out, are usually very small, and it is only those of wide, but scattered, dispersal that are likely to come into consideration. *Magnoliaceae*, which HUTCHINSON places at the foot of the Dicots, does, on the other hand, look like a primitive family, and is not unlikely to be related to the *Ranunculaceae*, also at the foot. They probably go far back into the days of wider divergence, and the small families that are often split off are more likely to be of the nature of sub-families, while one must not forget the possibility of polyphyletic origin of some of the structural discontinuity shown. *Magnoliaceae*, too, were probably not very capable of rapid spread in changing conditions, and might be overtaken and destroyed at times.

The suggestion in the *Gen. Pl.* is that the *Incompletae* may perhaps be, and in ENGLER that they are, primitive forms from which later families have been derived. A much sounder line appears to the writer to be that followed by HUTCHINSON, who recognises that many of them are themselves derived forms, and the work in this book goes strongly to support this supposition. While ENGLER puts 19 families of them, adding only the very small families of *Garryaceae* and *Julianiaceae* to them, in his first fifteen orders, and sixteen more follow in the next five orders, HUTCHINSON places the same families in his orders 6, 7, 16, 18, 19, 23, 44, 45, 46, 47, 48, 49, 50, of his 59 orders of *Archichlamydeae*.

Our work goes to show that in general it is probable that the very large and widespread families on the whole are at any rate very early. Divergence appears to have been one of the chief marks of evolution, diminishing in emphasis as time goes on and the material upon which to draw increases. But it is highly probable that at the very start of the flowering plants such families as *Magnoliaceae* took a large hand in the matter, being themselves slow both in evolution and in distribution.

A number of families like *Betulaceae* and *Fagaceae* have given much trouble in deciding their genetic position, which is by no means settled yet. The difficulty as usual seems to arise from the way in which more of the important characters than usual have been affected in the mutation that gave rise to the leader, so that they show a considerable taxonomic separation from any other families. Probably they are old, and date from a time when divergences were considerable, while at the same time they are woody, and slow in growth and reproduction. One great difficulty is to know how *Fagus* and *Nothofagus* came to be separated so far geographically, for they are alike in many respects, and were long considered as one genus.

11. *The sub-divisions of families* can rarely be made, if of any importance, to harmonise with the geographical distribution. The taxonomic splitting rests upon the assumption, commonly and necessarily made under Darwinism, that relationship is determined by structural characters

only, so that intermediates, destroyed by selection, were required in order to cover the vacant space, taxonomic or geographical, or both, between two things structurally closely allied. This explanation has been very hardly worked, and badly strained. We have more and more realised that structural alliance is compatible with gaps of considerable size, and any direction, and that it completely ignores such a geographical difficulty and such a barrier as is presented to the *Araceae* (pp. 268, 273) by a 6000-mile stretch of the PACIFIC OCEAN. And now that we have seen that selection to get rid of the intermediates is also a broken reed, there is really little support left upon which to base extensive destruction. It thus becomes practically impossible to explain the formation of widely separated subdivisions upon the old conceptions.

The real destruction that is almost all the time going on is a destruction of individuals which prove weaker upon the whole total of their outfit, as compared with those that are growing close to them, whether these belong to their own species or not. There is little evidence for any killing out of a whole species, unless it be one newly born and confined to a minute area sufficient to support a very few individuals. The extinct species that we find as fossils are very often quite local things, which cannot safely be considered as ancestors of things now living, when one remembers the laws of ASA. And their characters are as a rule "finished", not transitions.

The distinction between one tribe, genus, species, &c and a close relative of its own rank, is simply due to whatever divergence may have marked the mutation by which they were separated. And we have seen that in every family the same rule is followed, that the genus that begins, and heads the family, promptly breaks up into genera heading sub-families or tribes, these into the heads of sub-tribes, and so on, so that after a dozen or so of genera are formed, the future taxonomic division of the family is clearly marked out. Selection had nothing to do with it; it is a necessary corollary of the law of dichotomous divergent mutation. Each genus behaves like its immediate predecessor, but usually upon a rather smaller scale.

So long as classification tries to be genetic, so long does it lay itself open to criticism that it is practically impossible properly to meet, and so much the more will it make itself troublesome to use, by not taking full advantage of the help offered by the divergences which nature has so kindly provided, but which as often indicate close relationship as not.

12. *The small families.* Many of these have been created since the *Gen. Pl.*, for example some 58 of one genus each, 17 of two, and so on. Usually they are simply genera, often solitary or even monotypic, diverging rather markedly from the rest of a family to which they were once united, like *Adoxa* (*Caprifoliaceae*), or *Akania* (*Sapindaceae*). Some families have been much disintegrated, like the *Ternstroemiaceae* of BENTHAM and HOOKER, whose genera have been scattered among nine families, many of them new. These families in turn have been much shuffled in placing them in orders, but all this shuffling that goes on is mainly based upon different valuations of the various structural features displayed, little or no regard being paid to age, size, area occupied, or any other non-structural feature.

As is well known, it is not possible to take the " value " of a character in any one family as a standard for it elsewhere; the principal thing that gives it its value, its age in the family concerned, has been ignored. In such conditions the shuffling may go on indefinitely, leading nowhere. The logical termination of such work is that every genus, or small group of genera, shall have its own sub-tribe or other group, as we have seen in the *Araceae*, where 108 genera are put into 42 different groups, and the same in *Saxifragaceae* and other families. Families may take the place of genera, and the whole dispute about relationship may then begin afresh. It must be recognised that taxonomic work cannot, without great complication, lead to a genetic classification. Age, size, and area must in future occupy an important place in all such discussions. We need a great deal more knowledge of the incidence of character, especially now that we have seen what divergences may occur between the closest of relatives; and we must not forget the old and overriding genus from which two very similar things may spring in similar conditions at great distances apart.

Like the genera, the families are arranged in a hollow curve type of distribution by size, with an increasing increase downwards from the 45 given above. The small families are also considered below under *Behaviour of genera.*

13. *Pairs of families.* There are some curious pairs of families that should be worth more careful investigation in the light of what has been brought up about complexes, small families, and the like. The best known is *Ericaceae-Epacridaceae*, the difficulty here being the geographical separation, for while the *Ericaceae* only reach AUSTRALIA with a *Rhododendron* in the north, and a few other species, and while it would be absurd to try to bring in selection between the valueless points of difference, *Styphelia*, the leader of *Epacridaceae*, has 175 species, mostly Australian, but spreading into most surrounding countries. One cannot but connect them with the great abundance of *Erica* and others in SOUTH AFRICA, and in fact this connection seems to show in other families like *Proteaceae.*

Another pair is *Myrsinaceae-Primulaceae*, about which GUPPY has much to say, though it is not easy to trace any likely common ancestor in this case either. *Cunoniaceae* has been split off from *Saxifragaceae*, but with its leader *Weinmannia* mainly South American, with species in MADAGASCAR, NEW ZEALAND, and POLYNESIA, and most of the rest of the family confined to NEW CALEDONIA, it looks more like a polyphyletic sub-family of *Saxifragaceae.* There are other cases also. In dealing with such cases, it must be remembered that if the families are very old (headed by very large genera) they will probably go back to a time when greater variety was likely to appear.

14. *The behaviour of genera.* Nature seems to have nothing specially to correspond to our notions of species and genera; her object seems rather to be to increase the number of living things upon a plan in which increase in variety seems to keep pace with the increasing variety in conditions, and in the ways that are open for mutations, in fact, GUPPY's theory of evolution by differentiation. Each new thing, whose advent was apparently compelled by some sufficient change of conditions, must be suited to those conditions, or die out again. Except perhaps in extreme cases, it shows

no special structural adaptation. From the immediate ancestor it inherits enough of local adaptation to survive and reproduce, being, apparently, a more or less incidental product of internal changes that go on when the plant is becoming suited to new conditions. It is completely impossible to predict what may change at the next mutation, or to what it may do so.

We have already said a great deal about the behaviour of genera in *Evol.*, especially in Testcases I, p. 90 to V, p. 99, VIII, p. 101, IX, p. 110, XVI, p. 126, XVIII, p. 128, XX, p. 134, in which, incidentally, we called attention to the way in which the earliest and largest genera of a family tend to break it up at the very commencement into its future taxonomic classification, which in this book we have illustrated with so many tables, all showing the same thing, and all impossible of explanation, it seems to the writer, by adaptation or selection. The testcases continue with XXX, p. 158, XXXI, p. 161, and XXXII, p. 163, and *cf.* also pp. 184, 189-90 above.

Each genus in the dichotomous divergent series in turn tends to behave like its predecessor, which also remains living, so that, as we suggested in 1907, and have used as part of our working hypothesis ever since, there is now often no reason why the whole tree of a family should not now exist, alive, upon the earth. Evidence to the contrary is supposed to be provided by fossils, which indeed show that not every member of any family is at present alive, but do *not* show plants that are at once to be taken as ancestors of things now alive. If they were so, they ought at least to be reasonably large and widely distributed, and these are qualities that are rarely found. It is much more likely that they represent side lines of development, which were completely killed out in some catastrophe (*cf.* YULE on catastrophes in 158, p. 23), and with them, most probably, all their descendants, if any, which would occupy less areas than themselves.

There is little to suggest that many fossils may be direct ancestors of genera of the same family that are still living. Most families taper so neatly to a point in their largest genus, beyond which one cannot be sure of the ancestry *at all*, as the difficulties that occur with the orders clearly show, that it becomes a very bold assumption indeed to suppose that some fossil may be, for example, a direct ancestor of such a thing as *Psychotria*, *Acacia*, or *Carex*. It is clear, when one looks at the facts that we have now brought up in some detail, and indeed at the great difficulty that there is in placing *any* genus with any certainty, whether living or dead, as a direct and immediate ancestor of any head of a large family, that it is going to be a very difficult matter to trace ancestry back into past ages. We have so little to go upon that it becomes very largely a matter of pure speculation, and the application of inductive methods is greatly needed. We have applied these to geographical botany for the last 50 years, and have brought out several results that have a great deal of evidence behind them, though they have met with little acceptance, as they have been contrary to many received opinions. The writer must confess to considerable curiosity as to how the early breaking up into tribes, sub-tribes, genera, species, and sub-species will be explained away, to say nothing of other things.

Fossils belong in general to existing families, and even tribes, while any fossil that was a real ancestor of any leader of a big family might probably differ from it so completely that it would not be put into the family at all. The further back we go, the greater do the divergences become, and there is, for example, no proof that the mosses did not arise in one mutation from the algae. Now that we know how large and how divergent a mutation may be, there is little use in looking for transitions, for if divergences increase upwards from species to the leader of a family, there seems no reason why above that leader they should not be larger yet.

There is quite a possibility that the ancestor behind say. *Ranunculus*, going back so far as it must do, was a genus that may be smaller (even if living), and perhaps a good deal smaller, than is *Ranunculus*, for we are going back into a time when the material available for divergences was less, and when it is not improbable that mutations were fewer. This would be especially likely if the ancestors of flowering plants were woody Gymnosperms, and it is worth consideration if they did not descend directly from the ferns.

The " downward " direction of evolution, which we have seen to be the most probable one, takes the value out of any argument derived from a fossil that belongs to a sub-family or tribe now existing whose head is the second genus on the list or a later one, for these are younger than the head. A really ancestral fossil should belong to the first tribe, or even, much more probably, to a different family altogether.

If, as required by Darwinism, genera, tribes &c were later than species, it is rather a remarkable fact that most fossils show unmistakeable family characters, and even tribal may be seen.

It must also not be forgotten that any genus seems to tend towards giving off descendants of two kinds, species in which the generic characters go down more or less untouched for the greater part, and new genera, in which more of them have been touched, and that sometimes in a more emphatic way. The whole question of the value of fossil evidence requires careful study. There is no doubt that fossils represent facts, but the way in which on the whole divergence increases upwards till at the top, as our lists show, it is at the maximum, implies that any ancestor of any of these topmost genera should be separated by some marked divergence, and quite possibly even by several. This is a question which is very difficult to solve with the small amount of material at our disposal, and the simple fact that it cannot be treated as easily as herbarium material.

It is clear that to be ancestral to the leader of any family now existing, the fossil should probably be as widespread and as frequent, and should show such differences that were it living it would not be placed in any tribe that now exists, unless that of the parent leader, for only this is possible as an ancestor to the *whole* family. More probably it should occupy a tribe of its own, and still more probably a new family of its own. But so far as the writer is aware, new families do not often appear among the fossils, though the genera seem to differ in many cases, and some families and genera seem to go a very long way back.

Questions that require some kind of answer from inductive work, before we can properly value any fossil evidence, are whether, as the writer is inclined to suspect from such indications as Miss CHANDLER's *Stratiotes* (*Evol.*, 64), continual more or less specific change may be going on, and whether the tribal position of any of the fossils can be proved, and so on. We also need greater evidence of wide distribution, a thing which is at present very lacking. A point in favour of the idea of continual change is the way in which the *Podoste-*

maceae seem to go on producing new forms in extraordinarily uniform conditions (**136**) though it is true that one of those conditions is the perpetual action of the maximum force of plagiotropism.

We are very far yet from any understanding of what has gone on in the times that preceded the development of the bulk of the flowering plants, but what evidence we have will need to be interpreted in the light of what we have shown to be happening at the top of all our present families.

Let us now go on to take a few instances of generic behaviour, taking them from groups of families that we have so far left comparatively untouched, the Monocots and the water plants. As the matter is more simple to deal with in a small family, let us begin with the *Juncaceae*, which though small is evidently old by reason of its wide dispersal, the conditions of life that suit *Juncus* itself being also very widespread and uniform, probably putting little pressure on a species. Our list below includes the whole family :

Juncaceae by size in the world

1. Juncus	225	Cosmopolitan (montane in tropics)
2. Luzula	80	Temp., especially Old World
3. Marsippospermum	3	Southern S. Am., New Zealand
4. Distichia	3	Southern Andes
5. Rostkovia	1	Southern S. Am., New Zealand
6. Oxychloe	1	Southern salt deserts
7. Andesia	1	Southern Andes
8. Prionium	1	Cape Colony

The family evidently began with *Juncus*, and probably somewhere in the north, crossing the tropics at higher levels. The most widespread, almost cosmopolitan species, *J. bufonius* L., reaches 112 in BRITAIN, as do *J. effusus* L. and *J. conglomeratus* L., which though not quite so widely distributed in the world, exceed it in number of individuals.

Luzula, suited to rather drier and more shady northern conditions, was the first mutation from *Juncus*, and has not travelled so far. Only when *Juncus* reached the far south did it again, apparently, encounter conditions sufficiently different to give the needful stimulus for larger mutation.

Even in the tropics this does not seem to have been forthcoming; *effusus*, common in BRITAIN, is also common in the higher hills of CEYLON, and is one of the few species in common between the two countries.

The six southern genera show in S. AMERICA a structure that is largely co-ordinated with the drier and colder conditions to which they have been subjected, or, in the case of *Oxychloe*, to the conditions of salt desert. The results are seen in the well marked xerophytic characters, though we do not as yet know exactly how these were produced there. It is of special interest to notice that *Juncus* itself, the leader of the family, also shows cushion formation, one of the characters exhibited by these genera, in salt marshes and in similar places, so that it is evident that a tendency to that character is, so to speak, in the blood. It is evidently a case of like causes, like results, as one may see by comparing with the other cushion plants of the south, like *Azorella* (*Umbelliferae*), *Raoulia* (*Compositae*), *Restionaceae*, *Eriocaulaceae*, &c, or with many alpine xerophytes of the north.

In SOUTH AFRICA, on the other hand, the local genus, *Prionium*, and probably at a single mutation, developed a shrubby habit which enabled it to live more easily in the river beds, though we can see no reason why it should not have developed into something on the lines of the *Podostemaceae*; there was probably some internal reason.

The taxonomy of the large genera well illustrates the rule that we have been gradually making clearer—that the important taxonomic divergences are among the very first that appear in the history of a family, tribe, genus, or species. In *NP/1* BUCHENAU makes eight sub-genera of *Juncus*. Of these 1 and 7 have each only one species, in the Mediterranean and in S. Africa; § 6 (*Junci alpini*) has a number, mostly in the Himalaya, but also in the western mountains and arctic. This and the other five subgenera all occur in BRITAIN, and are in general headed by the most widely distributed species there, as we have seen in other cases; § 2, *J. poiophylli* by *J. bufonius* L. (almost cosmopolitan, British dispersal 112), § 3, *J. genuini* by *J. effusus* L. and *J. conglomeratus* L. (dispersal 112), § 4, *J. thalassici* by *J. maritimus* (disp. 55; this coast species could not reach more than about 80, but has not yet got round the north of SCOTLAND, though, as one would expect from the less broken coast, it has gone further north on the colder eastern side. The 5th section, *J. septati*, is headed by *J. lampocarpus* (disp. 110), the 6th by *J. triglumis* (25); § 8, *J. graminifolii*, is represented only by *J. capitatus* in JERSEY and GUERNSEY. The groups are thus headed by the most widely dispersed species in BRITAIN, as we have already seen in *Galium* (p. 179) and other genera.

The same thing shows in *Luzula*, whose three sub-genera are headed by the three most widely dispersed species in BRITAIN, which are therefore well divergent from one another —§ *Pterodes* by *L. pilosa* (111), § *Anthelaea* by *L. sylvatica* (110), and § *Gymnodes* by *L. multiflora* (111).

It is of great interest to see that all the small genera of *Juncaceae* have evidently arisen under the stimulus of altered conditions, and in the kind of broken and especially of mountainous country in which such conditions most readily occur. Those that occur on both sides of the south PACIFIC probably had other species on the now submerged land there.

By taking families from the top *downwards*, in the way in which nature evidently developed them, it thus becomes much more easy to trace that development, as we have just done in regard to *Juncaceae*. The taxonomic divisions soon become clearly marked out, though they are better shown in some families than in others (nature had not classification in view). Thus we find as leading genera:

Amaryllidaceae by size in the world

Agave	275	Heading	*Agavoideae*
Crinum	130	Heading	*Amaryllidoideae*
Bomarea	120	Heading	*Hypoxidoideae*

Araceae we have already seen on p. 267.

Bromeliaceae by size in the world

Tillandsia	400	Heading	*Tillandsieae*
Pitcairnia	170	Heading	*Pitcairnieae*
Aechmea	150	Heading	*Bromelieae*

and so on. The distribution of *Agavoideae*, in south U. S., MEXICO and C. AMERICA only, is much less than that of

Crinum, and it may be that the latter is really older than *Agave* itself. The fourth tribe in *Bromeliaceae*, *Navieae*, has only the genus *Navia*, with three species in AMAZONAS and GUIANA, marked by a supposed " important " character, few ovules against many, but one easily formed by a simple mutation (*cf. Farmeria* in *Podostemaceae*), and it cannot be regarded as on a par with the rest. If we look at *Tillandsia* itself, we find the two species with the widest dispersal, *T. usneoides* L. (CAROLINA to ARGENTINA) and *T. recurvata* L. (FLORIDA to CHILE), heading the two largest sub-genera, and so on. The law is quite general, and there are very few exceptions.

As one goes upwards, a family seems suddenly to stop at a very definite genus, the largest genus that one would put into the family without great hesitation. This, the oldest genus, was evidently that in which the "family " characters first appeared as a definite connected *combination*, which has subsequently remained comparatively unaltered. It has slightly changed at every mutation since it was made up, but has not changed the individual characters so continuously or so divergently one after the other that their presence as the family characters can no longer be recognised as a whole, sometimes A, sometimes B, changing, but enough remaining unchanged to be sure of the family concerned. Another family is

Hydrocharitaceae by size in the world

World size		Sub-family		Tribe	Distribution
Boottia	20	Heading	*Stratiotoideae*	*Ottelieae*	Trop. As. Afr.
Ottelia	15	2nd	Strat.	2nd Ott.	Warm
Blyxa	12	Heading	*Vallisnerioideae*	*Blyxeae*	Trop. As. Afr.
Lagarosiphon	10	2nd	Vallisn.	*Vallisner.*	Afr. Mad.
Elodea	6	3rd	Vallisn.	*Hydrilleae*	America
Halophila	6	Heading	*Halophiloideae*	No tribes	Trop. oceans
Hydromystria	3	3rd	Strat.	*Hydrochar.*	Trop. Am.
Limnobium	3	4th	Strat.	2nd Hydr.	Am.
Vallisneria	3	4th	Vallisn.	2nd Vallis.	Warm
Thalassia	2	Heading	*Thalassioideae*	No tribes	Trop.oceans

Here we can again see the growth of the family more or less marked out. *Boottia* and *Ottelia* differ little, and may even be sub-genera of one genus. *Blyxa* heads a new sub-family, and the last two sub-families, of oceanic dispersal and under almost completely uniform conditions, do not break into tribes as do the first two. They probably became marine at some big estuary on a nearly tideless coast, as at KALUTARA in CEYLON, where the river is fairly large. One is told by the local people that it is fairly safe to bathe at a certain belt in the estuary, where the water is about half and half, but that one is liable to be eaten by crocodiles upstream or by sharks down.

This is a small family, but being water plants they are more plastic, and have formed four subfamilies and eight tribes for about sixteen genera and about 90 species. Each genus behaves like its immediate ancestor, forming about the widest divergence possible at that particular stage, larger than in land plants perhaps on account of the plasticity. Each line of descent continues to divide when any excuse is given by the conditions, but the divisions tend to diminish, and, given time enough, would perhaps come down to a stage of sub-sub-species, or even Jordanian species.

The monotypic genera, as they make about 38% of all genera, while the ditypes make another 12%, require mention, but have been sufficiently discussed in many previous places, *e. g.* in *AA*, and in *Evol.*, and in (158).

15. *Generic sizes.* With the almost complete disappearance of adaptation and relicdom from the field of action, there seems little reason left for the great variation in sizes of genera, especially when they are all in the same family, and do not vary in concert with any other character that one can find, as all for example vary with age. Let us look at *Rubiaceae*, sub-family *Cinchonoideae*, with its eight tribes; the other sub-family, the *Coffaeoideae*, behaves in the same way.

Variation in sizes of genera in tribes of Cinchonoideae

Tribe	1	2	3	4	5	6	7	8	Aver.
Size of leader	20	180	100	5	40	50	60	125	72
Number of genera	12	48	24	5	43	10	48	86	34
Number of species	55	714	186	9	358	158	309	771	320
Av. size of genus	4.6	14.8	7.7	1.8	8.3	15.8	6.4	9	9.2
Number of ones	4	23	12	4	15	2	24	41	15

This is a remarkably incongruous set of figures. Let us place them in order by sizes of leaders

Tribe	2	8	3	7	6	5	1	4
Size of leader	180	125	100	60	50	40	20	5
Number of genera	48	86	24	48	10	43	12	5
Number of species	714	771	186	309	158	358	55	9
Av. size of genus	14.8	9.0	7.7	6.4	15.8	8.3	4.6	1.8
Number of ones	23	41	12	24	2	15	4	4

None of these sets of figures seems to have any correlation with the first set, or with any rule that one can think of, so that it is very hard to imagine that the grouping is genetic.

The *Coffeoideae* give a similar set of incongruous figures. Their leaders average 132 against 72, yet they have only 195 genera against 276, and 2381 species against 2560, and their average size of genus is 12.2 against 9.2.

16. *Taxonomic maxims.* We have already said a good deal about these in *AA*, pp. 217-18, and *Evol.*, p. 132, and this notice is simply a reminder that most of them are as easily explained by the new outlook as by the old. For example, two of the best known are that large and widely distributed species vary most, and that species of larger genera vary more than those of smaller. This is just what one would expect, as a simple and automatic consequence of all that we have learnt about the mechanical and automatic way in which evolution goes forward, and which we have seen illustrated by the incidence of varieties in the British flora (p. 186). Confirming this by looking at the first volume of the Indian flora, we find that 31 genera with 100 or more species *in the world* have 174 varieties, while 65 genera of less than 100 have only 168 in all, or less than half the percentage. As size and area go together, it is clear therefore that mere wide dispersal is probably sufficient to account for the variation seen. It may even be that at every birth of an individual in a definite line of descent there may be a tendency to a very small difference indeed; or again, it may be that as groups of characters are produced at each mutation, and that we make our genera by fitting together characters into the best marked groups that we can find, it is not unlikely that genera may be polyphyletic (*cf.* also BOWER's work in **16, 17**). But as yet all this is mere speculation, until we

know something about the laws that govern the phenomena actually seen.

Another maxim is that " those classes and families which are the least complex in organisation are the most widely distributed, that is to say that they contain a larger proportion of widely distributed species ". We have expanded this at some length in the chapter in *Evol.*, p. 65, and have there pointed out how it fits in with dichotomous divergent mutation and the hollow curve. We have dealt with the common maxims on p. 132 in the same book, showing how well they all fit in with our theories. There is also a long list of maxims in (68), vol. I, Dicots, pp. 6-7, but some of them may need a little revision to fit in so well.

17. *The discrepancy between taxonomy and geographical distribution* is often considerable, requiring explanation. The help that geography gives to taxonomy is more or less accidental, when it happens, as it sometimes does, that divergences in the two coincide. This often simply means that in that case there was no polyphyly; the marked character or combination of characters only appeared once, and was locally propagated. We have said much about this subject above, and may call attention to the most important statements. We have seen that dispersal is mainly governed by the laws of ASA, with the negative influences of barriers of all kinds. The closer relationship of the genera near the head of a family tends to be marked by wider divergence—a hopeless discrepancy. We have given many individual cases of great discrepancy, especially the *Monimiaceae* in Ch. X and *Araceae* in Ch. XI, the *Buxaceae* on p. 159, the *Dipterocarpaceae* on p. 153, and in places a reference or two to other families. We have described the cases of such genera as *Hibbertia* and *Schumacheria* on pp. 146-8, where there is no overriding genus in the family to bring similar features to two genera at great distances apart; *Tetracera* on p. 148 forms a very incongruous mixture of the two, and it is clear that it is the structural rather than the geographical side that must give way. We have also given details of *Siparuna* and *Mollinedia* on p. 246, and so on.

It is clear that one cannot neglect geographical propinquity, but if we try to add its results to those of structural likeness, we make our classification much more complicated, without making it any more genetical, for these two seem to be utterly incompatible in broad outline; a genetic grouping cannot be made upon a structural basis only, and it is better to keep them apart. The simple but universal branching out of the head of a family and its first descendants—its nearest relatives—into the heads of the tribes, subtribes, and so on, shows that divergence tends to be greatest at the top, in the region of closest relationship.

Discrepancy seems inevitable, and so widespread and common that it may almost be regarded as a law of geographical distribution. We can see it simply shown in such a case as *Rhamnus* (p. 143), where both in CEYLON and in MADRAS the same wide has mutated off an endemic in each country, and these two endemics are both sub-generically separate from the wide, as well as widely separated from each other. In fact, had their mutual separation been older and therefore commoner and more widespread, their difference would be sub-generic also, in all likelihood. The same difference as that between the wide and the endemic in CEYLON is common all over the range of *Rhamnus* and in one district there may be only one, in another the other. *Cf.* also *Tetracera* (p. 148), *Psychotria*, and many other genera.

The cause of this discrepancy was considered in *Evol.*, Testcase XXVIII, p. 154, and one may see it in another way in many monographs, *e. g.* that of *Siparuna*, head of *Monimiaceae*, in *PR* (*cf.* p. 246, and map on p. 224). It is broken up by the key into smaller and smaller divisions down to the single species, which approach one another structurally but not geographically; to get the latter, one must pick out species all over the list. There are some in every ten from the first to the eighth (last), in PERU, while there is also the overriding species 87, *S. guianensis*, practically covering all the rest. This type of distribution, with most of the structural subdivisions represented, is perhaps the most common of all. We have seen good examples in BRITAIN and in EUROPE generally, in CEYLON, and elsewhere, and have given a sketch of it, dealing only with species, in *Evol.*, Testcase XXVIII, p. 154. When we have realised what is shown in all the lists of genera at the heads of families shown above (condensed on p. 173) we shall of course expect this result. It is evidently a general law of evolution.

By no kind of shuffling, re-arrangement, or re-grouping, can one be sure of harmonising the structural arrangements, and with them the taxonomic grouping, with the geography or the genetic succession. Let us take *Phytolacca* (*PR*), which happens to be upon the table, as another illustration. Each sub-genus divides into those with hermaphrodite and those with dioecious flowers (*cf.* the *Restionaceae-Eriocaulaceae* complex in *Evol.*, Testcase XXIV, p. 138), showing that one or other of these characters must be polyphyletic. It is probably more or less as a result of this very common phenomenon that the tendency of taxonomic work is to continual subdivision of the groupings, so as to give to nearly every genus or small group of leader and satellites a separate position, as we have seen in *Araceae* where 108 genera occupy 42 different divisions, and even then, have not got over the difficulty.

With the structural differences largely valueless from an adaptational point of view, destruction of intermediates, whether geographically or taxonomically, cannot be called in as was formerly done, and the larger the family, the more difficult does the position become. This fact alone goes to show that the two are more, rather than less, independent of one another. The structural changes that the mutations bring about are not necessarily accompanied by increase in distribution, though they may be in cases where, as in xerophytes, there is a steady pressure in one direction. In a small and local family, where all the genera are living in much the same conditions as the head of the family, *e. g.* the *Penaeaceae* (p. 301), structure and geography agree well enough. But in a large and cosmopolitan family like the *Compositae*, reconciliation becomes practically hopeless, and indeed is not attempted, and the subdivision goes on as in *Araceae.* A single group in the monograph in *NP/1* taken almost at random, shows the following composition :

No. 557,1 CORSICA; 558,1 NEW GUINEA; 559,1 WEST AUSTRALIA; 560,1 CENTRAL AUSTRALIA; 561,7 S. AMERICA, and 562,2 CHILE. Obviously the only possible explanation is polyphyly; they are all young, and one could not get such destruction as would be needed.

The whole process seems to be largely the continual production of new permutations and combinations of characters that are handed down from above, each new one making others possible to its descendants.

18. *The incidence of character* demands much further enquiry. Why are family, tribal, genetic, and specific characters found in successively smaller groups? Evidently the family was the oldest, and we have hitherto looked at evolution as if it were moving backwards. What determines how long the bulk of some set of characters shall remain comparatively unaltered in a line of descendants? And why should there seem to be no reason why those particular characters should go together; why one family should have extrorse anthers and an inferior ovary, another get on just as well with introrse anthers and a superior ovary. We gave *Lauraceae* as an illustration on p. 115, but any other family would do as well. Except that the characters mark all the organs, there seems no correlation among them, except in such cases as climbing plants, where a weak stem accompanies the possession of climbing organs.

Why are the family characters on the whole so constant in incidence that they can be used as such, but why are they not exactly constant, one or two changing for every tribe, but almost never all or nearly all, and rarely twice the same, or in the same way? Why, to take a simple instance, does *Cucubalus* break away from the family characters of *Caryophyllaceae* to exhibit a berry fruit, the only one in the family? But why is this breaking away so common that in all families of more than four or five genera we have to qualify almost every character by " usually " or some such expression? And why is almost every character that thus unexpectedly appears one that is common enough somewhere else, even if not found in that particular family, like the berry, which is one of the commonest of fruit patterns, and in both Mono- and Dicots? And so on.

As an instance of a distinctive character found in several places in one family, but not outside of it, we may take the familiar red and black seeds (crab's eyes) of *Abrus precatorius* (*Legum. Papil. Vicieae*). This character, with the same exact straight line of demarcation, but with rather more black and less red, is found in *Adenanthera* (*Legum. Mimos. Aden.*) and in *Ormosia* (*Legum. Papil. Sophoreae*) and one or two more (*cf. Kew Bull.*, 1890, p. 1). Or again, take the case of cauliflory (flowers appearing on old wood), which is found in many tropical shrubs and trees like *Artocarpus* and *Ficus* (*Moraceae*), *Goethea* (*Malvaceae*), *Theobroma* (*Sterculia-*

ceae), and many more. In these two instances we have taken unusual characters, but if one take common characters, they are to be found all over the whole system of taxonomy.

Few actual generations are needed from top to bottom even in a large family, working as they appear to do by the 1-2-4-8- rule, and it is very unlikely that any divergence will strike all the family characters at once, after the first divergence from something outside the family that threw them all together, producing the genus A, which led the new family, and which had a set of characters that on the whole persisted right through it. It must be remembered that the beginning of a family, especially if large, tends to come at a period when divergence also tends to be large. The *individual* divergences in a small family (*cf. Evol.*, p. 199) are in general as large as in a big one, but the latter tends perhaps to have more of them in the early genera, so that there is less doubt as to its family rank. At an early period of time, possible mutations were probably fewer and therefore better marked.

At the second mutation the divergence will probably tend to be less marked on the whole, fewer characters, and especially fewer of the " family " characters, being affected. But they will still be so marked that the new genus B will go almost automatically into a new tribe, even though it is the immediate child of A, which will now become the head of the first tribe as well as of the family. Further mutations of B will give rise to still smaller divisions than tribes, though one must not forget that a large part of the importance of a character is due simply to its age; the older it is, the more descendants will show it.

When a divergence is very recent, and found only in one or two species of a large genus, like *Coleus elongatus* on Ritigala summit in Ceylon (*AA*, pp. 151-2), the taxonomic tendency seems to be to retain it in that genus, even with the divergence. The Ritigala *Coleus* no longer shows the usual calyx type of the genus, which could only be changed by a marked mutation. But if the mutation had been much older, so that there existed in Ceylon a group of species showing this calyx, there might be a tendency to give them a separate genus. We are more accustomed to find complexes in large genera than small.

On the whole, as one goes up from the monotypes at the bottom, the divergences seem to become rather more numerous, even if no better marked (*cf. Evol.*, p. 199). In a family like *Podostemaceae*, where all the divergences are rather striking, this seems to show well enough, and though both lines seem to have started from *Podostemon*, there is a great difference between the forms of AMERICA only, and those of ASIA only. As one gets near the top in a big family, one finds at last that the mutation that produced the leader A affected so many "important" characters that it is very difficult to say what was its probable parent. It is very noticeable in the list of the 45 leading families on p. 329, how many different orders they belong to, and how marked the tendency to put many of the large families each into an order, either by itself, or with a few satellites. In HUTCHINSON's list, we find such families as *Crucif.*, *Prot.*, *Malv.*, *Euphorb.*, *Legum.*, *Myrsin.*, *Gentian.*, *Borrag.*, each in an order of its own, and such as *Annon.*, *Ranunc.*, *Papav.*, *Cappar.*, *Viol.*, *Polygal.*, *Polygon.*, &c each surrounded by satellites. These are given in the sequence in which they occur in the list, so that one can see the great shuffling that has been done; it is clear that whatever arrangement we take, the families are difficult to place, for the simple reason that in many cases the mutation that gave rise to the head of the family altered a good many of the important characters of the immediate parent of that head. The difficulty of placing thus increases with the size of the head.

Working downwards in this way, order-family-tribe-genus-species, one may perhaps suggest that what is going on is something like this. At the "order" stage, divergences are few, but well marked, inasmuch, perhaps, as they have but a comparatively small number of diverse features of the different organs upon which to work, and possibly also because the available energy for making divergences may be greater. The new forms thus produced, in very early days more particularly, will tend to differ so much that we shall now look upon them as heads of families, and especially of large ones such as we see in the list above, beginning with *Compositae*, *Orchidaceae*, and *Leguminosae*. These in turn, when they come to mutate, will have rather more material, and perhaps rather less energy, and the result of later mutations will tend to be, at first, mainly heads of smaller and younger families.

The next stage will tend to be tribal, and so on downwards. But as no two will be likely to mutate at the same rate, or to begin doing so at the same time, we shall have a great mixture of all the different stages of evolution going on at the same moment. Each new mutation will more or less closely repeat the action of its immediate ancestor, having somewhat more material to work upon by reason of foregoing mutations, and perhaps rather less energy with which to do so. Those characters of the leader A that have been left comparatively untouched in the various mutations will be the family characters, and the same for tribal, generic and other heads, and as we come downwards in the scale, the chance of any mutation giving rise to something so divergent that it cannot be easily placed will become less and less.

In the very earliest days of the flowering plants, therefore, the new forms produced will have a tendency to be the leaders of new orders, made by comprehensive mutations that will cover a good many characters; whilst those characters, being developed at so early a period, will be regarded, now, if they have persisted, as very important, for we have seen that importance goes with age. Any new form produced at that early period will tend to be a member of a new family, or even order, when judged from a taxonomic point of view. In our present state of ignorance of such matters, it will be almost impossible to say with certainty what its parent actually was, for it may diverge in several important (old) characters. Hence our difficulties in making, or grouping and arranging, the orders.

At the same time, of course, the new form will be a new order, as well as a new family, a new tribe, a new genus, a new species. But to the botanist of that date, all this latter definition would be unnecessary, and what we now call a tribe or a genus would take the place of our conception of species, and be sufficient definition, though there would doubtless be frequent opportunities for dispute as to position.

As time went on, mutation would become less and less comprehensive, and it would become easier to place new forms in taxonomic relationships as marked out at the present day. A considerable number of what we should now call new families would appear, then tribes, and so on. But all these stages would be mixed up together, according to the different ages of the things concerned, and other factors.

There is probably much to be made out by a simple study of characters and their incidence, family by family, and it may be worth while to look, for example, at some of the satellites of the *Compositae.* In *Calyceraceae* the first three of its few genera are separated by mutations of the fruit. The fruits of *Boopis* (25 spp), the leader, are all alike, but the first mutation produced *Calycera* (10) with some fruits crowned, but not all, by a hardened calyx, while in *Acicarpha* (5) the ray fruits are united, and the disc flowers sterile. The family is confined to the southern ANDES, but has spread out upon the plains also. There is at present no possibility of explaining why these particular divergent characters are shown on these three leading genera. They show no correlation with any of the conditions of life, nor can one see any reason for the casual mixture of hard and soft calices in *Calycera*, or the union of the ray fruits in *Acicarpha.* For some reason quite unknown, the mutation united these particular characters in certain cases, which by our rules of taxonomy were new genera. But, as hardly needs further insistence, the chance that just these characters, and all at the same time, shall be chosen for change at the next mutation, is in the highest degree improbable, so that the genus will continue, though in each new species there will be a great probability that one or other of the characters will change. But it is therefore unlikely that a new genus will be formed from any parents but the older ones that have now so many species that they stand fairly high in the lists. In fact it is by no means impossible that most of the genera of a family are directly descended from one or other of the first dozen or so of genera that are shown in the many lists that we have now given. Very small genera, up to perhaps ten species at least, are unlikely to have much, if any, generic progeny with more than one or two species, progeny, that is, that for the present will count for nothing in the evolution of the family. As we have shown in *Evol.*, p. 101, in 41% of the families, the first genus has more than half the total of species in the family. Even in *Compositae,* the first 30 genera have 9055 species, while the remaining 1149 genera have only 9004 among them. It is the largest or oldest genera, derived from the earliest mutations, that have been the great, probably almost the sole important, factors in determining the later history of the family, especially its division into tribes and other groups. Except in small families with small heads, the little genera count for but little.

In other words, some of the characters that are being handed down may change at each mutation, though what the change may be, and why it should affect any particular character, is at present a mystery. Only in special cases like the *Podostemaceae* or other water plants, the plants of dry climates, parasites, saprophytes, and so on, does one seem to see any sign of cause and effect. The evidence that we now have of divergent mutation gets rid of many of the difficulties of the old school. The new theory makes no use of advantage and selection, needs no transitions, and will work equally well in either direction. But its laws need much further investigation.

If the genera of *Calyceraceae* were larger and more numerous, the descendants of *Calycera* would probably be regarded as a tribe *Calycereae*, contrasted with the tribe *Boopeae*. Age in the family, regardless of the intrinsic value of a character, is what gives it its importance. The writer has been preaching the supreme importance of age for fifty years, as enabling nature to carry out efficient and valuable change, and it was therefore a great pleasure to him to gather, from the papers and speeches at the Bicentenary of LAMARCK (79) that people seem to be realising this fact. Some of the most important characters are simply picked out by their age in their families, like the ligule of the grass leaf, the anteposed stamens of the *Primulaceae*, the tetradynamous stamens of *Cruciferae*, the ochreate stipules of *Polygonaceae*, the column of the *Orchidaceae*, the asymmetric leaf of the *Begonias*, and so on. It will of course be noticed that though this single insignificant and obviously mutational character is *a* mark of any of these groups, it is not *the* mark, unless found in combination with other characters. When the tetradynamous stamens are found in connection with a four-petalled flower, a superior ovary with a spurious division, and so on, we know that we are dealing with a crucifer, because that *combination* of characters is practically certain never to be found in any other group, unless possibly in *Capparidaceae*, which is very closely allied. The ordinary laws of chance forbid such a happening.

It is fairly probable that the *Calyceraceae* is an offshoot of the *Compositae*, one of which probably underwent a divergent mutation in which it happened that the erect ovule became pendulous (*cf. Buxaceae* and *Euphorbiaceae*), the cohesion of the anthers was lost, and a little endosperm appeared. All these are simple mutation characters, and it was what as yet we must call chance that altered them all at once, and made a new family. This particular chance, however, could only operate when led up to by the mutations that gave rise to the *Compositae*, and perhaps even the mutations that in the family of the *Compositae* gave rise to whatever genus it was that became the parent of *Boopis*. A very slight difference in the starting point will make more and more difference as the mutations go on, so that the final result may be something very different from that which began with a genus closely allied to the first.

The other very small and apparently satellitic family, the *Stylidiaceae*, has one fairly large genus, *Stylidium* (100), mainly centred in AUSTRALIA, distinguished from *Compositae* by simple mutation characters. The other two chief genera are *Phyllachne*, distinguished by absence of labellum, and *Levenhookia*, with shoe-shaped labellum. It is clear that all their characters may be obtained by simple mutation, but not why it should be so. There was no definite persistent strain in one direction, and so the mutations appear to be due to chance, though in *Levenhookia*, an endemic of the drier climate of WEST AUSTRALIA, the mutation has gone in the direction of small and crowded leaves (*cf. Juncaceae*, p. 346).

Even in so small a family as this, one can see early breaking up of a genus into its taxonomic divisions going on; *Stylidium* shows four sub-genera, and *Phyllachne* three sections, several of which have been regarded as of generic rank.

There are also frequent displays of greater complication, which may be lumped together as appearances of unexpected characters at various places, often widely separated geographically or taxonomically, or both. The *Rubiaceae* have usually an inferior ovary, but *Gaertnera* in AFRICA and *Pagamea* in BRAZIL have each a superior ovary, and must have obtained it by independent mutations, but why? Why are there no African descendants of the former, showing the superior ovary? It has 30 species, enough for considerable generic parenthood. Did the offspring return to an inferior ovary?

The adoption of divergent mutation makes the old positions untenable. We are presented with two *faits accomplis*, parent and child, no longer liable to crossing, as they were in the days of gradual transition, and too different for selection to come in as a guide. We have shown on p. 27 that adaptation does not operate to separate things, and on p. 34 how *Paeonieae* regularly show two characters that may be seen singly in various *Helleboreae*. It was this repeated occurrence of the same character in more than one place that suggested the idea that a family might carry a set of characters for kaleidoscopic use, which might be shuffled into various combinations, each of which, if of stable enough equilibrium (p. 372), might be represented by a different form, sometimes of one, sometimes of another, rank. Under my conceptions, adaptational value is not *required* in single characters, provided that they are not harmful; evolution is largely a display of permutations and combinations of the individual characters, on the whole increasing in complexity as time goes on and their number increases.

These considerations show the great importance that attaches to the phenomena of teratology (pp. 100-105), for they show clearly what large and unexpected mutations are easily possible. We have no proof that their usual non-viability may not at times be due to the fact that that particular combination of characters was not in stable equilibrium, or was not one which simply proved unsuited to its environment, and died out.

Such phenomena as we have been describing occur mainly in larger families, because, upon our conceptions, there have been more mutations, giving the chance of getting more of the less usual characters. One need no longer feel surprised that it is the large families that depart most from their prescribed family characters in one place or another, nor need one feel that one must spend so much time in trying to explain complexes and such phenomena, which are perfectly normal under the conceptions that we have brought up. A family simply happens to show in common a group of characters, often, so far as we can see, unconnected with one another in any definite way, but covering all or most of the parts of the plant.

The natural supposition seems to be that the combinations of characters that mark families and other groups are almost pure chance. At any rate, a large element of chance, as we must at present call it, is introduced into our taxonomy. A family (or tribe, genus, species) is defined by the general presence of such characters as *happen* to fulfil the necessities of divergence from others (result of divergent mutation), and constant or nearly constant occurrence throughout the family (tribe, genus, species), which is the result of early acquisition, due to comparative age. Only rarely does one find traces of actual structural adaptation about the characters, and then it is in such cases as for example the *Podostemaceae*, where the constant pressure of external conditions is largely in one definite direction only, and species that indicate suitability to that pressure are mainly favoured. But there must of course be some law or laws that determine what happens, for the happening is evidently compulsory.

In *Connaraceae* (p. 141), our first list of leaders of a family, the first three generic mutations divided the family into its four great groups, the tribes. The original set of characters, descending from *Connarus*, was thus being altered, but *differently* each time, by divergent mutation. We have now seen, in many lists of leaders, and in the tables on p. 173 and in *Evol.*, p. 199, that this is a law of evolution, closely adhered to by all families. Had *Connarus* remained the only genus of the family, its characters would have been the standard throughout, though of course necessarily altered a little in every species. But after the family has become early divided into four tribes we have to add the qualification " usually ", or some such word, to nearly all the characters that mark *Connarus*. All families, unless a few of the very small ones of 2-5 genera, show the same kind of thing. In *Ranunculaceae*, for example, *Clematis* shows a more or less woody habit with opposite leaves, and being now a large (old) genus, has passed most of its characters, but not all, on to various groups or single species, according to their relative age. *Clematis* itself is the overriding genus (151), covering all the localities of the others, and many people are still doubtful about the acceptance as independent genera of these "satellites"—*Viorna* (18 N. AM.), *Clematopsis* (10 MADAGASCAR, trop. AFR.), *Naravelia* (7 INDOMALAYA), and *Viticella* (1 EUR.). In many floras these genera are marked as " *Clematis* " p. p. and as they are evidently descended from it, it seems a matter of little moment how they are named.

The larger a genus, the greater the range of its characters therefore, and of necessity. We can easily see this by taking the number of lines given to a genus in *NP*. Taking the *Mussaendeae* of *Rubiaceae*, for example, we find :

Lines	Sizes of genera	Average size of genus
8-9	60, 30, 10, 10, 10, 5, 5	19 spp.
6-7	40, 20, 10, 8, 8, 7, 5, 5, 3, 3	11
Less	2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1	1.2

We have only to look at the many lists that we have now given, of leading genera in families, to see how complete is our ignorance of the important subject of incidence of character. It is impossible that selection or adaptation should range the members of a family by size in such a way that three quarters or more of the largest should head tribes in the way that we have seen to be universal. The only possible explanation seems to be that proposed by GUPPY and the writer, and by various earlier authors back to GEOFFROY ST-HILAIRE, that the process of evolution is in the reverse direction to that stipulated by " Darwinism ", and is in a " downward " direction towards species and varieties, not upwards away from them.

Such a list as that of the leading *Compositae* on p. 176 therefore indicates that *Senecio* was probably the first *Compositae* to appear, while *Hieracium* and all the other later genera in the list are all due to subsequent mutation of *Senecio* or its offspring. Here we come at once against a serious difficulty which is of the same kind as that felt in determining the orders of the flowering plants, or the relationships of any of the earlier groups of ferns, mosses, Gymnosperms, &c, to one another.

We cannot, by any means at our disposal, so far as the writer can see, determine which genera of the 20 (and the same is true of all the lists) are the immediate descendants of the leader *Senecio*, and which of them only belong to the second generation. The second genus in a list may probably be considered as nearly always a direct descendant of the first, but one must not forget the *Ericaceae* (p. 368), where the first two have changed places. But after the second, the determination of parenthood rapidly becomes a matter of guesswork. The third genus is most likely a direct descendant of the leader, and it seems probable that for a long period most genera will be so. We have seen in Testcase VIII (*Evol.* p. 101), which should be read in this connection, that for a long time the first genus makes up more than half the family with its species. The chance is perhaps greater that the earlier subsequent genera that belong to the same tribe as the leader may be its direct descendants, while those below the leader in any tribe are more likely to descend from the leader of the tribe, but as yet we have no information to go upon. It is only as the family grows in size that the genera following the first become large enough to be in their turn important as parents. This one may see clearly in the table on p. 102 (*Evol.*), where with one small exception the figures rise steadily with age.

As a general rule the incidence of characters seems to be governed by what at present we can only call chance, and examples of this are abundant. A frequent teratological phenomenon in *Cruciferae* is the production of bracts, which in this family are usually recessive; but in *Schizopetalon* (5 Chile) we get them regularly formed (p. 104), with no possible adaptational explanation, but apparently owing to the operation of some unknown law in the mutation that formed the genus. It is another illustration of the fact that almost any character may at some time or other appear anywhere in a family. *Cf.* pp. 133, 135-6, 142-43, 148-9, &c, &c. There seems no reason why such characters as in

Gramineae	Leaf net-veined in	*Olyra* and *Leptaspis*
Orchidaceae	Leaf net-veined in	*Corysanthes*
Liliaceae	Leaf net-veined in	*Smilacoideae*
Gramineae	Stamens 10-40 in	*Pariana*
	Stamens 6-120 in	*Ochlandra*
Orchidaceae	Pollinia ∞	*Calopogon*

to take just a few from the Monocots, should appear at all.

Pappus in *Compositae*, often regarded as an adaptation, is not a very efficient one, except in a few cases like *Taraxacum*. In many it is almost immediately deciduous, a feature explained by selectionists of the writer's youth as a design to drop the seeds not too far away from places where the parent had succeeded, though how such an altruistic arrangement came about was left to the imagination. Many show scales and bristles symmetrically mixed, and even the most enthusiastic selectionist hardly dared to suggest that if the one failed, there was the other to fall back upon. Others, like *Adenostemma*, have sticky glands as well as the pappus proper. In *Eriosphaera* the tips of the pappus hairs have a number of inflated cells, like a bunch of stalkless grapes. We have shown in (**155**) how the characters of pappus and other things vary from genus to genus in the usual apparently purposeless manner.

A convenient list of things that *may* happen, inasmuch as they *have* happened, is Penzig's *Pflanzenteratologie*, 2nd. ed., where great numbers of mutations are described, some of which were instanced on pp. 100-05. It is not clear why these changes are impermanent except in one or two instances, and one wonders whether they might be mutations that were in some way unsuited to local conditions. One cannot see any evident reason why they should be so temporary, as a rule.

If characters come together by what at present we can only call chance, such a case as the tribe *Brownlowieae* in *Tiliaceae* becomes more intelligible (pp. 156-7). Here we have a group which shows a number of characters in common, but is geographically scattered, while at the same time a number of characters, usually considered more important than those that mark the tribe, are found in various members of it. A few of the tribe fit together well geographically, and in the usual curve, and are probably a genetic assortment, while the rest have acquired certain characters by chance that have brought them into the same tribe.

Into the tribe *Shoreae* of *Dipterocarpaceae* we put things that show a certain group of characters, that may often be found singly in other parts of the family, as the imbricate calyx is found in *Vaterieae* or *Dryobalanopseae*. As we have said on p. 155, almost any character may turn up anywhere, for anything that we know to the contrary, though it is not common. Every genus tends to show some character that was not visible in its parent, where it must have been recessive, so that the probability is that all characters, or their potentialities, descend from the leader of the family.

19. *The lack of transitions between characters.* It used to be supposed that any character found was derived from some ancestral one with which it could be connected by a series of easy stages, so that there must have been enormous numbers of these transitions. But their destruction could hardly be so absolute as the facts would indicate; many would survive in odd corners of less competition, yet it is the rarest of occurrences to find anything that can be said to show an intermediate single character. What is usually found, especially in extinct groups (cf. pp. 168-9) is things that show a different *combination* of characters, some from one more or less related thing, some from another, usually together with some that show in neither. We have seen that the action of selection is little or nothing, and that dispersal is controlled, positively by the laws of ASA, negatively by barriers. We can therefore no longer expect to find transitions, except in very rare cases. This view agrees with the actual facts much better than the former one.

There are often great gaps in the geographical display of "finished" characters, like for example an anther opening by pores, formerly explained by the same hard-worked explanation of destruction of transitions; and the same criticism is applicable. One cannot believe in such enormous destruction, with no trace left, over such great distances, such large areas, in so many directions, and at such different times, and this unbelief is much strengthened when one realises that selection cannot be invoked, so that there is no apparent urge to force changes. A great many differences again are so divergent that transition is impossible, and we now know that divergence is the rule, and as the divergence does away with the risk of loss by crossing, it is still more probable that this is the right view to take of the matter, and that the old conceptions must be abandoned. As yet we cannot predict in the least what will happen at any divergence, but it is evidently governed by laws which we must try to make out.

The logical conclusion to all this is almost necessarily that all the characters of a family, or the possibility of producing them after one or two necessary previous mutations have, so to speak, prepared the way for their appearance, should be present in the original first ancestor or parent of that family, like *Senecio* or *Ranunculus*. The same line of thought may be carried right back to the beginnings of life, each new divergence opening the way for yet others, but with no guarantee whatever as to what the ultimate result should be. A very slight difference in an early mutation might ultimately lead to quite different results, as the people of Mars or the moon differ from man in the works of the imaginative writers.

We have been so much under the influence of the theory of gradual acquirement by selection, that we have assumed, for example, that the follicle must be an older type of fruit than the achene, for it is hard to conceive of the latter turning gradually into the former. We have therefore to make the *Anemoneae*, with their greater numbers and wider dispersal, a younger and more successful group than the more restricted *Helleboreae*, though they show no sign of relicdom, and their dispersal follows the laws of ASA and the hollow curve. The change either way seems equally easy to mutation (cf. Testcases XIV, XV, *Evol.*, pp. 122-6).

As having some bearing on the case, let us look at the fruit characters of *Ericaceae*, such characters being usually supposed of great value. The usual list is now headed by *Rhododendron*, which has proved larger than *Erica*. As it centres in the north, and the latter in the south, the question of polyphyly is at once raised (and remember the *Epacridaceae* on p. 342), but cannot be discussed here. There are four sub-families, and ten tribes.

Ericaceae in order of size in the world

	Spp.	Sub-family		Tribe
Rhododendron	700	Heading	*Rhododendroideae*	*Rhododendr.*
Erica	500	Heading	*Ericoideae*	*Ericeae*
Vaccinium	150	Heading	*Vaccinioideae*	*Vaccinieae*
Gaultheria	120	Heading	*Arbutoideae*	*Gaultherieae*
Thibaudia	50	2nd	Vaccinioid.	*Thibaudieae*
Gaylussacia	45	3rd	Vaccinioid.	2nd Vaccin.
Agapetes	45	4th	Vaccinioid.	2nd Thibaud.
Simocheilus	40	2nd	Ericoid.	*Salaxideae*
Leucothoe	35	2nd	Arbutoid.	*Andromedeae*
Psammisia	35	5th	Vaccinioid.	3rd Thibaud.
Arctostaphylos	30	3rd	Arbutoid.	*Arbuteae*

Two tribes only have no heads in this list, *Ledeae* (Rhod. 1), headed by *Befaria* (20 warm AM.), and *Phyllodoceae* (Rhod. 3), by *Phyllodoce* (10 N. circumpolar and boreal).

In *Ericaceae* we have an instance of divergence in the fruit. The first three mutations produce the types of fruit seen in the first four tribes, a dehiscent septicidal capsule in the *Rhododendreae*, a loculicidal capsule in the *Ericeae*, a berry or drupe from an inferior ovary in the *Vaccinieae*, and a fleshy calyx enclosing a capsule, usually loculicidal, in the *Gaultherieae*. This incidence makes the " naturalness " of the first three sub-families of *Acanthaceae* (p. 216) look somewhat doubtful, and goes to show how the value of a character really depends upon its age in the family concerned, and not upon the particular features that it displays. Berry-capsule is evidently a simple mutational divergence that is liable to happen anywhere, and without having properly understood this simple fact, we have given to the difference an importance to which it has no right except when old and inherited by many descendants.

20. *Complexes*. We have given an account of this phenomenon on pp. 211-14 to which little need be added. As all the characters of a family or genus are being handed downwards, there is little or no reason, so far as we can see, why any character in that family, or in its related families to a lesser and lesser degree as the relationship becomes more distant, should not appear anywhere, so that a complex is a normal occurrence. Nature is passing on potentialities that differentiate as the conditions differentiate, though it is but rarely that we can see any actual structural adaptation in any divergent change.

21. *Polyphyletic descent*. This comes into greater importance with the turning from back to front of our conceptions of the local direction of evolution. If the parent of a family hand down characters to all the rest in different combinations, it seems probable that the same individual character should appear in different places, perhaps even frequently. Ancient characters, visibly present in the early days of a family, tend to be inherited by many descendants, and especially those characters of flower and fruit which are less liable to be affected by outside conditions, and so become " important in the family ". But this rule must not be narrowed down to individual characters, as is well known, for any single character may at any birth be the subject of a divergent

mutation. The production of new species &c repeats to a considerable degree the phenomena of human birth and descent, but with great intervals of time between births. What is inherited by any individual is the large part of a certain number of characters, of which all or most occurred either visibly or recessively (potentially) in the original parent of the family. In spite of the change that is liable to happen to a few at any mutation—and those usually different, in whole or in part, at every mutation—enough of the original characters survive to mark all the members of that family as one related group. If a considerable number were to change at any single mutation, an event which the ordinary laws of probability show to be extremely unlikely, the offspring would automatically go into another group.

BOWER's work on the ferns (16) was perhaps the first to bring the question of possible polyphyletic origin into prominence, and it will be well to quote some of his remarks. He says that " early writers, taking one very conspicuous character for the genus *Acrostichum*, freely exposed sporangia springing from a considerable area of leaf-surface, mixed up a lot of things that were at first placed in sub-genera, and were gradually found not to be necessarily closely related because their divergences were too great ". We have pointed out above, however, that great divergence may go with the closest possible relationship. BOWER goes on to say " It is becoming evident that the Acrostichoid condition is not in itself a sign of affinity at all, but a state or condition, which may have been attained by ferns of quite distinct evolutionary history. If this be accepted, then *Acrostichum* is not really a genus of common descent, nor even a natural group. But it expresses merely that condition or state of soral development in which freely exposed sporangia spring from a considerable area of leaf-surface. "

" The case is parallel with that of *Polypodium*... Such single characters as those defining *Acrostichum* or *Polypodium* in the old sense are in fact too wide to be of service in a system which aims at a true phyletic grouping ". To this we would add that divergences are frequently so great that one needs to be very careful not to mix up a phyletic grouping with a supposed natural classification. One can hardly make up phyletic groupings for more than a few genera together, and will not get easy characters by which to classify.

If it be admitted as very probable that characters are all handed down from ancestors, and not casually picked up, then there is nothing to be surprised at if any character suddenly appears in a new form when there was no visible sign of that character in the parent. The surprise in fact would come if there were no such happenings. The evidence of the sudden appearance of new characters in the formation of local endemics, whether species or genera, in that of the very many small genera everywhere to be found, and in that of the evolution of the genera at the head of every family, is so complete that it is clear that divergent dichotomous mutation is a law of evolution, and the onus of proof that polyphyly does not frequently occur is thrown upon the other side.

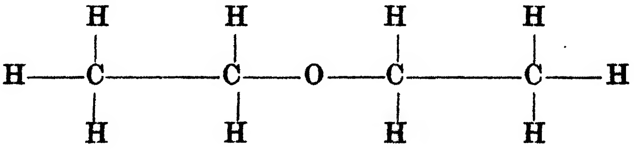
As a simple illustration we may take the case of the very well marked character of the reflexed calyx that turns up in so many *Ranunculi*. There is no single wide-ranging species that carries this character, as it is carried by *R. sceleratus* in the north, yet it is found in a considerable number of species in most of the range of the genus, *e. g.* in S. AFRICA. It would be absurd to attribute it to selection, and its source must therefore be the genus itself. Whether it were visible or not in the first *Ranunculus*, the potentiality must have been there, to appear at various independent places. This kind of thing is very frequent, as one may see in the red and black seeds of various *Leguminosae*, or in the frequent appearance of cauliflory in unrelated things (p. 355). It probably occurs more often than has been supposed, and is indeed one that should be expected to occur with some frequency.

The facts of teratology must come into notice here, for though they are not usually viable, they prove that a great number of unexpected characters can be passed on by the parent individual, which carried them in a " recessive " condition, and become visible, or " dominant ", in the sport. A study of the work of PENZIG (**102**) will show what a wonderful variety there is in such characters.

In Testcase XXIV, *Evol.*, p. 138 we have described a case which involves polyphyletic origin of the groups with monothecous and dithecous anthers, and similar cases are not infrequent, for example in the *Cochlospermaceae*, where two genera both show a division of this kind, or in the *Marantaceae*, where the first division is into 3-locular and 1-locular ovary, and each lot divides into those with one and those with two staminodes, and so on. Different sub-families of palms show division into those with fan and with feather leaves, and so on.

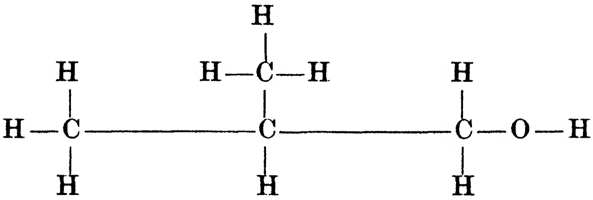
22. *The chemical analogies.* One cannot but be struck by the chemical resemblances that show themselves in these changes from one species to another. In the writer's youth, two bodies like ether and isobutyl alcohol were known to have the same crude formula $C_4 H_{10} O$, but were widely different in character and in properties, boiling for example at about 35° and 108° respectively. Beyond this, one could not then go, but now one knows that their molecules represent two different combinations of the same kind and the same number of atoms, both stable, but differently arranged and with different properties. This at once suggests that two allied species represent some kind of difference in the arrangement of the genes, or parts of genes, or even in the intimate physico-chemical arrangement of their molecules. The variety seen is probably due to their assumption of certain stable positions of equilibrium, as suggested in the working hypothesis that we have used since 1907. Some strain is supposed to be acting upon the nucleus, which presently relieves itself by undergoing some change in this way, a change which automatically brings about a change of structure. The change is not necessarily adaptive; adaptation is mainly internal and functional, the new species probably only changing that of the parent, born somewhere else, in such a way as to centre it upon the new conditions.

The ether molecule is represented by an assembly of two groups of two carbon atoms each, united by an oxygen atom in the centre, and with the remaining valencies satisfied by ten hydrogen atoms, each of which has a valency of one, while oxygen has two, and carbon four, represented by the lines that radiate from each. The whole molecule is thus made up, in a diagrammatic way



$$\begin{array}{ccccccccccccc} & & \mathrm{H} & & \mathrm{H} & & & & \mathrm{H} & & \mathrm{H} & & \\ & & | & & | & & & & | & & | & & \\ \mathrm{H} & — & \mathrm{C} & —— & \mathrm{C} & — & \mathrm{O} & — & \mathrm{C} & —— & \mathrm{C} & — & \mathrm{H} \\ & & | & & | & & & & | & & | & & \\ & & \mathrm{H} & & \mathrm{H} & & & & \mathrm{H} & & \mathrm{H} & & \end{array}$$

It thus forms a symmetrical and stable molecule, differentiated from isobutyl alcohol by the arrangement of the atoms, which in the latter make a pattern as follows



One can hardly talk of recessive characters in reactions like these, but the dominant (displayed) characters of ether are "recessive" in the alcohol. The combination CH_3 which has remaining valency of one occurs in two places in the ether-isobutyl alcohol pair, and perhaps may almost be looked upon as corresponding to a character in a group of plants.

A mere rearrangement of the atoms has thus made as wellmarked and complete a difference in the structure and properties of the resulting compounds as is the difference between one family or genus and another in living things. We can now make these chemical differences by the comparatively crude methods of the laboratory, and this is evidently the first step towards making them by nature's more refined and delicate methods, which do no harm to the living being. Already in the laboratory we have progressed a long way from the famous experiment of BERTHELOT in 1866, where he found that under the action of heat three molecules of acetylene became transformed into one molecule of benzene. A later discovery in this direction was that in the presence of zinc oxide, which acted as a catalyst without being itself altered in the reaction, carbon monoxide and hydrogen are transformed synthetically into methyl alcohol, at a temperature of 400° C. and a pressure of 160-200 atmospheres. Catalysts are not unknown in nature, and it would look as if there might be here an opening for work in what we may perhaps call phytochemistry. A good many substances hitherto only known in organic beings, animals or plants, are now being synthesised in the laboratory. The next step is evidently to find out how this is done by nature's methods. A conspicuous example is the synthesis of urea, formerly only known in animals, but now carried out on the large scale under the patents of the Badische Anilin und Soda Fabrik, producing one of the most useful substances of the celluloid kind. If a rearrangement of atoms can make at a stroke such complete changes in the structure, composition, and properties of lifeless substances, it is clear that similar mutational changes should make very important and evident changes in the structure of living things.

Chemistry was at first necessarily inorganic, carbon being simply one element among many, and not marked out for special importance until the appearance of life, which gave it great prominence on account of its combinations with hydrogen, oxygen, nitrogen, &c, which formed the basis of most organic substances, that have increased in number with the increasing variety of living things. The number of such compounds, most of them perhaps unknown in nature, that have been made in the laboratory is now, I am told, over 600,000, and no finality is in sight—if anything, it is the other way. The reactions produced in plants by colchicine, and other substances, are perhaps an indication of future possibilities.

This seems to the writer to be a fairly close parallel to the formation of species, vast numbers of which are known, especially in insects. We may perhaps call attention here to what has been said about the chemistry of plants and the possibilities of economic botany in *Evol.*, pp. 8, 89, 177. The great masses of facts accumulated, in such a book as WIESNER for example, at present remind one of the chemistry books of one's youth, before the study of the atom and the molecule had thrown so much light upon the subject.

I am deeply indebted to my cousin JEAN-PIERRE DE CHANAZ, who by his knowledge of chemistry has given me the information and help necessary in writing the above.

23. *Permutations and combinations.* The divergent mutation that is going on seems simply to be repeating upon a larger scale the kind of thing that goes on in human descent. Sets of permutations and combinations are being formed of the characters that are available, which in animals, more especially, are continually being mixed up by the agency of sex. One need not suppose that an individual in the

genetic chain carries all of them, or that any individual character is sure to appear in the offspring; the individual is carrying some set of potentialities, which may vary very slightly even between individuals. For all that we know, any character may at any time appear anywhere, but the greatest probability is, that if for example the plant is a crucifer, the potentialities will have a marked leaning towards cruciferism. By the ordinary laws of chance, it is very unlikely that more change will come at one mutation than will carry the offspring say into another genus, and not into monocotism or labiatism. Divergences like these belong to the older period of greater differentiation. Marked divergence is needed in several characters at once. The mere production of one cotyledon would not take a thing into the Monocots; one at least of the other common characters of that group, like the trimerous flowers, or the parallel-veined leaves is needed; that one cannot safely accept genetic relation on one character only has long been a maxim in taxonomy, and one can now clearly see the reason for it. The Monocots are in fact a group in which a particular combination of characters happened to appear at an early date, and the combination ran with only small changes through their descendants. Why this was so, we do not in the least understand, but whether, as is very probable, polyphyletic, or not, the group has had plenty of time to break up into families, tribes, &c.

A simple mutational change from some early Ranunculaceous plant, for example, might have made a monocot water plant which largely retained the less easily altered floral characters, and became leader of the *Alismaceae*, whose resemblance to the *Ranunculaceae* is well known.

The grand total of characters (*cf. Evol.*, p. 194) is less than that of species, so that the latter must depend for their number upon the possibilities opened by combinations of them differently made up. And it is upon the whole combination, not upon individual characters, that a species depends for its success or failure in the struggle for existence. And as this struggle varies from place to place with the variations in most of the factors, it is extremely unlikely that the whole, or even a large part of any single species should be killed out, unless at the very beginning of its life, when it represents but a feeble folk.

At mutation a new position of equilibrium has been taken up, and the new form, of whatever rank, is genetically as closely related as is possible to its also surviving parent. The new characters produced at any mutation seem to have nothing about them which should make them more likely to be preserved in heredity than their immediate ancestors. It is in the highest degree unlikely that the same *set* of characters should be altered at the next mutation, though one or a few may be affected. Thus on the whole the descendants of any particular grouping of characters will tend to inherit sufficient of them to be recognisable as probably related. Hence our familiar rule that genetic affinities can only be shown by agreement in two, or still better more, characters.

There is obviously a great element of what at present we can only call chance in the evolution that is going on around us. But nothing in nature occurs contradictory to her laws of operation, though there are evidently a good many of these at work. But they will gradually be discovered, as Mendel's law was discovered, by induction and deduction, and we shall slowly obtain a mastery of the processes of evolution, which will enable us to bring about desirable results influencing the future of mankind.

Nature is slowly constructing a great edifice by adding one atom to another, one molecule to another, and probably by increasing the complication of the genes, to say nothing of the cytoplasm. " Darwinism " laid too great a stress upon the " nature red in tooth and claw " side of life, making it the principal urge towards improvement, while its main function is to keep up the standard of work by taking the best individual for any particular job that has to be done under certain conditions that are local to that particular place. But as yet we have very little idea as to the aim of nature, if indeed she have one at all.

24. *Kaleidoscopic mutation.* An essential contradiction exists between the theory of evolution hitherto current, which implies that any character is descended from some other that was at least like it, and our system of taxonomy, as displayed in keys implying that there is somewhere a divergence between any character and some other. The possibility of making keys depends upon this. The difficulty of reconciling these two has long existed.

Somewhere or other in the familiar genus *Ranunculus*, which has been seen to be due to the branching out of parent species into younger and younger ones, these divergent pairs of characters must unite. They are so divergent, so unamenable to selection, and so valueless from an adaptational point of view, that it is clear that the union cannot be gradual, even were it possible, which is frequently not the case. It must rather be a case of one side of the divergence being sometimes dominant, sometimes recessive, and at any mutation, for all that we can tell, the positions may be reversed. Taking the characters of the buttercups from Bentham's flora, we find in Britain alone the following divergences :

Plant aquatic	terrestrial
perennial	annual
Runners	none
Stem erect	decumbent
Leaves undivided	divided
glabrous	hairy
Flowers yellow	white
Receptacle glabrous	hairy
Calyx spreading	reflexed
Petals five or less	eight or more
longer than calyx	minute
Head of carpels ovate or oblong	globular
Carpels smooth	tubercular or wrinkled
with stout beak	with short point

Many more divergences might be cited from other floras.

Looking at such a list, one can see no reason why the characters should go together at all, nor for the divergences they show, other than what we usually term chance. There can be little or no question of any special adaptation, nor of any selection among them. We can conceive no reason why *R. Flammula* should have a carpel ending in a short point, even if sometimes more or less hooked, while that of *R. Lingua* has a broad flat beak. The same difficulties are met with in any plants of an average mesophytic climate, like Britain. Only when conditions show a definite bias in one direction, do the plants sometimes show a corresponding structural bias, as in xerophytes.

Nor can we see any reason to account for the changes that take place when one species or genus gives rise to another. One cannot attribute it to adaptation, except perhaps in cases like that just mentioned, nor can we see any sign of law about the matter. It occurs in so many places geographically unconnected that its presence cannot be traced back to a common ancestor that showed it, unless that ancestor was the original ancestor, which even then might have been carrying the character recessively.

We have seen that the number of species is greater than that of single characters, so that the variety of species must be due to different combinations of characters. It will evidently be long before the laws that govern all this complicated inheritance will be clearly brought out, and in the meantime we need some kind of illustration to help any working hypothesis that may be formed. This must not do too much violence to the probable course of things in nature, and must afford changes not too unlike the natural ones, so that it may lead to suggestions. It is much too early yet to press the chemical analogy, and we shall fall back on the one that we have used for 40 years, the kaleidoscope, a familiar drawing-room toy of the writer's youth. One may imagine in a general way that a group of allied genera or species is represented by the series of slightly different patterns that one obtains by gently turning the tube. Each piece of glass may represent a character, and those that *happen* to be nearest to the top are those that will be most likely to change their relative positions. Thus the change of aestivation imbricate/convolute may happen to be near the bottom, as in *Acanthaceae*, and does not change again for a very long time, and thus is very important " in that family ", while in *Primulaceae* it is part way up the side, gets sooner changed, and is less important, marking only the difference between two tribes out of five. Or it may be at the top, become changed almost at once, and mark, as in *Rubiaceae*, only part of the tribe *Gardenieae* or *Rondeletieae*, or even only part of the very small group of small genera, the *Henriquezieae*, where its importance is trifling.

The total amount of light, and the individual amount of each colour, remains the same whatever pattern be displayed. But among the species of a genus, as we have seen, one character or another is liable to become recessive at any mutation, and to make the analogy more complete, it would perhaps be better to screen off one half of the circle, so that any piece of glass going behind the screen might represent a character becoming recessive, though sure to appear again (become dominant, or displayed, once more) as one continued to turn the tube, but in a different place perhaps, and in different relations to the surrounding characters.

Another thing that one must remember, that cannot be easily matched in the kaleidoscope, is that the characters of reproductive organs are, as compared with those of the vegetative organs, always more like the pieces of glass at the bottom of the circle, and it is not easy to design any way of showing this.

Sometimes two characters may be in contact by one pair of sides, sometimes by another. The permutations and combinations open to a dozen characters are almost endless, but it is all but impossible to pick out, except by chance, any one as definitely superior to another. A pattern is never twice exactly repeated. The way in which each individual bit of glass behaves is ordered by the laws of gravity, friction, and so on, but the total movement to the new positions is due to so complex an interaction of all these laws that one can hardly hope to disentangle them, for the present at any rate. We may therefore regard the formation of a new species, as we regard the formation of a new pattern in the machine, as being due to chance. A certain unpredictable combination of the available characters happens to be made under a certain stress, mainly of outside conditions, just as does that of the bits of glass. The result of a new combination of the latter is hardly ever seriously different from what went before, and the same is the case with species; there is little to choose among them, and practically no opening whatever for selection of one as against another. The differences that matter in the struggle for existence are more probably the *fluctuating* differences between individuals. This fluctuation, for example of height of plant, or of area of leaf, is not possible of representation in the machine.

In the operations of the kaleidoscope, one may get, apparently by simple chance :

1) The same two characters appearing in two allied species, but not in exactly the same mutual relationship—two bits of glass meeting by different edges in each.

2) The total value of the characters in any one of the innumerable possible combinations is the same—the light passing, and its colours.

3) The putting together of a new species out of characters carried, in a dominant or recessive condition, by the old. This might be easily shown by blackening out say an eighth of the circle; any piece of glass that went behind the screen might be regarded as having become recessive, the corresponding piece that had emerged as having become dominant.

4) The appearance of the same character in two different places—the same piece of glass in contact with A, B, C, D in one place, with W, X, Y and Z at another.

5) The re-appearance of a character that had apparently disappeared—a reappearance from behind the screen.

6) The appearance of an unexpected character—a piece that had long remained behind the screen, for some unexpected reason.

In (155) we have discussed the use of the Kaleidoscope at greater length.

25. *Concluding remarks.*

What it comes to then is in broad outline that the main stream of evolution runs on with little regard for other factors, which only deflect its line temporarily to one side or the other, the dominant direction being resumed as soon as the temporary interference is removed. The apparently needful stimulus for mutation seems to be provided by a change of external conditions, ultimately making so great a strain that mutation occurs. What exactly happens we do not know, but one result is evident, that there is such a re-arrangement of parts of the sexual cells that when the product appears it has quite a different structural constitution, especially in the fact that one or more of its characters have undergone a definite divergence, as we saw in the CEYLON endemic species quoted on p. 111-13 where the local *Ranunculus* showed a change from a divided to an undivided leaf, the local *Rhamnus* from 5-mery to 4-mery, and so on.

The characters found at times in tables are not the only points of difference, but are the most evident, those that are seized upon for keys. But in practically all the 51 Ceylon cases they are incompatible characters due to direct mutation and not allowing of transition. At some point in the ancestry of two such characters in two species of the same genus, we shall come upon the mutation at which they diverged. The original species of the genus could only show visibly one side of the divergence, but must have been carrying the other in some kind of potential or recessive, invisible, condition.

The divergences that appear in the very earliest days of a family seem largely to result in the production of sub-families or tribes, for about three quarters of the first few genera diverge markedly from one another in a few characters that remain more or less constant in the heredity, thus marking out a group in the family to which we give the name of sub-family or tribe. The two are not distinguished except by valuation, which says that in one case the divergences are of more " value " than in the other.

We must also realise that each head of a tribe thus formed is also at the same time a genus and a species in the family that descends from the original parental genus. For example in the *Connaraceae* (p. 141) the first four genera by world size each head a tribe, while only three of the first four *Dipterocarpaceae* (p. 153) do so. The characters that distinguish the tribes are much the same as those that distinguish genera elsewhere, but they are *combinations of characters* that appeared at a very early stage in the family history. By the ordinary laws of probability it is unlikely that this combination will again appear *except in direct descendants of the one that first showed it.* Simple age in the family is the secret of the importance of a character, for there has been time for it to be inherited by many descendants. Floral characters on the whole are better inherited, and less liable to frequent alteration, so that as a general rule they are more important. But in *Ericaceae* (p. 368) we have seen great variation in them at the very start of the family.

The individual characters that mark out the tribe are much like those that mark the distinction between the two genera in a bigeneric family (*Evol.*, p. 199), which there mark out its future classification when it has grown large. There is no doubt that the earliest mutations in a family give rise to its earliest divisions, these being followed by the smaller, but to work out in proper detail whether the earlier divisions show larger and more numerous divergences would need more time than is available to the writer at 80. On the whole, however, as one goes back through the past history of plants, it would seem that the smallest divergences, and perhaps the least numerous, mark the most recent divisions into species and subspecies, down to Jordanian.

On the other hand, as one goes upward, the divergences seem to become more clearly marked, and to involve more of the *available* characters, which will on the whole be less numerous in the early days of the flowering plants. Thus it comes about that above the leading genus of a family, which as the largest is growing the most rapidly (*AA*, p. 34), so that it occupies the tip of an acuminate apex, we are likely to find difficulty in tracing the ancestry further.

At the period when the leading genera of the family were formed, there were only the characters of the ancestors to draw upon for divergences, and these would be but few compared to the great variety subsequently developed as continually, and with ever greater rapidity, the family increased in size. Half a dozen divergences would affect, comparatively, a larger proportion of these ancient characters, and we have now seen that it is age which confers importance. Above the heads of such families as the *Compositae*, *Orchidaceae*, or *Leguminosae*, therefore, as there were but few characters to draw upon, there would likely be a great disturbance of characters at every birth, characters which would of necessity be old and " important ". The result of these mutations would thus be something which we now regard as widely different from the ancestor, though it would not strike the botanist of that date as anything out of the normal.

This consideration explains the great difficulty that exists in placing any family of the flowering plants into its proper " order ", as well as the tendency that there is towards giving a separate order[1] to each important family, which is often accompanied by what are obviously satellites. To place the orders into still larger groups becomes, for the same reasons as we have just considered, a very difficult undertaking indeed, and on the whole, the further back we go, the greater the difficulty of tracing even immediate ancestry, while if we go the other way, the immediate ancestor,

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[1] A better word than order, which has a different meaning in ordinary use, might be found, such as cohort, for example.

for example, of a lot of sub-species, is fairly evident. Divergence is more and more strongly marked as we go back in time, and affects more and more of the ancient and therefore important characters at a single operation.

All the time, or more probably, in the latter part of it at any rate, besides the production of new genera in a family, which at first largely head new tribes, there is a continual production of new species, and as the species grows, of new sub-species. This is probably owing to the continual production of more and more potential differences of character which enable more divergences to appear. It would seem more probable, if this be so, that most of the genera in the lists that we have given of the first ten or so of a family, are the immediate descendants of the head, so that it was quite probably the direct parent of most of the important tribes; and so on downwards. The larger or older the family is, too, the more sub-families or tribes shall we expect it to possess, for it goes further back into the period when fewer characters were available. With very old genera, too, it is more possible that some, or even many, of the descendants would diverge at once to new genera, and so on all the way down.

In going back through the past history of evolution we are necessarily somewhat handicapped by our now almost intuitive conceptions of variety, species, and genus, divisions that were probably not recognisable as such in early days, and to which there would certainly not be given the importance that we now attach to them. We shall see on p. 384 that it is not impossible that the list of the very earliest mutations known was something upon the lines of the list of the earliest mutations that followed the appearance of the head of a great family, like the *Compositae* on p. 176. In those early days the frequency of mutations was small, owing to the probable comparative uniformity of conditions, and to the small possibilities of divergence that were present with only a few simple characters. Mutations might even be millions of years apart, but when they did appear they would be such as we should *now* class as very important, because they have *now* lasted as marks for an enormous period of time, and so have become very important, by being handed down to a great number of descendants. The characters of reproductive organs, as less liable to serious interference from outside circumstances, have become, or rather have always been, of greater importance than those of vegetative organs.

In very early days, the differences between an alga and a fungus would be of no greater importance than that between say *Convolvulus* and *Cuscuta* now; it is age that has given such high importance to the former. It is by no means impossible that the very first mutations might have been upon something of the following lines

A. Heading Algae
B. Heading Liverworts
C. Heading Fungi
D. 2nd Algae
E. Heading Mosses
F. 3rd Algae
G. 2nd Fungi and so on

It is probable that later descendants of A would mainly keep to the group in which their leader is now found, as we may see in the *Senecioneae* on p. 177, where the great gap at the top was probably filled by genera that have mutated into other tribes.

As time goes on, the number of characters available at any mutation will probably be increased as the result of previous mutations, so that there will be greater choice, with less likelihood of a fresh and important mutation of some character lately changed, so that, judged by the botanical standards of later times, these later and younger mutations will be less important, and will less often give rise to new groups, which themselves will tend to be less important. This procedure of diminishing importance of the characters, mainly by reason of greater youth, will continue, and we shall arrive, in any given line, at the stage of orders, then of families, tribes, genera, and so on, while the simple divisions of early times will become of greater and greater importance as giving their characters to increasing masses of descendants. Age gives time for the results of changes to accumulate, and is thus one of the most important factors that are at work.

CHAPTER XIII

General distribution of plants.

We shall now try to put this subject into a more connected form, upon the lines adopted in the preceding chapter, beginning with an index

1. *Introductory*. The fundamental mass of facts upon which distribution is based, and which is always increasing in bulk and in accuracy, is the detailed working out by the taxonomist of the localities in which every species, genus, and variety or form, is to be found. The principal task of distribution proper is the study in broad outline of dispersal in large areas over long time, and its relation to the previous history of the world, geological, climatic, &c. The ecological branch of our subject deals with the way in which plants become grouped into communities, with the subsequent history of these. To the main line of the investigation, which hitherto

has been too much a field for great speculation, there have yet to be fully applied the inductive and deductive methods in common use, which we are here trying to show may be applied in such a way as to bring out useful and important results.

We began by working out inductively the law of age and area, with the first deduction, the law of size and space, both published in *AA*, 1922. The next deduction, age and size, followed automatically, and from these three, by the aid of the sub-conscious, which we have gradually made very subservient, a large number of other deductions, which have all proved correct on testing with the facts. Their success, with the further fact that illustrations have never had to be searched for, but could easily be found almost anywhere, has given the writer great confidence in the truth of these laws, which form the basis of the present work.

The long prevalent theory of "upward" change, from species through genus to family, is thus replaced by a "downward" from family to species, and if this be accepted, it means a great change in our way of looking at evolution, while it throws a good deal of light upon such subjects as taxonomy and dispersal. We have already considered the former, and keeping now to the latter, it is evident that age is one of the most important factors that have to do with it. But it has been completely ignored for many years; as GRISEBACH says, in talking of the work of his predecessors "they do not seem to have thought that mere age might come in". And this although such leaders as LYELL and HOOKER had called attention to it (*AA*, pp. 3-4). It is therefore of great interest to see the wheel of time coming round again (79, pp. 6-20). BUFFON had already said that "Nature's greatest workman is time", but it was LAMARCK who brought it into a notice and importance which it has never since wholly lost, though the opposition aroused by the writer's views upon age and area five and twenty years ago might have led one to suppose the contrary. LAMARCK said that "Nature has no difficulty on the score of time; she has it always at command; it is with her a boundless space in which she has room for the greatest as for the smallest operations". Dr ZEUNER's remarks should also be noted (*l. c.*).

The importance of age has been maintained by the writer for over 40 years. The chief active factors in distribution work with great slowness, except for the actual mutations, which seem to represent the giving way of something under increasing pressure. The result of age is to give all factors the time to produce their results as a combination of all. In this connection YULE's description of a "cataclysm" (158, pp. 23-30) should be read. If our "downward" theory be accepted, the whole position must be reconsidered. Local adaptation is an absolute necessity at the start, except in case of some fortunate accident, and it must be obtained for each locality in turn, so that much time is needed. Man, with his infinitesimal span of life, finds the slowness of nature difficult to realise, or to value, and is more impressed by her rapidity in the case of such things as cyclones, earthquakes, or avalanches (*cf.* 163).

In Chap. I we have given a general introduction to the subject, pointing out the great variety of conditions under which plants grow, so that the oldest or largest genus in a family, like *Ranunculus*, usually, therefore, by occupying the greatest area, occurs in the largest variety of conditions. This tends to result in a corresponding variety of species adapted to them by simple inheritance combined with adaptability. *Ranunculus* thus shows the greatest area, and size, as well as the greatest age. By reason of its age, it was able gradually to overcome the many barriers to rapid spread (*cf. AA*, chaps. I-V, *Evol.*, pp. 59, 69, 153, 176, and many places above) that are interposed by physical, ecological, and other conditions, giving it now such a lead in BRITAIN, for example, that it probably equals there the whole of the other ten genera of the family, whether in dispersal, in size, in variety of situation, or perhaps even in total of individuals. The tribe *Anemoneae*, to which it belongs, is in turn far ahead of the *Helleboreae* in number and dispersal in BRITAIN and in the world, not by reason of any superiority in the adaptation, if such should at times occur, but of the greater age of the seniors (not the juniors) of the group. This has given them the time needful to spread to greater distances, and to overcome more barriers, and also to produce more descendants, before the first appearance anywhere of the rival group. It is also not impossible that the action of mere age may be sufficient at times, or ultimately, to bring about specific change, with or without other stimuli.

We have continued this in Chap. II, where we have shown how the expansion of the area of a species is often definitely circumscribed by coming up against a practically insurmountable barrier like the CHANNEL or the PYRENEES, and in the rest of the book we have tried to indicate that change of conditions, which is everywhere found, is really also of barrier nature. The variations from place to place make time, or age, needful to overcome them. Sometimes this is done simply by the adaptability that every species seems to carry with it, and without which it would hardly survive the seasonal changes of weather. Sometimes, apparently, a new form, variety, or species has to be formed, but there is no necessary structural adaptation. The new plant seems simply to inherit its general adaptation, and to base its adaptability upon the new conditions, and so, if it arises in a direction in which the conditions are changing, it may be able to go further in that direction, or more quickly, than its parent. As for forty years we have imagined in our working hypothesis (p. 96), when the strain of this change becomes too great, some rearrangement seems to occur, in one or a few individuals, in the constitution of the nucleus. *Incidentally*, this will involve a structural change, but the new features are usually simply divergences from the old, like aestivation imbricate/convolute, and so on, usually with no adaptational value enough for selection to get any grip. Selection in fact seems to be of the best individuals, regardless of the species to which they belong, and upon the *total combined efficiency of all the characters* for the time, place, and conditions. If a character that is seriously detrimental should appear, its bearer will be punished, often by extinction.

The laws of ASA are of very great importance, and when once their meaning is fully grasped, one realizes that they alone, working upon the results given by dichotomous divergent mutation, have controlled with practical completeness all the distribution of genera containing ordinary land plants, up to a size of say 15-20 species or more, when the effects of the slowly acting factors, like geological and climatic changes, begin to show distinctly. Water plants, incidentally, tend to come into the range of these factors with much smaller numbers. It is age that gives their importance to characters, especially from a taxonomic point of view, for the older the character, the more descendants will show it.

2. *Endemism*. In the course of the last forty years, we have discovered so many interesting things about endemism,

whose proper explanation we have always regarded as the hinge upon which the understanding of distribution worked, that a separate book could easily be written about it. But if we always remember that with occasional exceptions in some places, especially within range of the ice, endemics are simply an illustration of the early stages of distribution, there is no need to repeat such chapters as *AA* XV-end, or a great part of the whole book *Evol.* We have yet of course to find out the exact reason why any endemic appears as it does, at some small spot, but the writer has for forty years used the hypothesis (p. 96) that there has been some unusual stimulus at that place at that time, and found nothing to go against it. Endemics, as we soon found out when we began inductive study, are in general simply young beginners as species. This was clearly shown by the way in which they were arranged in hollow curves similar to those shown by larger and more widely dispersed genera. When later we discovered the law of dichotomous divergent mutation, this view was strongly confirmed.

A large family is large mainly because it is old, and therefore has had the time to produce a great many smaller genera. It is not always realised how large a proportion of the species of the world are in the large genera at the very top of a family. To take one instance, the *Compositae*, the 30 genera at the top contain more species than do the 1149 below them, the figures being 9025/9014. The same thing is the case with genera and the areas occupied by their species. In the 325 species of *Ranunculus*, only the odd 25 really occupy very large areas, as a glance at the map of the New Zealand buttercups on p. 65 will show, most of the species occupying but small areas, and being endemic to the country. If we arrange them in order of the length that they cover (the breadth does not vary greatly, so that length gives a fair estimate of area), we find them upon

830 670 580 570 540 460 420 340 340 320 310 280 260 220
180 170 170 90 60 60 20 20 20 10 10 10 10 10[1]

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[1] It is not pretended that the thousands of figures given in this book are up to date. To make them so would cost years of labour, and they would then only be right in places for a short time. Figures from my *Dictionary*, when available, have been used, as they were all obtained upon the same principle, and so are still useful for comparisons.

Half these species thus extend for no more than one sixth of the full length of NEW ZEALAND (1080 miles). One can see, as usual, the increases at the bottom with the increasing number of possible parents.

If in CEYLON we take the Dicots, we find the proportion of endemics to increase with the local size of the genus, from 14% for ones to 21% for twos, 26% for threes and fours, 36% for fives, and 42%, or nearly half their species, for genera with more than five.

In the northern hemisphere there is a more or less well marked limit to the present northward extension of endemics, made by the long east and west mountain chain from the PYRENEES to the mountains of CHINA. In EUROPE, *many* endemics are only to be found in the Mediterranean basin; very few of the larger genera have crossed the ALPS long enough ago to have given rise to endemics on the northern side. In the southern hemisphere, on the other hand, with its more broken nature, there is no such barrier, and endemics may be found to the end of the land available.

The behaviour of endemics thus forms a miniature of that of the more widely dispersed species, and makes a good picture of distribution in general. A new species occurring in a country, whether an endemic making its first appearance anywhere, or a new invader, will behave in the same way, provided that enough adaptation for survival and reproduction has been inherited from its parent. A newcomer, endemic or not, will have a hard struggle at first to get through the net of selection, which will put it to a remorseless test of general efficiency as against the conditions ruling at that place and time. Conditions vary so much that at one time the test may be harder than at another. Having passed, the species will then begin to spread by any means open to it (*AA*, chap. II).

As time goes on, the number of possible parents will continually increase, and with it the number of new endemics, that will form the usual hollow curve of increasing numbers. The ones will of course usually show the maximum; they will be very slow in increase at first, and will be of different ages, so that they will not all form twos at the same time. When the number of species is large, one usually finds endemic species accompanied by endemic genera; in CEYLON for example, where about 750 endemic species are mixed with about 25 endemic genera.

Endemism evidently represents what for so many years we have been trying to bring home, the early stages in evolution and distribution. Starting with one genus, a family in time has two, then three, and so on, each beginning on a very small area, and gradually spreading, very slowly at first, and in the order of their birth. Ultimately the leader will cover an area that surpasses anything that people have been willing to class under endemism, and if time permit, the rest will gradually follow, unless any may be so shut in by barriers that they have not yet passed the stage of specialisation and localisation.

As a genus, as yet of the one species only, spreads, it will encounter new conditions now and then, and when these put upon it a strain more than usual, it may give rise to a new species, or even at times a new genus, which must be adapted to the conditions under which its parent lived, to have survived at all, while its adaptability will presumably centre upon them. It will thus begin life in a condition of specialisation and localisation, but will usually grow slowly out of that. The same process will be repeated at every new birth, and in turn the new species will expand its area, which at first will probably be within that of its parent, and perhaps usually within that of the first species of the genus, though probably, as we have seen, it will overlap in course of time.

As all new productions must begin as single species in very small areas, and as the potential parents will continually increase in number, the number of ones, at least after a number of genera have appeared, will go ahead of that of twos, these of threes, and so on, forming the usual hollow curve of compound interest, which when plotted by logarithms (p. 262) forms a straight line sloping downwards to the right. The grand total of genera in my *Dict.* (6th ed.) is 12,571, with 183,000 species, an average size of under 15 per genus. Of these genera, 4853 are ones, and 1632 twos, thus making up more than half the total of all, while the 921 threes raise it to 58.8%. But all these genera only contain 10,880 species among them, or less than 6% of the total of species. The larger genera, few though they be, contain the bulk of the species, and show the greatest extent of area occupied, of variety of form, and of ecological differences. The top 500 genera alone contain the bulk of those that are useful to man.

In chapters V, VI we have dealt with the characters of endemics, showing how their most marked feature of origin is their divergence; and also how, when there are two endemics descending from one wide, they take different lots of characters from it. On p. 111 there is a complete list of the 50-odd CEYLON genera each having one wide and one endemic. We have given the most evident characters for each, to show the divergence, which is so wide that structural transition is not usually possible. This behaviour of the endemics is permanent, not temporary, but it is very similar to the many teratological cases known (pp. 100-05) which look like imperfect exhibition of divergent evolutionary changes, that *might* at some time be made in a viable condition.

All our work has gone to show the great probability that evolution went downwards from family towards species, by dichotomous divergent mutation, the whole phenomenon suggesting that it is controlled by some kind of super-Mendelian law. The characters of the endemics must have come from the wides, their immediate parents, *whether these showed the character, or not.* While it is not impossible that the same divergence may appear independently in two or more places a long way apart, especially if there be an overriding member of the family in both or all, it is important not to call in this very facile explanation unless absolutely necessary, or it will soon be carried to absurd extremes, as was the formerly popular one of the extermination of intermediate forms.

Evolution of new species seems to be proceeding upon a definitely arithmetical basis, following some formula that we may look upon as laid down in advance. As YULE and the writer have said (**159**), vital factors cause deviations this way and that, but in general these are only temporary, evolution following up the straight line of progress (*cf.* curves at p. 260, which give straight lines when plotted by logarithms (p. 262).

Divergence at mutation is so outstanding a feature that it may be called a mark of evolution. An early divergence may be inherited by many descendants, and so become " very important in that family ", while a late one, in young parents, can only be inherited by few, and will be " unimportant in that family ". The characters are supplied ready made at the mutation, and their taxonomic importance simply depends upon the date at which they were supplied, provided that they have been continuously inherited.

Endemics, as we have shown, mark the progress of invasion. A newly born species will remain a local endemic for a very long time, or even almost permanently so if blocked by very insurmountable barriers, as many mountain and most island endemics are. A low-country endemic, on the other hand, may soon begin to spread to some distance, or even to ascend mountains that are near by. Thus endemics will in general be but slightly marked at the very front of an invasion, but will follow at some distance behind it. The actual leaders of an invasion, in their different families, will tend to be more of the nature of pioneers to which the local conditions that they meet will not be so important as to those further back. Later arrivals will find it usually more difficult to get a footing than did the earlier ones.

A theory has been brought up by STEBBINS (**121**) which tries to account for endemism by means of genetical hypotheses. Endemics are supposed to be genetically homogeneous, and therefore adapted only to a limited range of ecological conditions. This hardly seems to fit with what we have now seen about the way in which every new species seems to begin with specialisation and localisation. HARLAND's theory (*Evol.*, p. 62) seems more probable. Local adaptation and localisation come to every new species as it begins life, and whether it grow out of it or not depends upon the importance of the barriers with which it is surrounded.

3. *Adaptation.* If, as we maintain, a new species is born by a mutation probably forced upon one or a few individuals, then, unless these are suited (adapted) to their place and time of birth, they will be killed out by competition, like a crop of potatoes by an early frost. The conditions will differ for every individual. One plant may find among its immediate competitors a rapidly growing plant taller than itself; another may find a parasite that readily attacks it; a third may have to fight against an insufficient water-supply, and so on. In fact, it is to a considerable extent a matter of chance how any individual may succeed in its early stages; and even if it is lucky at the start, it may fail in some later conflict.

Supposing, however, a survival for some generations, and perhaps the establishment of some offspring near by, the most dangerous period of its life as a species will begin to come to an end, unless under rapid change of conditions. Each new individual in its turn will have to pass through the sieve of selection, and will usually only survive if its adaptation to local conditions is equal to that of its parent; and it must also have a certain amount of adaptability to enable it to meet the constant changes of conditions that are going on. In central Europe, for example, it may be tropical in July, arctic in January. If a seed from an equatorial country, where its ancestors, for many thousands of years, had been used to a constant succession of summer days, were sown in central Europe, it would evidently not survive the winter, nor would a seed from northern Europe have much chance of survival at sea level in the tropics, though it might do so at high levels. A more complete discussion of the matter will be found in *AA*, pp. 16-17, 22, 24-5, 29-30.

A seed taken only a short distance from its parent would not usually find any great difference in conditions, though the competitors would probably differ, and so would the warmth or the water supply, or the soil. But a species without temporary adaptability would never survive at all. Acclimatisation (*AA*, p. 29) to permanently different conditions can only gradually be attained, by easy stages, probably with some considerable time spent in each (*cf.* *Lantana* &c, below, p. 406). To put it briefly, a species starts with the needful local adaptation to its place and time of birth. It gradually spreads to any available place, usually near by (but *cf.* coast plants) to which that adaptation suits it better than any of its actual competitors, while it goes beyond that area as it becomes gradually acclimatised to the changes of conditions, a process which may need a long time. Naturally it will go more slowly in some directions, so that the area it covers will become more and more unsymmetrical, but it is not likely to be quite killed out. In regard to species in general, therefore, selection, however remorseless, does little more than select the best individuals, regardless of their species, and ten allied individuals will form a fairly safe unit by which to reckon.

A very important place has been given to adaptation in most works upon distribution, but we have now seen that it must be born with the new plant, and be strictly local in most cases, though some things, like climbing habit, or parasitism, may be at once useful in other places. Selection by adaptational value thus drops out as an explanation of distribution. Age allows the time needful for the acquirement as the new species moves into places with slightly different conditions.

The increase in number of species with age, which goes with area occupied, is also a difficult problem for the older theory. Why should more area need more species (p. 19)? Why could not the first one suit all the area, especially when, as so often happens, the area of the second is enclosed within that of the first, for a very long time at any rate. Why should there be more local species in a big genus than in a small, if size mean success? The fact that distribution by the laws of ASA is dependent so largely upon size in the world practically puts adaptation out of court (p. 28-9). The supposed operations of adaptation are described upon pp. 27-8.

The parent survives at a dichotomous mutation, even if the child ultimately prove superior to it in some places. The parent will have covered much ground, adapting itself as it goes, till perhaps some insuperable barrier occurs; and all this has later to be gone through by the child, so that the chance of its passing the parent everywhere is practically non-existent, in view of the long start that the parent has. The laws of ASA and of DDM give a more reasonable explanation of what is going on, and lead to the hope that we are working towards a clearer understanding of this subject, which one of its greatest students described to the writer 50 years ago as " beyond the scope of the human intellect ", a somewhat stimulating remark. Our new theories, at any rate, relegate explanation by selection to a very subordinate place, getting rid of the need for the many assumptions that had to be made under that conception (*Evol.*, p. 167, and *cf.* pp. 80, 109 above).

We have also discussed adaptation from the newer point of view in a paper (**156**), and have referred to its operations on pp. 27, 42, 45, 48, 54, 60, 88-9, 219-21, 250 seq. &c, above.

A species has been supposed to depend for its spread upon the acquirement of structural adaptation. As evolution was actually shown by structural differences, these had to be regarded, upon the selection theory, as being themselves of selection value, and it was their acquisition that was supposed to produce a new species by gradually endowing it with structural improvements which mounted up until the new form was different enough to deserve the name of a new species.

One great difficulty with this theory was how to prevent the loss of a slight improvement by simple crossing with an unimproved form. This was the basis of FLEEMING JENKIN's incisive criticism of DARWIN's work in 1867, and it has never been satisfactorily rebutted. DARWIN altered his conception of the matter by requiring that the slight improvement be made, not in one or two members of a species only, but in the whole number occupying some area of ground. This has always seemed to the writer to be an unsound position, for we have no evidence that such a change can occur; and if it does, it shows that the formation of a new species was also guided by outside influences, other than selection.

The original species, to survive and reproduce, must be adapted to the local conditions well enough to do so, and will only run the risk of destruction if the conditions change, or if a form that is still better adapted to them than itself should come into competition with it everywhere, a phenomenon that we have seen to be very unlikely. Competition depends upon the whole outfit of the competitor, and is not, or rarely, confined to some single item that may vary slightly, especially as it is highly probable that, upon the simple principle of compensation, an improvement at one place is likely to be set off by a deterioration at some other.

Another great difficulty has been the lack of any evidence, fossil or other, of these transitions, except at times in points too insignificant to form specifie characters; and yet they must have added up to countless millions. Yet another has been the widespread prevalence of incompatible differences, which could not be passed over by selection, between genera or species, such as we have instanced above, like aestivation imbricate/convolute, flower 3-merous/5-merous, and so on in great number.

Our conception of downward evolution, with new species produced full-fledged at one operation, as seems to have been usually the case in new forms, brings the whole matter into much greater clearness and simplicity. Both upon the Darwinian theory and upon our own, the species with which one starts is adapted to its situation, and its offspring inherit the adaptation. But while upon the old theory the older forms are gradually killed out, and substituted by new and adaptationally improved ones with gradual change of structure, on the newer theory the change comes suddenly, producing at one stroke a new species with divergent characters. Here it is probably only by chance that any adaptational improvement appears, and this seems to agree much better with the actual facts of the case.

Adaptation begins with birth, and further adaptation must be acquired for each serious change of conditions going beyond the limit allowed by the adaptability of the species. The result is that in the case of an old species like *Ranunculus repens*, which has had time enough to adapt itself to a great variety of conditions, one cannot say what were the original conditions at its birth.

Age is a far better explanation of the facts of distribution, explaining easily why things are distributed as they are, in numbers increasing from above downwards, and areas decreasing. Upon this law alone, or better upon the laws of ASA, one can make many predictions that prove correct when tested. After a species has spread to a little distance from its birthplace, the risk of its complete extermination by selection becomes less and less, and it is very unlikely to be continually accompanied by some species that is killing it out. The slight differences in adaptation that must exist between two species A and B, are enough to ensure that in some places A will succeed better, in others B, and there is little or no sign of any species being steadily killed out.

Barriers (p. 45) are the real obstacle to rapid spread, especially the very important ones due to gradual alteration of the conditions, that force upon plants a physiological change, so that much time is needed to travel any distance. Travel by land is the ordinary way in which things get about (p. 48), though an occasional seed may make a longer journey by sea or by air. On pp. 48-58 we have given illustrations of travel, and on p. 56 have shown how dispersal by the laws of ASA results in the production of contour maps.

Dispersal, it is clear, is mainly regulated by these laws, and it is difficult to see evolution producing adaptational improvements other than physiological. With the complete divergences that appear, it is a matter of almost insuperable difficulty to give the transformation any physiological meaning, or one capable of calling in the action of natural selection.

Under certain circumstances that we do not as yet understand, probably some kind of pressure from changed conditions, and even then perhaps only when it has been long continued (*cf.* **31**, or on p. 96), so that age comes in, a new species may be produced by a sudden mutation, and may show marked divergences. These may be of almost any rank, but are perhaps most often, at the present date, specific or varietal, though probably larger in very ancient times. The new form, if it survive, will inherit adaptation to the local circumstances, so that its history will tend to be like that of its parent, with only slight differences. There is little or no evidence to show that there is any *necessary* improvement in adaptation, for the structural features, that show that evolution has gone on, in general show no adaptational quality whatever, unless, as in the case of a slowly drying climate, there is a strong call for xerophytic features, and there seems to be a tendency in the mutations to go in that direction. In water plants, on the other hand, the adaptation seems to have been more sudden. Real adaptation would seem to be largely internal and physiological, and to have little or nothing to do with the structural changes that mark evolution, except in a few special cases, like climbers or water-plants. Being born with the species, it is probably variable between one individual and another. Its effects are mainly individual, and almost negligible in comparison with those due to the laws of ASA. We have worked this factor in evolution much too hard in the past.

The older a species grows, the more rapid will be its spread (*AA*, p. 34), though the rate will vary with the difficulties interposed by the barriers. It will thus increase the variety of conditions in which it lives, and diminish the chance of extermination. It will gradually cease to be a case of localisation and specialisation. The fact that a very young species is only adapted to a very limited range of conditions is no proof of limitation to them, but only of comparative youth. The general type of adaptation in a family tends to follow that with which the leader began, but increases as the family grows. Any single individual will have local adaptation, or die.

The area of occupation of a child will almost of necessity be within, or close to, that of the parent. In general, in a small family, the parent covers the range of all its juniors, but as the family grows, and its members become suited to greater varieties of conditions, one will tend to pass its parent in one direction, one in another. Thus the further that we go from the original centre of the family, the more will this be found to occur, and it will rarely happen that the leaders of all the families in a flora reach the very edge of distribution (*cf.* BRITAIN on p. 27). This is especially the case in the southern hemisphere, where the land is so much more broken than in the north.

There can be little doubt that the element of chance enters largely into the actual dispersal of any plant in BRITAIN or elsewhere. But in general, it is undoubtedly following the laws of ASA, and there is now little justification for the conception that a species kills out its ancestors. All As do not necessarily defeat all Bs. The visible differences between A and B are structural, and there is little evidence to show that they have much to do with the matter.

Adaptability is needed as well as actual local adaptation, for otherwise a species might be tied to its birthplace. Selection picks out, for each place and time, the most efficient individuals, and that ruthlessly. Good adaptation becomes generic by being handed down to further species, though even this need not be inevitable.

4. *Climate*, upon which such stress has been laid as the chief determinant of distribution, is dealt with upon pp. 59-62, and in more detail in *AA*, pp. 29, 40, 45, 138. But people have left entirely out of consideration the enormous effects due to mere age, which gives the time necessary for gradual adjustment, and for reaching the place under consideration. We have now shown clearly, and in many places, how the effects of the laws of ASA completely override those of any vital factors, when several allied species are considered together.

Any change of climate, which is bound to occur in going north or south, nearer to the sea, crossing a mountain range, or going upwards in the mountains, acts as a barrier, but one which an older species may have had time to pass by becoming in various stages locally adapted to the new climate. Any new species formed will have its adaptability centred upon the new conditions, but it will be very slow in starting to spread on account of its small numbers; and probably no two species, if not even two individuals, will be exactly alike in their reaction to the passing of a barrier.

The effects of warmth, or moisture, of soil and of other climatic features can only be seen in general phenomena, like the covering of one region with forest, or another with savannah, with halophytes or xerophytes. The dispersal of the plants in local detail is largely determined by these factors, while its general results depend mainly upon the laws of ASA. The action of natural selection is by no means excluded, but it consists more in picking out the best individuals for any particular spot. It is now no longer to be regarded as the guide of evolution by selecting minute differences in value between structural diversities, and killing out those that were inferior. It is upon function rather than structure that success mainly depends. Even a cripple is not necessarily a failure.

Climate is a barrier to dispersal by reason of its variations, which bar the way at one time, allow easy passage at another, but it is the laws of ASA which are the chief factors in dispersal, for they work always and inevitably in the same direction. Their results give us a good enough picture of evolution, when taken with those of the law of DDM. Large genera, which have had the *time* to do so, have become suited to an enormous variety of conditions. But they do not necessarily reach all points upon the globe, for they were born in different parts of the world, and did not all travel together. *Carex*, for example, with its 900 species, is found almost everywhere, even in such outlying places as the Hawaiian Is., where there are five species. Yet it does not occur in the Galapagos, whose different flora shows that they probably received their flora from some other source, where *Cyperus* arrived before *Carex*, and is now well represented in the Galapagos. *Ranunculus* occurs in the Hawaiians and not in the Galapagos, and *Amarantaceae*, though well represented in both, have no genera in common between the two.

It would seem probable that during the period of existence of the flowering plants, the climates of the world have become drier in a great portion of it. This would of course tend to restrict, and perhaps to slow down, the movement of new species formed under the new conditions, while the older mesophytic genera and species may have been able fairly easily to reach a great part of the world, where they are now to be found, sometimes discontinuously distributed by reason of the drying up of some regions more rapidly than the species could change their adaptation to suit.

As the differences between a dry climate and a wet might tend continually to increase at any such frontier between them as is made by a range of mountains running transversely to the wind, one will expect that the earlier (larger) genera would arrive at a time of less difference, so that their species might adapt themselves better to both sides of the frontier than the species of younger and smaller genera arriving after them. One gets a good illustration of this in CEYLON, where there is a well marked difference at the watershed of the high mountains, with a much wetter climate on the SW than on the NE side. The plants that occur in *both* zones belong to genera whose average size is much greater than that of plants that only occur in one.

5. *Migration and invasion.* We have now to consider how plants spread from one place to another. Differences in conditions occur between one place and the next. Warmth increases towards the equator, moisture with nearness to the sea or large lake, soil varies with local geology and climate, and so on (*AA*, pp. 10-53). Once a new plant is established to the reproductive stage, it tends to spread by any means open to it, the spreading being mainly conditioned by the barriers that interfere.

Movement from one country to another may be almost casual, especially when climate and conditions are nearly the same in both. Or, on the other hand, it may be a more regulated movement of a whole flora by reason of a change of climate, especially a change in warmth or in moisture, when the tendency is usually to move in the direction in which there will have to be the smallest possible change in local adaptation. But in all these movements one must not forget that both floras, of the invader and the invaded, consist of a few commoner and a good many rarer species, and that the latter will be more commonly killed out in both floras. Recent species or genera, unless born fairly near to the frontier, have but a small chance of reaching another country.

An outlying country like BRITAIN will in general owe its comparatively recent flora to migration or invasion from its nearest neighbours, chiefly FRANCE. Being so recent, there has not been time or opportunity for its species to form any important variations by mutation or otherwise. They are essentially the same as the continental ones, the smallest having been left behind, on the whole, at the various barriers encountered, not the least being the youth of so many species, which has limited them to small areas. One may easily see this effect in the British flora itself, where on the whole the dispersal goes with the size in the world, and in a quite emphatic way. The smaller genera steadily drop out as one goes north. As far as NORTH YORKSHIRE, the genera thus omitted have world sizes of 250, 235, 3/100, 60, 2/50, 2/45, 40, 30, 25, 5/20, 16, 15, 2/12, 10, 8, 7, 2/6, 2/5, 2/4, 3/2, 3/1, thus averaging only 36.

If two countries side by side have very similar climate and other conditions, invasion will be likely to go both ways, and the same large genera will mostly be found in both, while the small ones will tend to be different; it is simply a matter of age. MADRAS and CEYLON show this very well, both having a wet zone to the west and a dry to the east. The separation of the latter, even now, is only by a narrow and shallow strait, while that of the former is by a couple of hundred miles of deep sea. The flora of the CEYLON dry zone is almost completely a replica of that of dry MADRAS, but with numbers reduced, and a number of very small genera missing, while in the case of the wet zones, there has evidently been migration both ways, for some families and genera have more in CEYLON, others in MADRAS. The composition of these floras leads to many questions which there is no space to discuss.

The past history of plants, as of man, is largely a record of more or less successful invasion of countries that suit the invaders. Increasing numbers form the principal stimulus, so that invasion, with its usual effect of intermingling, becomes almost inevitable, especially when the conditions are closely similar. Unless specially organised, as in the case of many human invasions, they are individual enterprises, depending for success or failure upon the reactions of the individual to the local conditions.

It is probably a rare, or even impossible event that an invasion should be of the whole of a population, replacing the whole of that of the invaded country. Even in the invasion of BRITAIN after the ice, when the land was mainly virgin, the larger and better distributed genera would lead the way, reaching the greatest possible dispersal in the time available, while many of the smaller genera, and many of the little-distributed species of the larger, would be left behind on the continent. But if the invaded country is already populated by plants, it will be a case rather of infiltration, and that, of necessity, chiefly of the larger and more widely distributed species, which will be difficult by reason of the fact that the flora will already be grouped in communities, which will not be readily broken up unless the change in conditions is serious.

We have dealt with invasion in *AA*, ch. VIII, p. 76, and also on pp. 139, 234, and have there described the two chief invasions that seem to have reached NEW ZEALAND, one from the north when the climate was getting warmer southwards, one from the south when the reverse was the case. The diagrams reproduced on pp. 407-8 show the steeper curves of the southern invasion, indicating that it was the later, and the figures given on p. 478 show how the formation of COOK'S STRAIT in the middle of NEW ZEALAND did not affect the northern invasion, nor the wides of the southern, but is marked by a great drop in the younger endemics (those confined to the large islands, and not reaching the small outlying islands like the CHATHAMS) of the southern invasion, which form the youngest group of plants concerned. The figures given on p. 74 for the reciprocal invasion of CEYLON and MADRAS are also of interest in this connection.

6. *General development and spread.* So long as we have tried to find the causes of these phenomena in such external circumstances as climate, &c, we have made but little progress, and we have taken no notice of the most important factor, age. There is no doubt that wherever we may go, we find the plants suited to the local conditions of climate, soil, &c, but we have laid too much stress upon the conditions, and too little upon the plant itself and its hereditary

qualities, and upon the effects of the barriers to dispersal that everywhere exist, or have existed. We have looked upon the struggle for existence to which every individual is committed as soon as born, as a specific, rather than an individual, struggle, whereas it is really an individual struggle between plants in which it hardly matters what the species is, in most cases. Only when the one species, as in the case of *Mikania scandens*, is capable of overwhelming and destroying the other (p. 408) does it become a matter of life and death. There is usually a great intermixture of species, and as each fights for itself with its whole endowment of qualities, the struggle is in reality a very complex affair, not a simple quarrel as to whether a simple leaf is better than a compound, or an introrse anther than an extrorse.

Genera, as they spread, give rise mainly to new species, each suited to the place of birth, and also at times to new genera, equally suited to their birthplaces, but rarely overpassing the parent in number of species, or in area occupied.

7. *Spread of a species.* Since 1907 we have maintained that a species begins as a sudden mutation in one, or possibly in two or more, individuals, and have gradually developed this idea in *AA* (1922), *Evol.* (1940), and the present book. KOMAROV has taken the same line on different premises (78), and with this, and with all the additional work here described, especially the early splitting of the leader into sub-leaders, and so on, it appears now to be well upon the way to be established as the ordinary course of evolution.

If a species start at one very localised point, its spread will largely depend upon the barriers met with, and how successful it may be in overcoming them (*cf.* GRISEBACH on p. 386). Hence the great importance of mere age. A very gradual change of climate, for example, may probably be overcome by any species up to a certain point, without its actually needing to move, or to form a new species, *given enough time* to make the necessary adjustments. But a considerable space of sea, even if no wider than the STRAITS of DOVER, or a line of snow mountains, will probably set an all but insurmountable barrier in the way, and so will a sudden and well marked change of climate.

Thus it is clear that no two species are likely to behave in exactly the same way in regard to moving about, or to the spot where they shall settle, and it becomes dangerous to draw comparisons between species of different genetic relationships, or living in different countries and conditions. But time is everywhere the great underlying factor in their behaviour, especially when we compare groups of species geographically and taxonomically allied. The nearer together they are in their points of origin, the more likely they are to show much the same general adaptation to the conditions that surround them, and to behave in the same way towards any changes of conditions.

It must be remembered that the older in actual fact a species may be, the more open is it likely to find the country, and to act as a pioneer, for it will probably find spreading more easy. This will happen especially with early species of large genera, though on the other hand it is generally believed that such early species were largely woody, and likely to travel slowly.

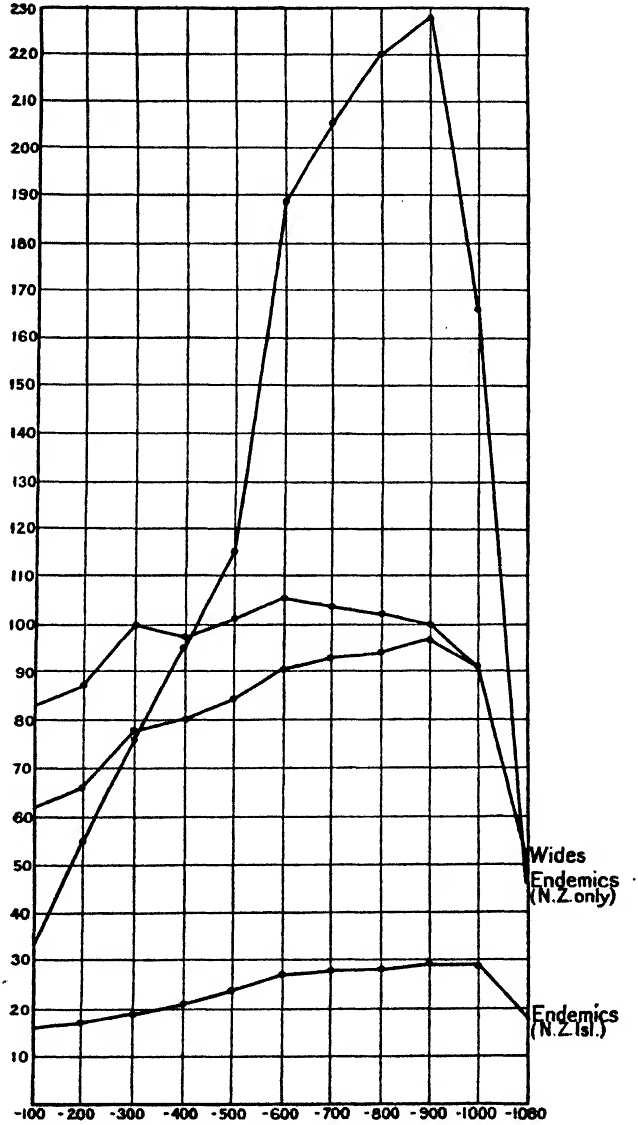
Species of different habit or mode of life may show much difference in rate of travel, but the travel is mainly determined by the laws of ASA and the barriers met with, and was almost entirely by land. Climate, formerly considered of supreme importance in settling what species should occur here, and what there, more often acts as a simple barrier by reason of its constant changes, its action being negative rather than positive. For example it is more uniform along than across a parallel of latitude, so that distribution goes more east and west than north and south. When its changes are well marked, they slow up dispersal, and tend to increase the formation of endemics.

A species usually begins with locally inherited suitability to its birth place, and as it moves away from that it adapts itself to the new places, but, so far as we can tell, without structural alteration except in very minor points. But extra strong stimulus seems to compel it at times to mutate into a form better suited to the immediate conditions than its parent, which however survives also. The structural alteration that occurs is apparently a necessary result of the mutational change, but has usually no perceptible result of an improvement in local adaptation. As it spreads, the species will settle chiefly in those places where the total effect of conditions is much the same as in the original birthplace, thus needing less acquirement of local adaptation. And the more the country fills up with plants, the more minutely adapted this local suitability will need to be. Thus, as a species spreads from its place of birth, it will come slowly and successively into other conditions, and settle in them wherever it can acquire the needful adaptation, so that the chief factor which settles its migrations is simply its age, for the older it is, the more time will it have to become locally suited. Given time enough, a species may go anywhere within the limits open to it.

It is practically certain that selection does not destroy whole species, except in their very earliest days, when they are confined to a very small area. It destroys those individuals that do not come up to whatever may be the standard imposed by the local conditions, as we have often pointed out in *AA*, *Evol.*, and above. The adoption of our view of evolution gets rid of many of the difficulties that beset the older views, especially that of how the crossing of old with new was avoided, as it is avoided by our conception of complete specific mutation, giving isolation from birth.

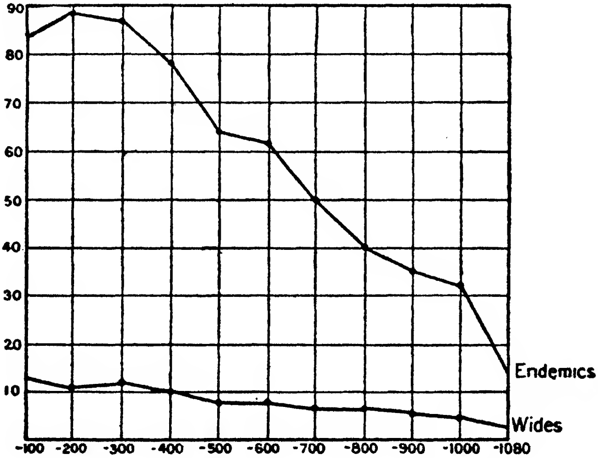
The earlier a species arrives in a country, the less variety will there be in the vegetation, and the more easy will it be to force an entry. In the writer's early days at CAMBRIDGE, about 1887, the rivers and ditches of the fens were a mass of the Canadian water-weed, *Elodea canadensis*, only the female plants of which had been brought over. Gradually, as time went on, it diminished in abundance, and is now no longer especially noticeable; possibly the absence of the male plant had something to do with this.

When in 1896 the writer went to CEYLON, great areas of rather recently abandoned coffee land were covered by a dense growth, a few feet deep, of the introduced prickly scrambler, *Lantana aculeata*, which occupied the ground " in pure stand " (to use the convenient forestry expression), practically excluding everything else, and killing out all smaller weeds by its dense shade. It had been introduced about 1825, and after a number of years began to spread on waste land, perhaps needing those years to adjust itself to the local conditions, soil, &c. About the eighties, another introduction, of 1851, began to spread. This was the Mexican sunflower, *Tithonia diversifolia*, which grew to a greater height, and was able, by vegetative reproduction, to force its way into the *Lantana*, gradually becoming common in



SOUTHERN INVASION OF NEW ZEALAND

places formerly occupied only by *Lantana*. Since the writer left CEYLON, another introduction, *Mikania scandens*, which was just beginning to spread in 1911, has now fully established itself, covering both the *Tithonia* and the *Lantana*. It is quite possible that this in turn will be largely suppressed, and so on, till some kind of forest growth may ultimately cover most of the waste land. The account of climax vegetation, in (**123**), pp. 222 seq., should be read in this connection. An important point in these introductions is that they do not owe their success to any adaptation *for the purpose*, but to the accidents of early arrival, of finding unoccupied land, of taller growth than their predecessors, of vegetative reproduction, and so on, that happened to prove useful in the conditions. Had *Tithonia* been the first arrival, *Lantana* would not have had so good an opportunity.



NORTHERN INVASION OF NEW ZEALAND

Another weed that has spread very widely in CEYLON, like the Canadian waterweed in the fens, is the beautiful water-hyacinth *Eichhornia crassipes*, which was introduced and distributed without the writer's knowledge, though he has been accused of doing it (it is a well known pest in hot countries). It has become abundant in irrigation tanks, paddy fields, &c, and a staff of ten men has to be employed to keep it from further spread.

On the other hand, it is much more difficult for a new-comer to enter and spread in an established community. The Botanic Garden at HAKGALA in CEYLON is largely surrounded by natural forest, into which few species have penetrated at all, the only noticeable one being the shrubby *Bocconia cordata*, which has spread for a few hundred yards on the rocks at the side of the little stream. A parallel case may be seen on the BAIE (little river) DE CLARENS, near MONTREUX, where an introduced *Buddleia* has taken kindly to the rocks by its side.

A factor that is probably of importance in cases of introduction is the exhaustion of certain constituents of the soil—the principle, in fact, that has guided rotation, and mixtures, of crops. Mixture of woody crops is very common in eastern countries, and the soil produces a result for much longer time (154).

A man, with his short span of life, cannot expect to see much more of the gradual formation of a flora than what we have just described, but it is not improbable that a good deal of land has thus been colonised, each new arrival finding it on the whole more difficult to enter and spread, so that a great deal of time must be allowed. But the order in which things follow one another, and the rate at which they spread, has a great element of chance in it.

A beginning has thus perhaps been made towards a regular community of plants of waste ground in CEYLON. The available space and resources were evidently not fully used by the pure stand of *Lantana*. Each of the first three has found the entry fairly easy, but it will probably become more difficult in time. The process is akin to the settlement of a new piece of country, like BRITAIN after the ice, by immigrant plants. Those that are old enough, and whose equipment best suits the conditions, will be those most likely to get a footing. One may see the same thing with human emigration. When the writer's ancestors went from YORKSHIRE to NEW ENGLAND in the days of Charles II, most of what was needful, beyond the capacity to fight continually with a skilful and ruthless enemy, was to be able to grow or prepare the simple necessities of life. But such is no longer the case, and a man with no better, or rather with no more specialised, equipment, would soon find himself in difficulty in NEW ENGLAND at the present time. There is always room at the top, and the great competition is at the foot. A new arrival in a country, plant or animal, is like one in the form of a local endemic species. Inheritance will give it a chance of survival, but it will have a hard struggle at first, which will be repeated for most of its descendants, individually, against selection. But when it gets established in a few different spots, the chance of its extermination will soon shrink.

8. *Communities of plants.* As the species in a country increase in number, they will tend more and more, by the work of competition or natural selection, to sort themselves into different communities, each made up of those plants best suited to some set of conditions that is not too rare. One species will suit one, another another. Thus the calcicole or lime-loving plants, marked *ca* in the list in (122, p. 176) are well marked in the community of chalk grassland. Once the pioneering stage is over, plants are usually only found in places to which they are well suited, or where there is little or no competition; otherwise they would soon be killed out. There is no absolute necessity for a pioneer, however common it may have been, to remain dominant, as may be seen with *Lantana* in CEYLON, once so common, now being largely exterminated by *Mikania.*

A community is not usually very large. The chalk grassland with 146 flowering plants is about the largest in BRITAIN, for plants suited to chalk land would arrive up to the moment of separation near DOVER. Any community, unless quite closed, is subject to infiltration from elsewhere.

Other factors than adaptation have taken a great part in the formation of a community, especially age, size, and area, whose importance is slowly beginning to be recognised. The most widespread and abundant members of a community are commonly those that are widespread elsewhere, or large in the world by number of species. Being old, they were very early arrivals, and have had time to adapt themselves to many different kinds of conditions, while later comers have found the ground already covered and have had to force their way in.

It is worth while to make an analysis of a couple of British communities from a new point of view. TANSLEY expresses the commonness of members in eleven groups in (122) : let us place the plants of chalk grassland (122, p. 176) and of the *Quercetum roburis* (l. c. pp. 76-83) of damp clay in these :

	Chalk		*Clay*	
Group	Number	Average dispersal	Number	Aver. dispersal
1. Dominant	1	112 vice-cties.	1	105 v. c.
2. Locally dom. or sub-dom.	2	104.5	3*	99.6
3. Abundant	34	100.2	38	103.5
4. Frequent	55	89.4	29	100.5
5. Locally abund.	14	69.9	11	100.9
6. Occasional	15	61.5	19	97.9
7. Locally freq.	3	50.3	4	84.5
8. Local	7	47.5	12	74.5
9. Rare	10	26.9	1	68
10. Very rare	4	16.2	—	—
11. Very local	2	12.5	—	—
Average of all		77.0	**	98

* *Carpinus Betulus* (27 v. c.) occasionally locally dominant, bringing the average to 81.5.

** The total is larger than the actual 113, because some of the plants appear twice, *e. g. Hypericum* f to a.

In both communities, and especially in the second, which ranges further north, where we have seen that the average of dispersal is increased, the dispersal is much above the average, except for the small groups 7-11 in the chalk.

A reference to the entries of each species in the index to (122) gives a somewhat rough estimate of the degree to which each has gone in joining other communities than the one in which it is most familiar. Each entry of a page in the index is counted separately, and though the chalk plants are 146 against the 113 of the clay, their total of index entries is only 569 against 673, or an average of 3.9 against 6. It is perhaps worth while to give the detailed figures :

Chalk	37/1*	24/2	23/3	11/4	13/5	14/6	10/7	4/8	1/8	2/10
	1/11	2/12	3/13	—	—	—	1/17	—	—	—
Clay	6/1	16/2	18/3	12/4	13/5	13/6	7/7	7/8	2/9	3/10
	3/11	2/12	4/13	1/14	1/15	1/16	1/18	1/20	1/22	1/23

* 37 each with one entry only, like "*Aceras anthropophora,* p. 178".

This is a very interesting result, and the writer regrets that want of time has prevented his making a complete analysis of all British communities. It is evidently a case largely of "first come, first served", with acquisition of the last detail of local adaptation after arrival (" first catch your hare ").

As one goes north into more hilly country in BRITAIN, the earlier arrivals of species show a greater extension of the area that they cover. By the time that plants had reached some elevation in the hills, members of their species at lower level had had more time to spread about there. If we take the two communities of grass moor on the Pennine hills (122, pp. 284-5), the *Molinietum coeruleae* and the *Nardetum strictae*, we find their members to show dispersal as follows :

	112	111-101	100-57	56-1	Total	Average dispersal
Molin.	11	8	7	—	26	104.3
Nard.	14	12	2	—	28	108.1

A very high dispersal indeed, with none below the mean.

If we go still further north, and yet higher, we come to the Scottish arctic-alpine grassland described in (122, pp. 300-301) and above. The 48 species of list B must have come from the south, and show :

26 19 2 1+ 107.5, or omitting +, the *Viola lutea*, which is a Highland form, 109.4

The maximum possible dispersal is reached in pastures formed on ploughlands in the HIGHLANDS (122, p. 294), all of whose plants show a dispersal of 112, and are evidently very old species in the neighbourhood, which have had time to become used to the conditions there.

Thus the average dispersal of the members of the various communities seems much to surpass the average dispersal in BRITAIN. The bulk of the many species of small dispersal do not figure in the communities at all, though there are exceptions like *Erica vagans*. Many have not had time or opportunity to do it. It is evident that the larger half of the members of a large community tends to be made up of the species that are estimated as dominant, abundant, or frequent. Taking from (122) all the dominant, sub-dominant, and locally dominant or subdominant species, though we may have missed some, 44 show a dispersal of 112-110, 15 of 109-101, 28 of 100-57, or 87 above the mean, and only 15 below it. Or if we look at the family *Compositae* on the chalk, we find, out of the 30, 13 abundant, 10 frequent, and only 7 below that, thus averaging 82 for the total. The grasses give a very similar table.

We have given a sketch of the distribution of the communities on p. 7 seq., and have pointed out how new arrivals may get their chance to spread when the composition of the soil ultimately begins to alter, while such changes may occur in vastly less time than geological ones. A plant tends to travel with its community so long as conditions will allow. The leading species, with the largest dispersal, have had the longest time to accustom themselves to different conditions, and occur in the greatest number of them, the most dispersed being the heather *(Calluna)*, the second the tormentil *(Potentilla erecta)*. Those near the foot of the list may only occur in one or two communities, while those not marked at all have hardly found their way even into one. The whole process rather resembles the settlement of immigrants in a new country.

The laws of ASA thus lie at the root of dispersal, exercising much greater influence than any adaptation, when dealing with large areas and long time. Adaptation pulls every way, and in varying degree, while the laws of ASA pull steadily in one direction, thus producing an overriding effect upon that of any other laws.

9. *Abundance of members of communities.* It is clear that however great the local adaptation of a species to the conditions of its community may be, there is always visible the influence of age, or of date of arrival in the country, which is shown by the fact that the leading species of a community are usually well above the mean of distribution in Britain (56.5). Species with less distribution are rarely even so prominent as " frequent ". The five frequent species in chalk grassland whose dispersals in BRITAIN are 56, 44, 40, 38, 35, are all marked ca (lcicole) or + (specially abundant on chalk) In the " abundant " species there are only two, *Hippocrepis comosa*, and *Cnicus acaulis*, both ca. The great majority of the species on chalk grassland have

been old enough to spread beyond the chalk, and make themselves at home under different conditions at first perhaps those rather like the chalk conditions.

In BRITAIN, it is evident that the number of vice-counties reached must largely represent the time spent in reaching them, and in becoming suited to all kinds of small and more or less permanent variations in conditions, so that time, here rather local age, is the most important factor in their dispersal. So, in general, if the area occupied is large, the species must be old, though this rule may suffer modification in the case of water plants.

10. *Change of composition of a community.* As in time conditions become altered, the composition of a community gradually alters also (p. 9), and its plants tend to go more or less different ways, in those directions principally, where conditions suit them best, and require the least possible alteration in their local adaptation. This is what happens in human communities, except in the case of emigration to distant countries, and even there similarity at least in language and climate is sought as much as possible.

In countries where there is a strong stimulus from any cause, as for example with the variation in dryness of climate, and general desiccation of climate, as in S. AFRICA, any endemics formed, which will perhaps tend to be more numerous than usual, seem to show a tendency at times to become better adapted to conditions by slight changes in the direction of xerophytism, whereas in a uniform mesophytic climate like that of the equatorial forests, one can see nothing in the new structure of an endemic that suggests that it is an adaptation to anything.

In BRITAIN, plants as they move about the country need much local adaptation to the great variety of different soils and other conditions (p. 9), so that movement in general will be slow, except for a few early pioneers, to which, as there would be little competition except between themselves (thus incidentally keeping their local adaptation up to the mark), the small differences of local conditions would probably matter but little. As the mixture of species grows, these small differences become more and more important, and dispersal grows slower and slower.

On the other hand, there is little evidence to show that structural adaptation occurs; it is rather physiological (p. 11). A new species probably inherits enough for the moment, and each new generation will perhaps be very slightly better adapted, so that, given time enough, and opportunity, including the absence of insuperable barriers, it may get anywhere.

11. *Ecological influence in the development and spread of new species.* Though these things seem accidental, there is always law behind. While the laws of ASA and of DDM are the chief ones that govern the whole matter, there are many subsidiary laws, and if ecological influences always tended in the same direction, they would probably be looked upon as much more important than they now are. A new species, born upon a small area, will die out if not suited to it. This suiting is of course due to simple inheritance, though in addition there seems sometimes to be a tendency at birth towards changes suitable to the ecological demands of the neighbourhood, as towards xerophily in a dry country, like S. AFRICA or the RIVIERA (124). Plants temporarily exposed to such conditions frequently show similar changes; plants moved uphill, or nearer to the beach, develope slight xerophytic characters, but lose them again if taken back to their original homes. But supposing that these plants were kept in the new conditions for hundreds of generations, it is quite possible that the cumulative result (of engrams) might in the long run have a permanent effect, producing a new form, variety, or species that would not go back to the old form without at least very long exposure to the old conditions.

Such a species or genus, with its new xerophytic outfit, would probably find it easier to go forward towards increased xerophily, than back towards mesophytism. Evolution, once started on a definite route of specialisation, seems to go on with it, rather than return. But it is worthy of note that in such a region as S. AFRICA, while the largest endemics have only about 100 species, *Senecio* alone has 222 (55), modified enough to suit the local conditions, and some so far modified that they have been regarded as new genera, especially *Doria* with 27 species, and *Kleinia* with 18, both now included in *Senecio*. Only in very ancient cases of complete isolation like the HAWAIIAN Is. do the local endemics exceed the old genera of wide dispersal in the numbers of their species.

This idea brings in its train, of course, the long-standing difficulty about the inheritance of acquired characters. But we are inclined to think that characters may become heritable in this way, if *time* enough be allowed. Many species have so enormous a range that they must be under very different conditions in different places, yet they are suited to them all, each plant in its own place. Nature has spent vast periods of time in acclimatising plants to all kinds of conditions, often producing new species for the purpose, and has thus made innumerable new species, each acclimatised to the *immediate* neighbourhood in which it is living, but having to compete on more or less equal terms when it moves away from that.

The turning of evolution back to front, as we have seen, almost does away with some of the old sources of dispute, like the questions of localisation and specialisation, local adaptation, and perhaps the inheritance of acquired characters, making them of less importance. But the fact that we have brought more law into plant-distribution does not do away with the many new problems that now present themselves with an insistent *embarras de richesses*. We have been working at one aspect of the problems of dispersal since 1906 at least, and have had the good fortune to break through into an untilled field. Many of our results do not agree with suppositions that have long been regarded as more or less axiomatic. The geneticists work at another aspect, and Prof. SMALL at a third, and at present it is difficult to see where these will interlock. But there is no need to quarrel about interpretations at present, for one day all the work will fit into a harmonious whole. SMALL, for example (**118**, **119**), has done much work upon the senescence and probable death of old species, whereas my work has chiefly concerned itself with their behaviour at the other end of their life, millions of years away, so that there is as yet no overlap that one can see. My work goes to show the importance of the laws of ASA and of DDM, of the automatism of adaptation, and other things, which have as yet no apparent relation to old age and death, but where the connection will some day appear. The geneticists, on the other hand, are working more or less at right angles to SMALL and myself, so that it is only at times that there is liable to be any serious conflict of opinion.

The supposition of reconstruction made in the working hypothesis that we have used since 1907 (p. 96), is based upon the results obtained in the early days of Mendelism, but it has produced the results shown in this book and in its two predecessors, *AA* and *Evol.* We shall now look to genetics for further progress, which for a short time, with so many new avenues open, should be fairly easy.

The whole question of adaptation is much simplified. A species is born adapted to its place and time, if it is not promptly killed out. It slowly spreads, suiting itself to each new place in turn, if that be possible, while at times, when the strain is great, it produces a new species. This will probably at first be more or less surrounded by the parent, but as time goes on, it will tend to go more quickly than the parent in certain directions, and may even get in front of it, so that the outline of the whole dispersal will ultimately no longer be simply that of the area occupied by the first parent.

The actual characters that are produced in the new species will depend upon the characters, not only of the immediate parent, but also to some extent (perhaps according to some law like that of GALTON) upon those of ancestors further back. If the conditions are changing in some definite direction, the characters may take a definite impression of that, as for example if they are changing in the direction of xerophily. How exactly this is done we do not know; it may be simply that selection kills out, usually at birth, anything that does not change in the necessary direction.

In general nature does not draw very marked frontiers between different conditions, so that gradual acclimatisation is possible in most places, except against such an insurmountable barrier as the sea, a range of high mountains, or a desert. Such a process would be simple enough in the case of such things as xerophytes, halophytes, arctic and mountain plants, &c, but in such cases as water-plants, climbers, parasites, &c, a definite sudden mutation from the ordinary type of plant is probably needed (cf. **137**, **146**). While the well known complete families of water-plants date very far back, there are many cases of more recent acquirement of the water habit, like *Menyanthes*, or *Bidens*, and many more.

The old theory of selection involved many assumptions, of which there is a list of 33 in *Evol.*, p. 167. Our theory seems to us to explain or avoid most of them. We have as yet no proof that the adaptation of a flowering plant to its conditions of life is in any way superior to that of an alga or a fern; though it may be more complicated, that is no proof of actual superiority. There seems as yet to be a considerable element of chance in it all. But our theory of adaptation does seem to offer a small change for the better.

Suppose that we look at the flora of the Mediterranean region, which is fairly dry throughout, and shows very well the earlier stages of a xerophytic flora. Upon the principles that we have enunciated, one will expect to find all, or practically all, of the genera that are confined, or endemic, to the region showing there xerophytism, as they are young, and were mostly *born* under these conditions. But the great bulk of the flora is made up of the species of the large genera (as we have now seen in many examples of various kinds), which range often to great distances beyond the Mediterranean. These are much older genera than the young local ones, and probably arrived before the region became so dry as it now is, and they have had plenty of time to suit their species, and especially the new and endemic ones, to the Mediterranean conditions, as the xerophily of these gradually increased. The oldest species will probably on the whole tend to occupy spots that are more or less sheltered from the dry conditions, but the young and strictly local genera have been forced to be xerophytic from birth, and have only had time to migrate a little way from their birthplaces. They thus form in reality a very insignificant part of the flora. Leaf-reduction seems one of the first xerophytic characters to be acquired, and it is an instructive exercise to look at the plates in THOMPSON's flora of the RIVIERA proper (124), to which we shall now confine attention. One sees at once the relatively small amount of leafage, even in British genera and species. Two endemic genera, *Spartium* on Pl. X, and *Coris* on XX, emphasise what we have said about the characters being fixed at birth, for these are the first and only species in these genera. Let us take the *Leguminosae* as an example. Omitting *Oxytropis* as living at too high a level, there are 32 genera on the RIVIERA with about 200 species, as against 16/72 in BRITAIN. All the British genera are included, with 59 of their species. There are ten genera of the family endemic to the Mediterranean, and each has one species upon the Riviera. If we place these in order, with the type of locality described for each, and opposite to it place some British species of the Riviera whose localities are also given, the two match almost to a word.

Genus	Total spp.	Riviera sp.	Locality	British sp. in same or closely similar spots
Dorycnium	10	1	Damp places near sea	Genista tinctoria
Pisum	6	1	Woods, hedges, thickets	Lathyrus Nissolia
Scorpiurus	6	1	Fields and dry places	Ulex europaeus
Calycotome	4	1	Dry hillsides and woods	Genista pilosa
Anagyris	2	1	Dry stony limestone slopes	Hippocrepis comosa
Dorycnopsis		1	Woods, railway banks, hillsides	Lotus corniculatus
Biserrula	1	1	Arid slopes and hillsides	Anthyllis Vulneraria
Bonaveria	1	1	In crops	Lathyrus tuberosus
Hymenocarpus	1	1	In crops	Lathyrus tuberosus
Spartium	1	1	Slopes and dry woods	Vicia sepium

The genera in the righthand column are all large, and their species are all British. With the lapse of sufficient time, all these species have been able to adapt themselves both to Britain and to the Riviera, but that is not saying that they are now adapted to both at the same time. Seeds taken from one and sown in the other would probably take several generations at any rate to become fully suited. Each is adapted to its own situation, but could probably be adapted to the other by slow travel, as is nature's way (*cf.* the acclimatisation of *Coffea liberica* to the hills in Java, in *AA*, p. 29).

Not only do the British species greatly outnumber those of the local endemic genera on the Riviera, but so do the British genera, though not to such an extent. The first four British genera have 103 species out of 200 *Leguminosae.* The old views, so tenaciously held, that there was something peculiar about an endemic, especially its commonly small number, which under "Darwinism" was a proof that it was dying out, and was therefore a relic, evidently have little or no foundation. Each new plant in a country whether of a wide or of an endemic genus, and whether newly arrived from abroad, or born in the country, will only in general survive, if it be sufficiently suited to the local conditions to do so. In the case of species arriving from a markedly different climate, the chance of survival is little or none (*cf.* the tropical seeds that so often arrive on the coast of CORNWALL), and in the case of species *born* in the country (endemic), whether from foreign or from endemic genera, the chance is the greatest possible. But so far as one can tell at present, the advantage (if any) of the endemic genus, whose adaptation centres upon the local conditions, only comes fully into play when its species proceed to expand their area without having to put so much strain upon their adaptability as the others perhaps do, so that they may thus be able in greater or less time to go ahead of them. But there seems no reason why this advantage should be very great; even yet the S. African species of *Senecio*, 222 in number, are much ahead of any other genus, endemic or not.

The most common and popular division of the vegetation of the world is into trees, shrubs, and herbs, divisions which on the whole follow increasing dryness, so as to make it not improbable that the first covering of the world was by trees, and by such a family as the *Rubiaceae*, of which so large a part grows in moist and hot conditions. Shrubby growth is largely characteristic of drier regions, such as much of the Mediterranean coast, of parts of CALIFORNIA, &c, where it goes by the collective names of maqui (macchie) or chaparral. It forms communities of more or less xerophile plants in many parts of the world, mostly sub-tropical. Herbaceous vegetation is characteristic especially of the rather dry arctic and alpine regions, of the heaths of the north of EUROPE, the savannahs of the tropics, and so on.

In all these types of vegetation one may see at work certain general principles, when one realises that the process of evolution has gone in a direction different from that which we have so long regarded as the normal. The first comers would be the large and old genera, some of whose species would perhaps give rise to forms better suited to the conditions, which at that early period were probably not so pronounced as they are now, in regard to variety of climate, especially of dryness. The changes of climate were quite possibly slower than they now are, and the differentiation of forms would be correspondingly slow, though the work in this book gives good reason to suppose that on the whole the changes were probably larger — generic or family rather than specific, in many cases.

Smaller genera would come later, perhaps finding it more difficult to modify their new species to suit the now drier or otherwise altered climate, and finally would come the period of the endemic genera, which in time, as our list of the *Cynareae (Compositae)* on p. 445 shows very well, would grow to cover so large an area that many people would deny them the title of endemic, though their larger ancestors (like *Centaurea* in *Cynareae*) had evidently at one time been themselves endemic. When in a well defined region like the Mediterranean one finds endemics of considerable size, it evidently means that that region is old as it stands, and has long been inhabited by plants; when they are only very small, this is probably not so. But until the new conditions have lasted for a very long time, the species of the endemic genera will be far behind the endemic species of the larger genera in number, as one may see in S. AFRICA or CHILE (p. 440 below).

As it is on the whole probable that early flowering plants were meso- rather than hydro-, or still more xero-phytic, one may predict that genera that occur in the mesophytic country will be larger than those in the xerophytic, and those that occur in both larger still. Taking the first hundred genera from a list I have made of genera over 50 species, there are five xerophytic averaging 125 species each, 37 mesophytic averaging 158, and 58 of both zones averaging 260. This really follows from the law of size and space; the larger genus occupies more space, and occurs in a greater variety of conditions, to which, as being older, it has had more time to suit itself.

It may be well to say a few words about individual groups of specialised plants. Water-plants form a well-known class, found all over the world, consisting mainly of a number of families that contain water-plants only, and therefore probably very old as evolution probably is very slow on account of the uniform conditions. On the other hand they show a marvellous variety of form, indicated in the way in which they are taxonomically broken up, few though they are, into many sub-families and tribes; and carried to the greatest extreme of variety that is known in the tropical family *Podostemaceae* (cf. pictures in 148).

There are a few water-plants that have begun so much later in life that they have not got beyond the stage of sub-families (*Menyanthes* and *Limnanthemum* in *Gentianaceae-Menyanthoideae)*, or even genera (*Bidens*, *Jussieua*, *Nipa*, *Pistia* &c).

Parasites also deserve mention. If our theories are correct, the earliest parasites would probably have to take as hosts the larger and more widespread genera of the present time. Only late comers as parasites would be able to find any of the younger genera common enough. We have taken the sizes of all the hosts that we can find mentioned in the great taxonomic works, and find them to be 24 of 250 species or more, 36 between 250 and 60, 24 between 60 and 15, and 36 between 15 and 1, the average being the large figure of 155, which indicates a very old genus.

Climbing plants form a large group, belonging to many families, and very commonly only to portions of families, or even to single genera or even species. The habit is so common that it is evidently very easy of acquisition, and cannot all be traced back to one, or even to a few, parents; it is very polyphyletic. They cannot owe their adaptation to selection, for it would be very disadvantageous were the correlation not complete — a weak stem with climbing organs, as we have often pointed out, *e. g.* in *Evol.*, pp. 57, 171. Its appearance must be the result of a single direct mutation, but what the stimulus is, we do not yet know.

Saprophytes, to judge by the number of species in their genera, would appear to be a very young group, but one must remember that they live in very constant conditions, like water-plants.

12. *Leaders and sub-leaders.* In *Evol.*, p. 31 and in more detail on p. 134 (Testcase XX) we outlined one of the most striking facts brought out by deduction from our theories. This, which will evidently be of great importance in the study of distribution, is the way in which the original leader of any family promptly gives rise to sub-leaders of tribes, these to leaders of genera, subgenera, and so on, right down to sub-species. This is shown for all families down to 50 genera on p. 173, and in more detail for many important individual families later (list under Leaders in Index). The further back in a family that some character begins to be handed down, the more descendants does it tend to mark,

and the more important is the group so formed. In the very early days, when a family has but few genera, and those but small, the main taxonomic lines of its classification are already marked out, as indeed may be seen in the bi-generic families in App. III, *Evol.*, p. 199.

The first generic mutation of *Justicia*, leader of *Acanthaceae* (pp. 206, 218), produced *Ruellia* by a number of divergences, larger and smaller. That in the aestivation, from imbricate to contorted, proved to be so permanent in inheritance that almost all the *Acanthaceae* show one or the other. This is perhaps partly due to the fact that it has no adaptational value whatever, and makes no difference to the amount of material used. The first division of the family is thus into *Imbricatae* and *Contortae*. Of course we do not yet know whether any appreciable amount of polyphyly or of cross-mutation from one to the other has gone on, but in general the division is sound. As adaptation does not seem to have any opening in this or in other divergences at the tops of families, we may leave it out of account, dealing with dispersal by the laws of ASA.

The mere fact that, as we have seen, the leaders of all geographically possible sub-groups seem usually to appear in BRITAIN or elsewhere, is another great argument against the influence of selection. The structural alteration was probably due to some rearrangement of the genes and chromosomes, inevitably bringing about the change without which we should not know that evolution had gone on. Carrying no apparent disadvantage, they were not interfered with by selection, and they allowed of no transition forms, by reason of the divergences. This rule seems so general that we can leave selection out of account, except in details of ecological dispersal, remembering to take our species in groups of allies.

This early formation of sub-leaders from leaders is so universal, that together with the formation of the leaders themselves, it is evidently a law of evolution, and will repay more detailed study. Clearly, by mere analogy, it should hold all the way down to sub-species, as indeed proves to be the case.

There is a great gap in size between *Senecio* and *Othonna*, the next genus in the *Senecioneae* (p. 177), which suggests at once that the early descendants of *Senecio* are to be looked for, not in the tribe, but in the family, among the earliest genera given on p. 176. The second genus, be it *Hieracium* or another, must be the direct descendant of *Senecio*, and it looks as if a number of the later ones were so as well, and indeed this fits in well with the geographical dispersal of the *Compositae*. But these later genera in the list all *belong to other tribes* showing that the early mutations of *Senecio* are so divergent as to cross the line of distinction at one stroke. When the genus is newly formed, and this seems to hold for all leaders of families, and more especially for early ones like *Senecio* or *Psychotria*, it would appear to start with more decisive mutations than those to which it gives rise at a later period. This rule seems—one cannot prove it as yet—to run right through the vegetable kingdom from the very beginning. In the early days, it would not seem impossible that such distinctions as those between algae and fungi, mosses and liverworts, algae or mosses and ferns, and so on, might have appeared at a stroke, probably at very long periods of time apart.

There is a possibility that at its birth such an old genus as *Senecio* has not yet the command of any great variety of characters upon which the kaleidoscopic mutation that goes on can ring the changes, so that at the very start of a family there are not many characters that are likely to escape from some change or other at some point. Those that *do* have the luck to descend right through the family till a comparatively recent time will be the most " important " of the family characters, while those that became changed at an early date will be " unimportant ". But a very noticeable thing that will at once strike anyone who begins to work with taxonomic characters is that when one gets down to the smallest, most numerous, and most recent genera—the " ones "—there tends to be, owing to the many mutations needed to produce so many " ones ", perhaps hardly a single " family " character left that has not been altered somewhere. One gets very quickly into the habit of accepting as a member of a family anything that agrees in *most* of its characters with the type of the family, and not necessarily in all. A mere glance at any list of characters of a family or genus will show how continually the words often, frequently, usually, and so on, have to be used.

A good way in which to study such matters is to spread out the families by tribes, arranged in order by size, giving with each genus such information as to its dispersal as may be required. But to do it requires very large books, and it would be quite impossible here. But, if proper secretarial help can be obtained, we hope to work up into good shape for use, many of those that we have already made, and to leave them to such institutions as Geneva, Kew, Brussels, &c, as they will save future workers very much time and labour.

Rank in the family, tribal or other, is owed mainly to age (p. 188). At a kaleidoscopic mutation some of the original characters are lost and are replaced by others, divergent from them. The number of species is greater than the number of important characters, so that differentiation depends largely upon permutations and combinations of the characters (p. 189). A character varies in importance with its age in the family : the older it is, the more important is it. The parents carry the potentialities of all characters, and the laws that govern their incidence much need investigation.

Divergence is automatic, probably electrical, and seems to become more marked, probably because characters are fewer, as we go further back in time, though every now and then individual species seem to show more marked characters than usual. This increase of divergence as one goes back seems to offer a better explanation of the very marked differences between the great classes than we have hitherto had.

A question that soon arises is as to how far the leader continues to lead, or even to be present, as the group led increases in size. Statistics of the British genera *(LC)* show that the leader does not always lead. The first genera in a few families show as follows, the leader in italics : *Nymph.* 96, *92*, *Papav. 94*, 96, 108, *Cruc. 32*, 112, *Caryo. 104*, 112, *Legum. 68*, 112, *Umbel. 55*, 112, and so on. A good many large families show this kind of thing. In most of the more tropical families, like *Malvaceae*, the leader does not often appear in BRITAIN at all, unless the family is so old that it has given time for the leader to appear, like *Panicum* in the grasses, which barely reaches BRITAIN. The leader in BRITAIN appears more often in the tropics, for it can find a cooler climate in the hills.

One will expect a large leader to be followed in general by a large family, and in fact we find, taking averages over the whole number of families

Size of family	No.	Total spp. in leaders	Average of leaders
1-24 genera	214	15,174	71
25-49	27	4.730	175
50-74	20	4,035	202
75-99	13	4,030	310
100-199	14	5,665	404
200 or more	15	8,850	590
	303	42,484 (23.2% of all spp.)	140

The first genus of a family necessarily defines the centre of its distribution, but the second may start to the east of that, the third to the west, so that it is unlikely that they will arrive in any new country in the order of their birth (*cf.* Britain, pp. 177 seq.). If the family develope upon the dichotomous principle, we shall expect the tribes to do the same, and this in fact proves to be the case everywhere, a phenomenon that one would hardly expect if competition came into the matter, just as one would not expect the variety of tribes that show everywhere (*cf.* the Seychelles on p. 469).

Now that we have seen that the degree of change seems to grow less emphatic as we come downwards from ancient times to the present, it would seem probable that production would become more an output of lower than of higher forms, while in old times it may have been almost entirely of what we should now call higher forms, genera, and even higher.

We have seen how simple it becomes, under the new conceptions, to trace the gradual adaptation of the members of a small family like *Juncaceae* (p. 346) or *Hydrocharitaceae* (p. 349) to new conditions, and we may see the same kind of thing going on with the small genera in a large family, like the frequent production of coast species among the " ones " in the *Rubiaceae.*

To go now a stage lower, we find, as we have already seen on pp. 181-4, that similar phenomena as to leadership are repeated with the genera, and as this is a very important point, we shall give one or two further instances. If we take *Juncus*, which must be one of the oldest genera in Britain, we find :

British spp.	Dispersal		Sub-genera
J. bufonius	112	Heading	§ *Poiophylli*
effusus	112	Heading	§ *Genuini*
conglomeratus	112	2nd	Genuin.
sylvaticus	111	Heading	§ *Septati*
articulatus	110	2nd	Septat.
squarrosus	109	2nd	Poioph.
bulbosus	109	3rd	Septat.
others of above groups at 96, 91, 63			
maritimus	55*	Heading	§ *Thalassici*
others of above groups at 41, 39			
triglumis	25	Heading	§ *Alpini*
others of above groups at 19, 19, 14, 12, 8, 5, 3			
capitatus	2	Heading	§ *Graminifolii*

* The maximum possible to a coast species is about 80.

The two unrepresented sub-genera of *Juncus* (*cf.* BUCHENAU in *NP*/1) have each one species, one in the MEDITERRANEAN, one in S. AFRICA.

If we look at *Luzula*, the other British genus of *Juncaceae*, which has only three sub-genera, we find

L. pilosa	111	Heading	§ *Pterodes*
multiflora	111	Heading	§ *Gymnodes*
sylvatica	110	Heading	§ *Anthelaea*
campestris	110	2nd	Gymn.
others at 29, 22, 8, 1			

If we take the best dispersed species of *Lamium*,

L. purpureum	112	Heading	§ *Purpurea* (Briquet)
amplexicaule	99	Heading	§ *Amplexicaulia*
hybridum	85	2nd	Purp.
Galeobdolon	72	Heading	§ *Galeobdolon*

If we take the first five British *Scirpus*, we get :

S. setaceus	108	Heading	§ *Eu-isolepis*
caespitosus	104	Heading	§ *Baeothryon*
lacustris	101	Heading	§ *Schoenoplectus*
fluitans	97	Heading	§ *Eleogiton*
pauciflorus	94	2nd	Baeothr.

The British *Saxifragas*, following ENGLER (*NP*/2) give

S. tridactylites	85	Heading	§ *Tridactylites*
granulata	85	Heading	§ *Nephrophyllum*
hypnoides	70	Heading	§ *Dactyloides*
stellaris	46	Heading	§ *Boraphila*
aizoides	34	Heading	§ *Xanthizoon*
oppositifolia	33	Heading	§ *Porphyrion*
nivalis	17	2nd	Boraph.
Hirculus	12	Heading	§ *Hirculus*

The Irish forms are largely in § *Robertsonia.*

The British *Violas*, following Mrs GREGORY (161) show

V. Riviniana	112	Heading	*Caulescentes rosulantes*
palustris	105	Heading	*Acaules eflagellatae*
canina	102	Heading	*Caulescentes arosulantae*
odorata	81	Heading	*Acaules flagellatae*
hirta	75	2nd	Ac. eflag.

The same kind of thing shows in other countries. The heads of the taxonomic divisions are among the very first to be formed, and so appear among the earlier arrivals everywhere; and as selection seems to have little effect, they remain in much the relative positions in which they arrived. *Desmodium* in CEYLON, with eight out of twelve sub-genera represented, is a good example, and there are many more as good. The *Rhamnus* quoted on p. 107 is another very good illustration of this, and also of a very widespread polyphyly.

This work shows clearly why it is easier to distinguish species in a single flora than to try to puzzle them out in a monograph, where species from all kinds of localities are mixed up together, and as they often tend to show slight variations to correspond with the particular sets of conditions in which they live, show much more overlap than is usually the case in one country.

We may even go a step higher than the family, and deal with the top orders, as headed by the top families. The first twelve of these give the following result :

Family	Genera		Order		
Compositae	1179	Heading	*Sympetalae*	11	*Campanulatae*
Orchidaceae	726	Heading	*Monocots*	11	*Microspermae*
Leguminosae	675	Heading	*Archichlam.*	24	*Rosales*
Gramineae	548	Heading	*Monocots*	4	*Glumiflorae*
Rubiaceae	506	Heading	*Sympetalae*	9	*Rubiales*
Asclepiadaceae	352	Heading	*Sympetalae*	6	*Contortae*
Cruciferae	350	Heading	*Archichlam.*	22	*Rhoeadales*
Umbelliferae	334	Heading	*Archichlam.*	33	*Umbelliflorae*
Euphorbiaceae	326	Heading	*Archichlam.*	26	*Geraniales*
Acanthaceae	273	Heading	*Sympetalae*	7	*Tubuliflorae*
Liliaceae	269	Heading	*Monocots*	9	*Liliiflorae*
Scrophulariac.	259	2nd	(Sympet.		Tubulifl.)

Five of these twelve are *Sympetalae*, four are *Archichlamydeae*, and three are *Monocots*, a fact which hardly goes to support any notion that the *Sympetalae* were derived as a single group from the *Archichlamydeae*. The table also goes to show that the grasses, lilies, and orchids are ancient families, whatever many of the other *Monocots* may be.

All the first ten families in the above list, at any rate, are widely separated taxonomically from one another; in fact the first three are as far apart as it is possible to be with our present system of classification, were it fully natural. Yet they are quite possibly, in reality, closely related. One feels, however, that *Compositae* and *Orchidaceae* are perhaps in a higher position that that to which they are really entitled.

13. *Overtaking of leader by younger genera.* As we have seen, conditions change in many directions, and often more or less continuously, for example in the directions of greater heat, cold, dryness and moisture. When a descendant is born along one of these directions, the chances are that *in that direction* it may in time overtake, and even pass its parent, so that if we go round the edge of the map of dispersal of a family, while on the whole the leader will reach the margin at more places than any other member, it is not unlikely that at some places, especially in the older families, and far away from the original centre, we shall find places where one of the younger genera has passed the older.

To take a single example, the *Malvaceae*, a mainly tropical family (p. 156). Its leader, *Hibiscus*, has spread out toward the colder zones, but its most northern limit seems to be the south of FRANCE. But other and smaller genera have been born further north, and have been able to move more quickly northwards than *Hibiscus*, as for example the Mediterranean genus *Lavatera*, that has a coast species which has reached 17 vice-counties in BRITAIN, or *Althaea*, which seems to have been born further north yet, and has reached 30. Finally *Malva*, also northern, is one of the commonest weeds in southern BRITAIN, and has reached 96 vice-counties. If we go to the Antipodes, and look at NEW ZEALAND, we find *Hibiscus* just reaching the islands with a couple of species scattered over the warmer parts, while *Plagianthus*, a genus of AUSTRALIA of 10 species, evidently born there, has three species, all endemic to NEW ZEALAND, one along the whole length of 1080 miles, one from 60 to 1080, both also reaching the CHATHAMS, and the third reaching from 60 to 900. There is also a NEW ZEALAND endemic genus, *Hoheria*, evidently a descendant of *Plagianthus*, to whose tribe it belongs. It has one species from 300 to 900, well within the bounds of *Plagianthus*. There are other *Malvaceae* that have behaved in this way, and suited themselves to colder habitats, like *Kitaibelia* in SE. EUROPE, and *Tarasa* in CHILE, both monotypic. Such examples may be found in most families of cold countries, whose leader is tropical.

14. *Development and spread of a genus.* A genus is in general a recognisable stage between a tribe and a species, but when and how the formation of species, as distinct from genera, began, we do not know, and probably it would not be simultaneous everywhere. Divergence at birth seems on the whole to be greater the further back that one goes. The very old genus *Senecio*, for example, seems at first to have given rise, not perhaps to any species of *Senecio* itself, but to new genera, so divergent that we now class them as heads of tribes. In *Psychotria*, another very ancient genus, large divergences appear as it developes, but seem to appear more than once, and at different places, thus at once suggesting that the kaleidoscopic mutation that was going on had but few characters, but those usually well marked, upon which to draw, so that at a mutation, some of them were liable to be used over again in a polyphyletic way. These, at so early a stage in the history of the flowering plants, were likely

to be largely characters that we should now class as generic, but which a botanist of a few million years ago would probably have called specific. But this is as yet speculative. With the knowledge that we now have, we know what we mean by a genus, though it is very difficult of definition. All, however, admit that its characters are in general more distinctly divergent from those of its relatives, and the divergences more numerous, than those that mark a species.

Commencing as one species, and probably as only a few individuals, early growth and dispersal, which will be largely determined by the obstacles to be overcome, will be extremely slow, though becoming quicker as time goes on (*AA*, p. 34). Sooner or later, upon our working hypothesis, some extra stimulus will cause a rearrangement of the parts of the nucleus, with two results, (1) that the nucleus will better suit the extra, or the differently applied, pressure, and (2) that this will automatically cause the appearance of a new form, even at times a new species or genus, inheriting from its parent enough local adaptation to be able, in general, to survive and reproduce, and probably slightly improving its adaptation with every succeeding generation. But it is unlikely, with the structural changes that go on, that the adaptation will be the *same* in detail. Some parts will be better, some worse adapted, but the total result will be much the same, except that the child will probably find itself better suited to go in some directions, worse so in others, than the parent, so that their areas of dispersal will not be quite the same. One may go more into drier country, the other prefer the wetter, for example.

Owing to the continually increasing number of possible parents and the fact that a new species must begin as a one, the ones will be much the most numerous as the genus begins to expand, and the species as a whole will give the usual hollow curve.

Plotted in logarithms, it forms a straight line running downwards to the right (p. 262), and YULE actually traced a great many of these curves, both in plants and in animals, thus showing incidentally that what we have said in this book will probably apply to animals also, with modifications in various directions. One must remember that the statements here are largely statistical, and can only occasionally be applied with safety in individual cases. A genus may have been born a very long time ago, and still be only a "one", perhaps because now shut in by insurmountable barriers, and under such circumstances, it would be unlikely to form any new species. But such species are "lost in the crowd" in statistical work, which shows how widely and generally operative are the laws of ASA &c.

Let us take a few instances from CEYLON endemics of the early formation and dispersal of species of a genus. *Monoporandra (Dipterocarp.)* has two species; one, with stalked panicles and many flowers, is not uncommon in parts of two provinces, while the other, with small racemes of 1-4 flowers, occurs only at one spot in warmer and wetter conditions, 300 m. lower. *Schumacheria (Dillen.)* has a leader common in the moist low country, with large terminal panicles of relatively large flowers, while the other two species, with axillary panicles of small flowers, are found one in the hills about 1000-1500 m., the other in the extreme south of the moist low country. One could go on for a long time with such examples, which bear out the general description that we have given of the formation and dispersal of the species of a genus.

Several monographs well showing how a genus grows and spreads have appeared in recent years. In (**120**) STEARN has dealt with *Vancouveria*, a small genus of *Berberidaceae* of the NW. U. S. (map on p. 429, *l. c.*). *V. hexandra*, which appears to be the original parent, ranges like the line (a) in the plan given here, *V. planipetala* like the line (b), and *V. chrysantha*, which is evidently fairly recent, is found only at the spot (c), just on the frontier of CALIFORNIA. Species (b) evidently began somewhere there, in rather drier conditions than (a) (OREGON is a very wet country), and went ahead of it to the south.

```
a
a
a
a
ab
abc
 ab
 ab
  b
  b
  b
  b
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Cymopterus, described as to dispersal in (**93**) is the third American genus of *Peucedaneae* (*Umbell.*). The map given by its author shows that *C. acaulis* was probably the original parent, which appears to have arisen somewhere in the region of DENVER, COLORADO, at a height of say 5000 feet (1500 m.). From there it spread into the region of the MISSISSIPPI, into the SW corner of CANADA, and into MEXICO, so that it covers a big area.

West of DENVER is a region of high mountains, in which travel would be slow and conditions continually changing, so that a number of new species, all of fairly restricted areas, have been formed there, or in the desert and semi-desert country beyond. Such species are, for example, *C. globosus* in the mountainous country of W. UTAH, NEVADA, and eastern CALIFORNIA, *cinerarius* in the high mountains of NEVADA and E. CALIFORNIA, *deserticola* in the MOJAVE desert of CALIFORNIA, and, probably the most recent of all, *megacephalus* at one spot in northern ARIZONA.

Another, and perhaps even more interesting case is that of *Haplopappus* (**93**), where the author gives many suggestions as to the mutations which might have produced the various species upon much the same lines as we have suggested above, but space will not permit of quotation.

There is no doubt that in general the dispersal of a genus corresponds with reasonable closeness to its size or area, so that the oldest or largest genus in any circle of affinity will occupy most area, and be the leader in most places, as will the species in a genus that occupies most area. Until the family becomes fairly large, the leading genus tends to cover all, or nearly all, of the area occupied by the family. Even in so large a family as *Compositae*, *Senecio* does so to a very great extent. There seems no reason why a genus should not become as nearly cosmopolitan as geology will allow, and time will permit. Under our views of evolution, a genus does not necessarily kill out its ancestors, as was once believed.

15. *Development and dispersal of a family.* A family begins as a single species and genus, but with what we consider more marked divergence than that which we regard simply as a genus of some family already existing. As usual, it is of necessity adapted to its birthplace, and has enough adaptability to be able to withstand the usual climatic changes, &c. When it comes under some extra stimulus, it will give rise to another species, and at first, especially, will tend to give rise to new genera. All the time, at a steadily increasing speed, it will be extending its area, and coming into new conditions and producing more new species and genera. If time enough be allowed, it will thus ultimately come into the bulk of the combinations of conditions that exist, and may have produced species locally suited to them. These species

in turn, as they extend their areas, will come into other conditions, and produce further new species or genera, and so on Adaptation coming in this simple way is much easier to understand than adaptation that depended upon selection.

Working upon these principles, we may take a small family like *Juncaceae* (p. 346), or *Penaeaceae* (p. 301), and watch the family growing in size and in differentiation, while every new form produced is suited to whatever conditions it met with. But of course in a large family, so much adaptation has been done, and so many new forms have been produced that to trace out the ancestral history of any one plant becomes a very difficult and complex task, which is usually quite beyond any knowledge that we may have at the moment. One must be content with some knowledge of what seems to have gone on at the ends of the twigs of growth, as for example one may see in the *Rubiaceae* a number of monotypes adapted to life under the conditions of existence upon the coast, with fewer ditypes or larger numbers ; or several monotypic myrmecophilous plants, and so on. In all or most of such specialised adaptations, one seems to get a hollow curve — many monotypes, fewer ditypes, and diminishing upwards. In *Juncaceae*, *Juncus* and its oldest and almost cosmopolitan species like *bufonius*, *effusus*, and *conglomeratus* were evidently adapted in their early youth to the conditions in which they live, which are common all over the world (in the mountains in the tropics). Their first generic mutation was *Luzula*, suited to rather drier conditions, and starting probably near to *Juncus* when this was 1-2 species-generations old. It followed *Juncus* almost everywhere, and these two were so well suited that they did not have any more generic mutations till in the extreme south, when cold would come in as an extra stimulus, and they, or quite possibly only *Juncus*, as the older, mutated off the small genera like *Rostkovia* or *Andesia* found on small areas in the far south.

If we turn to water plants, we find them living in conditions that are very constant, and rarely provide much in the way of stimulus, with the result that we get very few genera, even in so ancient a family as the *Nymphaeaceae*. On the other hand, a submerged water plant has little fibrous tissue, and so is very plastic, and when a stimulus comes along, it may be that it produces a much greater effect than usual, so that the divergence of the new genus may be regarded as of tribal or even sub-family rank, as one may see in such a family as *Hydrocharitaceae* or *Potamogetonaceae*. The greatest variety of structural form known in the flowering plants is shown by the *Podostemaceae*, of which an illustrative set of photographs will be found in (148). But to go into this question in detail would lead far beyond the space that is available.

16. *Polyphyly*. We have pointed out various cases (*e. g.* pp. 158, 369) in which independent development from two or more ancestors seems the most probable explanation of the appearance of the same character in different places. For many characters of very great importance, like inferior ovary or alternate leaves, this must be true; in fact wherever it shows in two or more families that are not closely related.

It is, however, a very facile explanation for anything of this kind, like the old one of destruction of intermediate forms that were supposed to have existed. It is therefore very important never to call it in unless all other possibilities have been tested without result, or it will soon be as absurdly overdone as was the old explanation. But it must be accepted as a possible explanation, which may be commoner than we think in its application.

We have seen, under teratology (pp. 100-105) that the changes of character that may appear at a single mutation are quite numerous, large, and *unexpected*, while the usual general working theory has been that every character was descended from something not unlike itself in previous generations. We have dismissed sudden and divergent changes as practically impossible, in spite of teratological evidence to the contrary, and we have assumed that the intermediate stages have been killed out. This has led to great difficulties, which have become practically insurmountable now that we have seen that evolution goes the other way. What were the intermediates between *Justicia* and *Ruellia* in the aestivation, and why were they killed out completely? They are among the most important characters of *Acanthaceae*.

Teratology *proves* that a great number of unexpected changes may take place, and apparently without difficulty, but as they are not viable, they have been dismissed as unimportant. But they show that *the parent was carrying the possibilities of production of characters elsewhere found in* *the family*, and that under some stimulus, here perhaps food-supply in some cases, they might appear. For instance, the first one quoted on p. 100 shows *Clematis* producing more than one ovule, which is the most marked character of the other tribe *Helleboreae*. No. 7 shows the appearance in *Anemone* of another character of that tribe; and so on. Given this possibility, which cannot be denied, there is little or no reason against the viable occurrence of such a thing (*cf.* in PENZIG the occurrence of bracts in over 30 genera of *Cruciferae*, and their viable occurrence in *Schizopetalon*, p. 104).

We have seen that there is evidence that the same character may appear in more than one place, but usually in the same family, and if we consider, which is now quite permissible, that the possibilities of production in any member of a family may include any of the characters of any member of that family, we shall no longer feel surprised at the unexpected appearance of any character. Teratology gives ample evidence of such appearances; *e. g.* in *Ranunculus*, petals to sepals, petalisation of stamens, synanthy, female flowers, honey-scale to petal, condensed stem with leaf rosette, apetalous flowers, multiplication of petals (as permanently seen in the Nilgiri mountain *R. reniformis*). One will not in general, however, expect a character that is not shown somewhere else, and especially in the family (*cf.* the blue flower, p. 103).

By the ordinary laws of chance, that one character should appear again may happen frequently enough, but that two should do so is rare, unless they are linked like a weak stem and the possession of climbing organs are so often linked, and that three should do so is rarer still. Rarity perhaps increases as we come down to small genera, where the kaleidoscopic mutations have more to draw upon. When we consider this possibility with what has been said above, it would be in no way a surprise if polyphyly were very frequent, and that some of the large families, like *Compositae*, owed their origin to more than one source.

A point that requires study is whether a given step in mutation tends to be followed by steps that are also alike or nearly so. This is part of the question of incidence of characters, mentioned above as one of the things urgently calling for investigation. In the *Araceae*, for example, the inheritance of endosperm does not seem to follow what at present we are accustomed to consider genetic lines. We have also seen in *Acanthaceae*, pp. 207-8, how structural characters in pollen, than which it is not easy to imagine anything more "useless", may turn up in different places there. A character may be clearly marked in detail in a descendant, when the parent showed no sign of it.

Numerous instances could be produced to show how a character that occurs in one place in a family may appear again in another widely separated place, where it is very unlikely that the genera concerned, which may be widely separated with no linking genus, had a common parent except at the head of the family. It must have been a character whose potentiality of appearance was handed down from above, even from the head of the family, in the way in which which we know that ancestral characters may appear in human inheritance at intervals. A great many cases can of course be accounted for by the overriding genus *or genera*, and these need not necessarily show the character, but may be carrying it in a recessive condition.

It may be well to quote another instance of the kind of phenomenon where it seems as if polyphyly must be invoked. *Triuridaceae* has only four genera, *Sciaphila* (20 spp.), the leader, in INDOMALAYA and in BRAZIL, followed by *Andruris* 6 INDOMAL), *Triuris* (2 BRAZIL), and *Seychellaria* (2 MADAG., SEYCHELLES). The distribution is very discontinuous, and the occurrence in the SEYCHELLES (p. 469) shows that the family is probably old enough to have gone through a good deal of geological change, but even so one does not feel convinced that the family is genetic without polyphyly. It is, however, of special interest to note that *Sciaphila* has both its two sub-genera in BRAZIL and in INDOMALAYA also. This might be thought a proof that great destruction has gone on in between, till one notices that in CEYLON, where the genus has one wide and one endemic, the latter belongs to the second, the former to the first, sub-genus; or in other words, the sub-genus must almost certainly be polyphyletic.

17. *Dispersal of the Compositae.* Having used this family to illustrate taxonomic work on pp. 175-81, let us now use it for dispersal, and our method of dealing with this under the laws of ASA and of DDM. We give below the floras of *Compositae* of BRITAIN and NEW ZEALAND thus displayed,

though there is not space for all the information that might be entered.

These countries have only one really important genus in common, *Senecio*, leader of all, and the most likely genus to be found anywhere. BRITAIN has ten species, all fairly widely dispersed elsewhere, while NEW ZEALAND has 30, one wide (S. *lautus* AUSTR., N. Z., CHATHAMS, KERMADECS) with 29 endemics, 15 of them only in the south island, six in the north, six in both, the rest on the outlying islands. All are probably direct or indirect descendants of the wide. The problem of whence this *Senecio* came cannot be attacked with much hope of success till we have a much better knowledge of incidence of characters, geological history, &c, and we are now out to show that inductive reasoning and deductive treatment are of value in this kind of work. Our figures are of course not up to date, but there is no reason to expect relative positions of genera to be much affected by additions.

It is instructive to compare relative positions and other arithmetical data in these two islands, which are as far separated as it is possible to be. BRITAIN has 43 genera (including *Mulgedium*) with 7274 species in the world, NEW ZEALAND only 24/3277, an average size of 169 against 131, or with *Senecio* omitted from both, of 125/53, a large difference. BRITAIN has a much larger proportion of genera at the tops of the tribes, and it is of interest to note (numbers to the left of the name show position in the tribe) that she has *all* down to 11 in *Cichorieeae*, and to 6 in the *Anthemideae*, indicating that the source of these tribes was not too far away, and with somewhat similar conditions. But the NEW ZEALAND *Compositæ* as a whole much outnumber the BRITISH. NEW ZEALAND also has three endemic genera, with 4, 3, and 2 species, thus indicating considerable age. But as usual, the bulk of the endemics are in the larger and older genera, *Celmisia* 42, *Olearia* 35, *Senecio* 29, *Raoulia* 17, *Helichrysum* and *Cotula* each 16, making 155 out of 200 in these six genera. It is of special interest to see that two endemics are in genera that are very small locally. *Crepis*, a very cosmopolitan genus, has one endemic, only, ranging the south island, *C. novae-zealandiae* Hook. f., while *Sonchus* has two " weeds " on the main islands, and one endemic on the CHATHAMS, which would be of great interest if genetically proved to be a descendant of one of them.

BRITAIN has 15 of the first 20 *Compositae* (p. 176), while NEW ZEALAND only has *Senecio* (with 30 spp.), *Helichrysum* (16), *Gnaphalium* (10), *Sonchus* (3), *Crepis*, *Picris*, and *Taraxacum*, 1 each.

Britain	Spp. World	Spp. Brit.	Max. Disp.
1) *Senecioneae* (tribe 8, p. 177)			
1. Senecio	2000	10	112
15. Petasites	15	1	110
x. Tussilago	1	1	112
2) *Cichorieae* (tribe 13, p. 178)			
1. Hieracium	800	10P	111
2. Crepis	240	6	112
3. Lactuca	100	5	76
4. Scorzonera	100	1	1
5. Hypochoeris	60	3	112
6. Sonchus	50	4	112
7. Leontodon	45	3	112
8. Picris	40	2	66
9. Tragopogon	35	2	94
10. Taraxacum	30	4	112
11. Mulgedium	25	2	2
x. Lapsana	10	1	112
x. Cichorium	8	1	68
x. Arnoseris	1	1	24
3) *Cynareae* (tribe 11, p. 179)			
1. Centaurea	650	12	112
3. Cirsium	225	8	112
4. Saussurea	150	1	27
7. Serratula	40	1	64
8. Carduus	35	3	89
10. Onopordon	25	1	51
x. Carlina	20	1	85
x. Arctium	6	4	92
5) *Astereae* (tribe 3, p. 180)			
1. Aster	500	2	70
3. Erigeron	180	2	70
6. Solidago	100	1	111
x. Bellis	15	1	112
6) *Eupatorieae* (tribe 2, p. 181)			
1. Eupatorium	450	1	99
7) *Inuleae* (tribe 4, p. 181)			
2. Gnaphalium	150	5	112
3. Inula	100	2	59
4. Antennaria	85	1	89
x. Pulicaria	30	2	82
x. Filago	12	5	93
8) *Anthemideae* (tribe 7, p. 181)			
1. Artemisia	280	4	111
2. Chrysanthem.	180	2	112
3. Achillea	125	2	112
4. Anthemis	125	3	77
5. Matricaria	50	2	111
6. Tanacetum	30	1	108
x. Diotis	1	1	10
9) *Heliantheae* (tribe 5, p. 181)			
1. Bidens	150	2	87
10) *Arctotideae* (tribe 10)			Nil
11) *Mutisieae* (tribe 12)			Nil
12) *Helenieae* (tribe 6)			Nil
13) *Calenduleae* (tribe 9)			Nil

New Zealand			
1) *Senecioneae*	World	N.Z.	Endc.
1. Senecio	2000	30	29
x. Erechtites	15	6	4
x. *Brachyglottis*	2	2	2
2) *Cichorieae*			
2. Crepis	240	1	1
6. Sonchus	50	2	1
8. Microseris	40	1	—
8. Picris	40	1	—
10. Taraxacum	30	1	—
3) *Cynareae*	Nil		
4) *Vernonieae*	Nil		
6) *Eupatorieae*			
x. Ageratum (weed)	1		—
7) *Inuleae*			
1. Helichrysum	350	16	16
2. Gnaphalium	150	10	6
x. Raoulia	25	17	17
x. Cassinia	20	5	5
x. Craspedia	4	1	—
8) *Anthemideae*			
x. Cotula	50	19	17
x. Abrotanella	15	7	7
x. Centipeda	5	1	—

	Spp. World	Spp. N.Z.	Endc.
5) *Astereae*			
5. Olearia	100	35	35
7. Brachycome	60	5	5
x. Celmisia	50	43	42
x. Lagenophora	15	6	6
x. Vittadinia	8	1	—
Haastia	4	4	4
Pleurophyllum	3	3	3

	Spp. World	Spp. N.Z.	Endc.
9) *Heliantheae*			
1. Bidens (weed)		1	—
10) *Arctotideae*		Nil	
11) *Mutisieae*		Nil	
12) *Helenieae*		Nil	
13) *Calenduleae*		Nil	

Genera in italics are endemic to New Zealand.

p Nominal x among the small genera where there is much overlap and duplication.

Celmisia and *Olearia*, the largest, are southern endemics of Australia and New Zealand. *Celmisia*, probably coming from the southern continent, was only just in time to reach Australia, where *Olearia* leads the whole family in species. What happened to *Aster*, leader of the tribe, and where, has yet to be discovered. *Gnaphalium* looks like a fairly early arrival in New Zealand, with four wides and six endemics.

There are two endemics of *Inuleae* reaching beyond New Zealand to Australia &c, while *Craspedia*, the last of the tribe, has one species, reaching also Australia and Tasmania. A proper treatment of the *Compositae* would need a long chapter, but there are a few points that need special mention. We have just seen that *Senecio*, *Helichrysum*, and *Gnaphalium* are the only genera of the " big 20 " (p. 176) to appear seriously in New Zealand, and it is worth while to look at other southern countries to see what they may have to show.

Senecio evidently got a good start, as it shows everywhere, and in such numbers. These are mainly in southern countries, so that it is evident that the place of origin of *Senecio* is yet to seek. Chile alone has 264, S. Africa 222, while in the latter the second genus is *Helichrysum*, itself a southern genus, fading out to the north. But a number of other tribes seem to have sprung directly from *Senecio*, two in America, *Mutisieae* and *Helenieae*, two in Africa, *Arctotideae* and *Calenduleae*, and also the tribe of *Senecioneae*, the *Othonninae* (p. 177).

Let us look at the Chilean *Compositae*, which by size, from the flora of Reiche, are for the top few :

Senecio	264	*Senecioneae*
Haplopappus	86	*Astereae*
Leuceria	51	*Mutisieae*
Gnaphalium	44	*Inuleae*
Hypochoeris	39	*Cichorieae*

followed by *Baccharis*, *Conyza*, *Trigeron*, and *Mutisia*.

Senecio was evidently first to arrive, strongly asserting its leadership of the family. *Astereae* is not headed by *Aster*, as one would expect anywhere in AMERICA, but by *Haplopappus*, a genus common all along the ROCKIES and the ANDES. *Gnaphalium* is in much greater number than usual, but *Helichrysum*, the actual leader of *Inuleae*, is not present, probably because the connection to the south was severed before it could cross. An interesting tribe is the *Mutisieae*, largely confined to S. AMERICA, and there represented by *Perezia*, its leader (75 PATAGONIA to TEXAS), *Mutisia* (60 S. Am), three with 50 each (do), and a tail of 40, 35, 30, 30, 25, 18, 18, 15, 12, 12, 10, 10, 10, 10, 8, 5, 5, 4, 3, 3, 3, 2, and 27/1, practically all confined, except the first, to S. AMERICA. *Hecastocleis* has its only species an endemic in the deserts of NEVADA.

So far, *Mutisieae* make a very good example of a small tribe, but they are not confined to S. AMERICA, but have a section in the Old World, headed by *Gerbera* (45 S. and trop. AFR., INDIA, CHINA, SIBERIA), too large and widely dispersed to be a descendant of *Perezia*, mainly in the mountains of S. AMERICA, and only at most twice the size, so that it would only have two species and be very local when *Gerbera* began in AFRICA or ASIA. It may quite likely be a case of polyphyletic appearance of the tribal characters, or of enough of them to put the two in the same tribe.

Helenieae is also American, but more northern, with several of its larger genera represented by a few in S. AMERICA. *Pectis*, its leader, is not large (60 ARIZONA to BRAZIL), but is followed by over a hundred small genera, forming a very long tail for so small a head—3/35, 30, 4/25, 5/20, 2/18, 4/15, 4/12, 10, 2/8, 3/7, 2/6, 3/5, 4, 10/3, 15/2, 41/1. This is a phenomenon which shows in a number of places. It does not contradict anything that we have said, but an explanation would considerably advance our knowledge of the whole subject of evolution, now that we are beginning to comprehend the rules that govern it. It is also noticeable, and needs explanation, that there are a number of genera of N. America, especially of California, that have representatives in Chile, but not between.

The few non-American *Helenieae* are a bit of a puzzle, and need investigation, for which there is not space. *Jaumea* is perhaps the most interesting, and there are monotype genera in Angola and in SW. Cape Colony.

Turning now to Africa, where there are also some local tribes, *Arctotideae* may be noticed, for it is practically confined to S. Africa, except that one or two of its large members reach Abyssinia &c, and *Gundelia* has one species from Syria and Armenia to Persia and a genus *Cymbonotus* (now usually merged in *Arctotis*) with one species in Australia. In S. Africa itself, it consists of *Berkheya*, the leader, with 80 species, reaching tropical Africa also, *Arctotis* (65, do.), *Ursinia* (60, do.) and 18, 15, 5, 4, 4, 4, 4, 3, 2/2, 3/1. This little group is probably locally a direct descendant of *Senecio*, which has 222 species in S. Africa (old figures). *Gundelia* and *Cymbonotus* require genetic investigation to find their real relationships; being only of one species each, and so far away, close relationship to other *Arctotideae* seems improbable. But for practical purposes they should remain where they are.

Calenduleae is another little tribe of *Compositae* whose main stem, headed by *Osteospermum* (40 Cape to Natal &c) is S. African, but which has other members, structurally allied, far away, *Calendula*, a Mediterranean genus, (15 Canaries to Persia), *Dipterocome* (1 Persia), and *Eriachaenium* (1 Tierra del Fuego). Here again genetic investigation is needed, before one can accept them as genetically part of *Calenduleae*, though for practical purposes of identification they must remain in that tribe.

Othonninae, a subtribe of *Senecioneae*, is another group of *Compositae* with its headquarters in S. Africa, and headed there by *Othonna* (p. 177), followed by genera of sizes 35, 12, 3, 2, 2, 2 (note that there seem to be no ones), and here again there is one member, *Werneria*, with 35 species reaching the whole length of the Andes from Venezuela to Patagonia, which can not, so far as one can at present see, be fathered upon *Othonna*.

Another small subtribe of the *Senecioneae*, the *Liabinae*, headed by *Liabum*, which follows *Othonna* on p. 177, and has 60 species from MEXICO to ARGENTINA and in the WEST INDIES, may be noticed, for it indicates that probably both *Othonninae* and *Liabinae*, as well as perhaps *Werneria*, just mentioned, may have had *Senecio* itself as their immediate parent. There are only three other genera in the sub-tribe. *Allendea* (1 MEXICO) is probably a direct descendant of *Liabum* and there are two in AFRICA to be accounted for.

It is when we come to AUSTRALIA that we find so many *Compositae* that differ from those in the rest of the world. There are a great many endemic genera, giving the impression of a flora that was very early isolated, and had to make itself up by the production of new genera from those that already existed in the country. There are 43 endemic genera in *Inuleae* alone, 8 in *Astereae*, 4 in *Anthemideae*, and one each in *Arctotideae* (or possibly two), *Vernonieae*, and *Senecioneae*, corresponding roughly to the numbers of species in the genera that might be parents. All this goes to show very long isolation, which in the north at any rate is supposed to have lasted since the Eocene, and in the south was probably longer than it was in NEW ZEALAND, to judge by the much greater number of endemics that NEW ZEALAND has in common with JUAN FERNANDEZ than has AUSTRALIA. Few of the great Composite genera of the list on p. 176 reached AUSTRALIA at all, where none of the genera are very large compared to those of S. AFRICA and S. AMERICA. In fact only the following exceed 20 species in all (old figures):

Astereae	Olearia	63	*Inuleae*	Helichrysum	52
	Brachycome	36		Helipterum	30
Senecioneae	Senecio	28		Angianthus	22

Senecio and *Helichrysum* are the only leaders of tribes old enough, and so placed, as to reach AUSTRALIA before it was cut off, and to give rise to many endemics, and we have seen how numerous these are, especially in the *Inuleae*, which has many more species in its leaders. It is worth while to look at a list of the Australian *Inuleae*, grouped according to our rule of size and space:

Australian Inuleae, by size in Australia

Helichrysum	52	*Rutidosis*	7	*Stera*	3
Helipterum	30	Pluchea	6	*Acomis*	2
Angianthus	22	*Waitzea*	6	*Millotia*	2
Cassinia	13	Athrixia	5	Raoulia	2
Gnephosis	12	*Ixiolaena*	5	*Toxanthes*	2
Podolepis	12	Monenteles	5	*Ammobium*	1
Calocephalus	10	*Podotheca*	5	Antennaria	1
Gnaphalium	8	Craspedia	4	*Cephalipterum*	1
Leptorrhynchus	8	*Humea*	4	*Coleocoma*	1
Myriocephalus	8	*Chthonocephalus*	3	*Decazesia*	1
Blumea	7	*Ewartia*	3	*Eriochlamys*	1
Pterigeron	7	*Gnaphalodes*	3	*Gilruthia*	1

Gratwickia	1	*Schoenia*	1
Griffithia	1	*Scyphocoronis*	1
Ixodia	1	*Stuartina*	1
Nablonium	1	*Stylolepis*	1
Neotysonia	1	*Swinburnia*	1
Parantennaria	1	*Thespidium*	1
Phacellothrix	1	*Thiseltonia*	1
Pithocarpa	1	*Tysonia*	1
Pterygopappus	1		
Quinetia	1		

Endemics in italics, including all ones but Antennaria.

One can see the history of the *Inuleae* in AUSTRALIA written out for all to read. *Helichrysum* was the first arrival from a common source with S. AFRICA, where it is much more numerous than in AUSTRALIA, while *Helipterum* had a common source nearer to AUSTRALIA, where it is the more numerous. *Angianthus* was evidently a descendant of *Helichrysum*, and so probably were most of the many other endemics, which become more and more numerous as the number of possible parents increases, while when they are of one species only, their rate of growth is very slow, and so is their dispersal. Other wides, like *Gnaphalium*, *Blumea*, and *Pluchea*, have come into the country at a later period than the two leaders of *Inuleae*, and a very few of the endemics may possibly be their descendants; and of course *Angianthus*, and probably some others of the larger endemics, may also be parents in their turn. But the fact stands clearly out, that the flora of AUSTRALIA is largely local descendants of the few leaders, or nearly leaders, that managed to be there early. The same may be seen in CHILE or S. AFRICA.

Let us now look at the dry region of the eastern Mediterranean, which if one count the transition zone through AFGHANISTAN, reaches into northern INDIA. It contains a great many genera and species of *Compositae*, worked out with great care and skill in BOISSIER's flora (**13**). The first thing to strike one is the great prominence of the *Cynareae*. We have already seen that *Senecioneae* is a comparatively insignificant group, for the early mutations of *Senecio* seem largely to have given rise to the leaders of other tribes (p. 176). *Cichorieae* is fairly well represented in BOISSIER, but seems to have begun in a region of greater dampness, for it is better represented in western EUROPE. Let us therefore consider especially the *Cynareae*.

This is a tribe of moderate size, with one departure from geographical continuity, apart from the crossing of the ATLANTIC, *Centaurodendron* in JUAN FERNANDEZ. Laying it out by age size and area, we get :

	World	E. Medit.	General distrn.
1. Centaurea	650	254	Medit., Eur., As., Am.
2. Cousinia	250	136	E. Medit., As.
3. Cirsium	225	74	N. temp.
4. Saussurea	150	3	N. temp.
5. Echinops	80	42	Medit., Eur., As., Abyss.
6. Jurinea	60	44	Medit., C. Eur.
7. Serratula	40	16	N. palaeotemp.
8. Carduus	35	20	Medit., Eur., As.
9. Onopordon	25	14	Medit., Eur.
10. Carthamus	25	10	Medit., Abyss., NW. Ind.
11. Carlina	20	8	Medit., Eur., As.
12. Atractylis	20	6	Canaries to Japan
13. *Carduncellus*	20	1	Medit.
14. *Cynara*	12	3	Medit.
15. Tricholepis	12		Indomal.
16. Rhacoma	10		W. I., trop. S. Am. (Cent. p.p.)

and

at 6 or 5 spp.	*Staehelina*, *Xeranthemum*, *Zoegea*
4 spp.	Arctium, *Cardopatium*, *Galactites*
2 spp.	*Amphoricarpus*, *Centaurodendron*, *Crupina*, *Myopordon*, *Plagiobasis*, *Silybum*, *Thevenotia*,
1 sp.	*Acantholepis*, *Autrania*, *Carbenia*, *Chardinia*, *Cnicus*, *Cynaropsis*, *Giraldia*, *Goniocaulon*, Hemistepta, *Koechla*, *Microlonchoides*, *Polytaxis*, *Russowia*, Schmalhausenia, *Siebera*, *Tyrimnus*, *Wettsteinia*, *Xanthopappus*.

Endemic genera in italics.

When one sees a list like this, or that of the Australian *Inuleae* above, and similar ones may be made by scores, the notion of regarding endemics as relics becomes absurd. And as one goes up to the top of the list, among the larger genera, one sees that they are simply those that have had the time and the opportunity to spread beyond the limited area to which most people try to confine the use of the term endemic. *Centaurea*, directly or indirectly the parent of the rest, has had time to spread over a great part of the world, and *Rhacoma*, the W. Indian and S. American genus, is usually taken as part of *Centaurea*, which is also found there. The same is probably the case with *Centaurodendron*, for there are several *Centaureas* in CHILE.

This kind of distribution may be seen in many different places. Such work as we have been describing all goes to show that its size is one of the most important characters belonging to a genus. The first thing to be done in investigating a problem in distribution is to get the genera, and their known dispersal, all arranged in order of size, and in their taxonomic relationships. One can at once learn much from such a table, or find things that require investigation. We can see the effects of the laws of ASA and DDM, and see how greatly dispersal depends upon the past geological and climatic history of the world, and how important isolation has been in providing time and opportunity for so many countries to people themselves to a greater or less extent by the production of endemics, which of course belong as a rule to the same groups as the wides that have already reached the country and acquired a certain age there. Endemics are very obviously the young beginners, and are not relics of past vegetation except in rare cases.

Finally, let us call attention once more to the variation in size of tribes, described on p. 327, which requires explanation, especially when one looks at the figures of the genera in such a tribe as the *Helenieae*, with its small leader of 60 followed by over 100 genera with fewer species. We may also refer to p. 187-8, where we have pointed out the great difference between the six top tribes with 5050 species in their leaders and only 6006 in 482 followers, while the seven lowest tribes have 1060/5586 in 674 followers. One gathers an impression that mutation out of the tribe is not confined to *Senecio*. It is evident that all kinds of new problems are cropping up, and space will not permit of any further discussion on these lines. We have tried to show how a problem in distribution may be handled by the use of the new methods based upon the laws of ASA, and how one begins to feel that at last one is "getting somewhere", as one never did in the days of speculation.

18. *Development of a flora.* The flora that gradually forms in a country is of course a mixture, the result of migration from elsewhere, and will depend upon the sources and what they can supply in the time available, and also upon how long the country has been open to inflow. Except for a few Highland plants that came from further north, the bulk of the British flora has come from FRANCE and BELGIUM. The country itself only became available towards the end of the ice period, and was later cut off again by the formation of the CHANNEL. But in the intervening time, it received most of the larger (older) French genera. Taking the first two volumes of BONNIER's flora (14) we find

Genera	in France	in Britain	Not so	% of non-British
of 1 sp.	73	23	50	68
2-4	44	22	22	50
5-10	24	21	3	12.5
Over	11	11	0	0

There is no evidence here for any selection other than by age (size). Age has evidently been much the most powerful factor in determining the composition of the British flora, and probably of any other, for we do not find any results that conflict with that conception. Vital factors vary too much in location and intensity to have any marked general effects that can be easily measured. If evolution, as now seems to us fairly well proved, go downwards towards the species, the whole problem of dispersal is much simplified, and adaptation is not due to selection, but to simple heredity, though improvements, or rather perhaps complications, appear in it at times.

Following the laws of ASA, old families, genera, and species are thus to be found in most countries, and how many of the smaller ones also appear rests upon how long and how open the lines of communication remained by which they had to travel, and along which the older and larger would be the usual leaders. On p. 333 we have a list of the thirty largest genera in the world, and on p. 173 of the largest families. In BRITAIN, 13 of the genera, and 12 of the families down to 15 appear, and 8 more from 16 to 30. In the tiny group of the SEYCHELLES, only equal to the county of RUTLAND (the smallest in Britain), there are 12 of the 30 largest genera, 13 of the first 15, and 11 of the second families, so that these islands have 24 of the first 30 families represented. CEYLON has 18 of the genera, and NEW ZEALAND only 10.

As a genus or species expands its area, it usually increases its commonness in the country where it began. This is exactly parallel to what we found with the distribution of family names in BRITAIN, taking our facts from GUPPY (162), and it shows also in our (unpublished) results with the names in Canton VAUD (*cf. Evol.*, pp. 35-39, figures on 40). The dispersal of plants behaves like that of family names, where it is inconceivable that selection should come in except in individual and local cases. As GUPPY has said, selection could not produce an ordered world, for it is of necessity so local in its effects.

The flora of a given country will therefore depend mainly upon what plants reach its boundary in time to pass any obstacles that may there exist, and be able to enter the country. Whether, or how, they extend far into that country will depend upon what obstacles they may encounter, but on the whole the older and larger genera will lead the way, and in those the species that have the largest dispersal elsewhere will lead.

The subject of geographical botany, as we are dealing with it here, is thus largely concerned with the original time and place of birth of every species, genus, and family, *i. e.* with its evolution and subsequent dispersal. In the former, it is mainly subject to the law of DDM, and in the latter to the laws of ASA. The changes that go on at mutation will have a great resemblance to those that occur when one slightly turns a kaleidoscope—a slight rearrangement of the pieces of glass, which we take to represent the characters of the plant.

Everywhere it will be the oldest genera that on the whole are the first to arrive, and in the case of a young flora like that of BRITAIN all the genera and practically all the species will also be arrivals from abroad. In an older country there will be a few endemic or locally born species, in one older still there will be, as in CEYLON, a few endemic genera as well (CEYLON, as p. 109 shows, contains 25 endemic genera to 750 or more endemic species), and in a very long isolated island like AUSTRALIA there will only have been time for a comparatively few large genera to arrive, and the rest of the flora will be made up of local endemic genera, some with considerable numbers of species, as shown on p. 444.

The difference between one flora and another, within say a single continent, is mainly a difference in the smaller genera, and in the numbers of species of small dispersal within any genus. Obviously its formation will be very complicated, when one remembers all the possible differences in every possible factor, and in the plants upon which these factors are to act. But if one keep in memory that the principal ultimate factors which are obeyed to a large extent by everything in the process, are simply the laws of ASA and of DDM, one may get a very fair conception of what is likely to be found, in any country north of the ALPS, for instance.

An essential principle of taxonomic subdivision, in fact one without which subdivision would be practically impossible, is divergence, which on the whole seems to be less marked as time goes on, or perhaps it would be better to say, less obvious. The number of characters upon which kaleidoscopic mutation can work seems to increase continually with the formation of new ones, as does the number of possible chemical combinations with the formation of new ones, a phenomenon that shows clearly with the formation of carbon compounds. If only a limited number, or proportion, change at every mutation, the chance that one of the obvious characters, like 3-locular ovary, two cotyledons, extrorse anther, and so on, will be changed at any single mutation, becomes less and less at each, and we gradually come down to smaller more numerous and less obvious characters like those that mark sub-species. The chance of new generic mutations, for example, diminishes as time goes on, whereas if we go in the opposite direction, upward, it becomes greater and greater, so that there may even once have been a period when what we now call generic mutation was perhaps rather the rule than the exception, and there may perhaps even come a time when generic mutation will be very rare indeed, specific rarer, and sub-specific the rule.

This conception makes comparatively simple the explanation of why the great divisions of plants into the large groups like seaweeds, mosses, ferns, conifers, and even the flowering plants, all took place at very distant periods, while nothing comparable appears now, nor has done for millions of years. In the year *x* B. C. there were probably but few characters available upon which to ring the changes, while change was apparently always in some way divergent. If, as seems to be the usual rule, the new feature produced was always of similar type and rank to the old, like leaves alt./opp., simple/compound, and so on, it is clear that a mutation there might easily have the effect of producing what we should now consider as new family characters, or even higher like those of class or phylum. It is not being suggested here that such characters are only equal in value to other characters of the kind usually shown in mutations at the present time, but they are apparently equal as units in the mutation. The older a character, and the longer that it has been inherited, the more " important " it is, as we have been trying to make clear in this book. But these very old characters, when they were but few in number, would be much more liable to sudden change than they are now, when mixed with many others of different values, often of lesser importance.

But if we work evolution downwards like this, and look upon characters as handed down from ancestors in a " dominant " or " recessive " condition, we get a much simpler conception of the whole process of evolution and its meaning. The evolution of things suited to every set of conditions that may be met with has not been a selection of suitable characters when they happened to turn up, which would be a very complicated process, but has been by sudden mutation, producing a new form at once, suited by heredity to whatever the local conditions may be. But there is no necessary useful adaptation in any new structural character that may appear.

The new form will soon begin to spread, and to find its way slowly into the places best suited to its constitution. These at first will probably be within or very close to the range of the parent, but will ultimately tend to go beyond that, in directions that prove best suited to it. But it must not be forgotten that the parent will in general have a good start of the offspring, and that the latter is never likely to pass it in all directions.

A new family being thus created by an early mutation, its next step will be to mutate divergently, and as there are as yet but few characters with which to work, the divergences will tend to be well marked, and as it is unlikely that all will be lost in subsequent mutations, enough are likely to remain as important characters marking tribes &c. If development is thus dichotomous, each new form will get a good start of its immediate follower. If the latter was born, as is most probable, on the side of A where the greatest change of conditions had occurred, for example where the climate was drier, it would be most likely to spread upon the side away from A, in the direction AB rather than BA, and on that side it may ultimately overtake and pass the parent. Expansion will slow down as conditions change, but given *time* enough, which is reflected in the number of species in the genus, or of genera in the family, any place not cut off by an insurmountable barrier is ultimately attainable, so far as we can tell as yet. It must not be forgotten that early genera of a family may be able to pass a barrier which later becomes more formidable, like an arm of the sea which is just beginning to cut off an island. For somewhat similar reasons, the order of arrival in a country of genera or of families will rarely be in their exact order of age. Among other differences, they will start at different places.

The new offspring that are thus formed in the early days of a big family will probably be almost all genera, but as time goes on the rate of genus production will probably slacken, and more species will be produced, usually, as we have seen on pp. 427-8, each in its own sub-genus at first. And so on; as time passes, production will tend to become of lower rank, though it must not be forgotten that the importance of a character largely goes with its age. Sufficient work has not yet been done upon the incidence and the real value of characters for it to be safe to make any more categorical statement.

The whole process of evolution and dispersal of plants, the subject of this book, thus appears to be at bottom a simple matter, depending upon the results of the laws of DDM and ASA. But an extraordinary complication is brought into it by the operations of other natural laws that are governing the facts of geology, meteorology, and other sciences concerned with the formation of the world and of its covering, as they stand revealed to us at the present time, and as they have existed in the past. But as our figures seem to show, when handled by a master of statistical work like YULE (158), evolution is proceeding upon what, when plotted as a logarithmic curve, should evidently be a straight line that slopes downwards from left to right, but which is interfered with by all kinds of outside influences, which cause deviations this way and that from the straight line. But the dominant plan of evolution along the straight line holds all the time, and the deviations from it are only temporary, though they leave very often permanent traces of their operation. When evolution began, it was not already laid down that it should reach the Dicotyledons; it might equally well have resulted in something different. The laws of nature work blindly, but remorselessly. To take a single example, *Stachys palustris* did not come to BRITAIN for the ecological reason that there were there, or were going to be, reed-swamp and alder-willow communities, but because it was the most widely distributed *Stachys* in Europe, with a distribution right round the north temperate zone. The whole of this zone obviously does not contain these two communities, and the *Stachys*, in the course of its journeyings, has suited itself to various conditions of life, but found, when it met these communities, that they suited it unusually well, and especially perhaps in the conditions that rule in BRITAIN.

The things mainly missing in BRITAIN as compared with SPAIN are chiefly the small families and genera of the Spanish flora, whose rate of travel and of overcoming obstacles was too small to allow them to arrive in good time. Taking the first family to appear in opening the Spanish flora (157), the *Onagraceae*, we find *Epilobium*, with 17 species, with 4 endemics of which two reach FRANCE, to be well represented in BRITAIN, its four best dispersed species reaching 112, 111, 107, 103. Next comes *Circaea* with 3 species, none endemic, showing two in BRITAIN at 106, 36. *Chamaenerium*, the third genus, has two Spanish species, one an endemic in the SIERRA NEVADA in southern SPAIN, that do not appear in BRITAIN, while the other two genera are monotypes, and both water plants, one of them, *Ludwigia (Isnardia)* reaching BRITAIN in two vice-counties, the other *(Trapa)* not reaching it. The family was evidently mainly governed by the laws of ASA in determining what of its members should reach BRITAIN, but one cannot pick out the small genera that will do so, with any certainty.

We have gone into this matter in Chaps. II, III, IV, but it is perhaps worth while to call special attention to the certainty with which one may predict the arrival in BRITAIN of the larger genera. There are 112 genera of Dicots in SPAIN with more species than the average of 9.2. Of these we find no less than 105 in BRITAIN, the only missing ones being *Alyssum*, *Biscutella*, *Cistus*, *Delphinium*, *Phelipaea*, *Sideritis* and *Thymelaea*.

Development of a family thus seems to go in a downward direction under the laws of DDM and ASA, without the wholesale killing out that used to be demanded. Selection seems to have little to do with the dispersal of a family, except in a small and local way. The family grows by the law of DDM, spreads by the laws of ASA, and the spread is mainly hindered by the presence of every kind of barrier. It will be quick or slow according to the number and kind of the barriers, and the time that it takes to surmount them by gradual physiological adaptation to the changing conditions. Selection might act upon a whole species just at its start in life, but as soon as individuals are established in places at some distance apart, and more or less different in conditions, it will act almost entirely upon each individual separately, in fact in the way in which it acts in daily life, where it was, for example, one of the factors at the back of the great emigration to new countries that went on in the writer's youth, when he used daily to pass through the crowds leaving the LIVERPOOL landing stage, hoping to find some place where the competition was not quite so great, and travelling at the now almost incredible fare of 30/- each to NEW YORK, carrying their own food and bedding with them.

19. *Floral regions and zones of vegetation.* A vast amount of work has been devoted to mapping out the world into what are usually known as floral regions, distinguished from the more ecological " zones of vegetation " by showing marked predominance of certain families of plants, whereas the zones ignore taxonomic relations. There are six zones generally recognised, and divided generally by broad ecological similarities. They tend of course to pass gradually one into another where they meet : there is not usually an abrupt line of change. They are (1) the northern glacial zone, where one finds mainly low-growing somewhat xerophytic vegetation of an " alpine " type, with a short vegetative season, though often a very warm and dry one; (2) the mesophytic northern zone of cold winters lasting three to six months, a zone originally largely covered by forest, with heaths in the drier openings, and which passes gradually into (3) the northern zone of hot summers, where there is no serious winter, and where it is dry enough to require a xerophytic character in its plants once more. Next comes the (4) equatorial tropical zone, where it is again wet enough for the flora to be once more mesophytic, especially in the shade of the heavy forest that characterises so much of it, though there are also many open spaces, or savannahs, where the sun-exposure ensures xerophytism. Next follows (5) a southern zone that corresponds to (3), whilst the other two southern zones are generally counted as one, (6) a southern cold zone, for there is not enough land suitable to plants in the southern hemisphere to make it worth while dividing.

These zones, it will be seen, are zones determined by the climate, and we have now seen that one may find members of any family in any zone to which it has had *time* to acclimatise itself, a stipulation which reduces to a very few the fully cosmopolitan families. The range of a family is ultimately, so far as it has gone as yet, determined by its age, changes of climate simply acting as barriers that must be overcome; and only when the climate alters with great suddenness, as at the ANDES watershed, does it become a practically absolute barrier like the sea. With any gradualness in the conditions, new species may be born that suit the new climatic features. With sudden change, it may be impossible, or it may not—we cannot as yet say. But it is always at least possible that at a far back period the change was less; if for no other reason, because the mountains were often less high, so that passage would be more easy, and the difference between one side and the other perhaps less. This is shown in CEYLON, where there is a well known difference—fewer species, and more xerophytic, though mostly belonging to the same genera, on the drier eastern side of the mountain range. On the west side (wet zone) there is a wet season for almost all of the SW monsoon, with half or more of the NE as well, the dry season being a couple of months or so. On the east side (dry zone) the dry season lasts for half the year, so that a certain amount of xerophily is required. The flora does not contain the Malayan element so noticeable on the west side, nor do the climate and other conditions encourage the production of endemics, which are but few. The flora is in general a reduced copy of that in the dry part of MADRAS Presidency.

But the idea lying behind the conception of floral regions was that they should be marked by the possession of large numbers of certain families, which might be regarded as characteristic of them, as *Cruciferae*, *Compositae*, and *Umbelliferae* are of the MEDITERRANEAN region. But the larger a family, the more territory does it occupy (size and space) and only very small families are confined to a single region ; those just mentioned are cosmopolitan. The Mediterranean region is one of the best marked, consisting as it does of all the territory around that sea, up to the line of the mountains (ALPS, &c) in the north, the tropical forest to the south, and having the ATLANTIC on the west, and extending eastwards to PERSIA, and including AFGHANISTAN and BELUCHISTAN as transition countries. Yet even here there are gaps in the barriers, like the valley of the RHONE, or of the DANUBE, and the escape over towards Central ASIA. Only a very small family remains (for the present) within the region in which it is born; the great majority cross its frontier at some time or another. An old family, too, might find some of the barriers less awkward than they have since become.

Large families are thus of little use in marking out floral regions, and small ones are usually comparatively rare, so that it is a very difficult matter to trace them out, and as their definition seems to lead nowhere, it does not seem worth while to make the effort. The development and spread of the *Cynareae* (p. 445) makes a good illustration of what we have been discussing. When younger, it was evidently confined to the MEDITERRANEAN region, but its largest genera have now passed beyond its boundaries and have become common in various countries at greater and greater distances away, till *Centaurea*, the leader of all, is almost cosmopolitan. And this phenomenon is the general rule everywhere, distribution being a dynamic subject, and not a static, as was so long supposed.

There are quite a number of families which have their headquarters in the MEDITERRANEAN region, and this is a point that helps to give this region the status of a real floral region. For example, the *Cistaceae* show in the Old World genera of 80 (*Helianthemum*, the leader of the family, mainly MEDIT., but reaching much of western EUROPE, including BRITAIN, and also Central ASIA), 16, 12, and 7; and in AMERICA and the WEST INDIES genera of 30, 15, and 3. There must evidently have been land communication, unless the family is polyphyletic, and the American genera being smaller, it looks as if the family perhaps went westwards. The land junction may have been in the north, or it may have been what it may save space to call Wegenerian, somewhere in NORTH AFRICA.

Another small family also showing Mediterranean origin is the *Cneoraceae* (2 genera). *Cneorum* was old enough to reach the CANARIES, where it gave rise to the local endemic *Chamelea* (1 sp.). *Cynocrambaceae* has its only genus reaching from the CANARIES to Central ASIA, *Cynomoriaceae* is even smaller, with one species only, confined to part of the region. *Globulariaceae* shows *Globularia*, the leader, reaching beyond the MEDITERRANEAN region, as do most genera of that size if they were not born near the centre, and has one genus at either end, one in SOCOTRA, one in the CANARIES and AZORES. *Moringaceae* (1/4) probably began in the eastern MEDITERRANEAN, for it reaches INDIA. *Punicaceae* (1/2) has one species in the mountains from the BALKANS to the HIMALAYA, one in SOCOTRA, evidently cut off, by the drying of the country in between, from closer communication. *Resedaceae* is another definitely Mediterranean family, but there are some Californian species of *Oligomeris* which may owe their origin to polyphyly or to Wegenerism.

One may also find tribes belonging to the Mediterranean region, like the *Anchuseae* of *Boraginaceae*, or to other regions, like the *Semecarpeae* of *Anacardiaceae*, which are confined to INDOMALAYA. The *Scandicineae* of *Umbelliferae* is mainly Mediterranean, with its larger genera also going beyond the region, and it shows a very good hollow curve, headed by *Chaerophyllum* which reaches to 99 in BRITAIN, and *Caucalis*, also British, and below them 25, 15, 2/12, 10, 8, 3/4, 3/3, 2/2, 8/1. The small tribe *Echinophoreae (Umbelliferae)* is completely Mediterranean, with 8, 7, 2, 2/1.

A good instance of the improbability of selection acting to any serious extent upon one family as against another is obtained by comparing the two families *Cruciferae* and *Umbelliferae*, both of which show their maximum development in the Mediterranean region. Adding up the latest figures that I have collected for my *Dict.*, including the *Cruciferae* of NP/2 and the *Umbelliferae* of NP/1 with all the additions in Supplements to the *Index Kewensis*, we find

Found only in the Mediterranean region, and not going *beyond* its boundaries :

	Ones	Twos	Threes	Total
Crucif.	51	19	8	78
Umbell.	54	18	9	81
Found only in the rest of Asia :				
Crucif.	18	7	4	29
Umbell.	21	10	10	41
Found only in America and the West Indies :				
Crucif.	39	14	5	58
Umbell.	36	10	10	56

These are remarkable figures when one looks into them, and give no support to the notion that distribution is based on adaptation, or that the small genera are relics. There is but little in common between these families except *size*, yet they behave in the same way and in different places.

20. *The floras of mountains.* One is used to being told that the ascent of a high mountain will show, and much more rapidly, the phenomena that one would see in going toward the pole. This in outline is true enough, especially in botany. In SWITZERLAND, for example, one ascends through the region of deciduous trees corresponding to the forests of central EUROPE, to the region of conifers, like the forests of northern EUROPE, and higher yet to the open regions peopled by plants like those found in the far north. Other factors than climate, and very especially the laws of ASA, are also at work, and one must not press the analogy into too great detail. Age, by allowing the necessary time for adaptation to various climates, exposures, and soils, is the most important of all, for the barriers are liable to change so quickly in going upwards that they are much more formidable than on the plains, and upward movement of plants is made very slow indeed. But similar changes are in general taking place in the two directions, horizontal and vertical.

Age alone will enable us to predict a very great deal of what actual distribution will show us. There are perhaps, or probably, extreme limits beyond which a plant cannot go in acclimatising itself, or in producing new species better suited to any given spot, and probably acclimatisation becomes slower and slower as we approach these limits. A new species, however, born under different conditions from its parent, will probably be able to go further than the parent in the direction in which the conditions are changing. An alpine endemic will be able in general to go higher than its parent.

There is no doubt that the larger and older genera are, in their various species, suited to a great variety of conditions, and so are found covering very large areas of the world, but they owe this to their age, not to adaptation, which *time* allows them to acquire as they move. There are so many examples of unrelated water plants, for instance, that the habit of water life is evidently easy to acquire, and this is easily understood, once we have seen what mutation can do. The same formation of species suited to new conditions evidently takes place upon mountains.

A chain of high mountains is a very formidable barrier for a species to encounter, though it may be possible to go round, or to cross by some low pass. We must also remember that some mountains are so recent that species may have crossed when they were lower, or with a warmer climate. Mere steepness is a great obstacle, and a greater is the rapid change of climate as one ascends. When a range is parallel to the sea, like the ANDES, the GHATS, or the mountains of NORWAY, and crosswise to the wind, the difference of climate upon the two sides may be so great as to form a very formidable barrier, owing to the dryness of the descending wind on the far side. Even with the moderate height of the CEYLON hills (highest summit 8296 feet or 2528 m.), the climate and flora differ on the two sides, the SW. side of the mountain mass being in the wet zone, while when one crosses the watershed, one rapidly comes into the dry zone to the NE. It is thus of interest to find that the genera with species in both zones are on the whole twice as large in world size as those with species only in one, or are absolutely considerably older. In this connection one may note the behaviour of the Para rubber, *Hevea brasiliensis*, introduced from S. AMERICA in 1875. In the wet zone (at a low level) it flowers in February, in the dry in August, owing to the alternation of the seasons with the monsoons, which blow from SW. and NE. for roughly six months each way. It is clear from its behaviour that a plant can make the needful functional adjustments to local differences within a short time. Introduced weeds in CEYLON (p. 406) seem often to be a number of years before they spread.

The flora of a range of mountains will depend usually upon that of the plains below, except that some species may be carried along the range at high levels, above the trees, as is well shown in the ANDES. But from the plains the ascent will be long and arduous, by functional, and by occasional specific or even generic adjustment to the changing conditions, and one must not forget that the climate of the whole region may also be changing, and making the ascent more difficult, or more easy. Some plants may even be killed out in the plains, or driven north (*cf. Diapensia*, p. 66). In CEYLON one finds the buttercup and many other northern plants in the high mountains, with their nearest congeners in the high mountains of INDIA, hundreds of miles away.

If the slope of the lower part of the mountains be gentle, change in the flora will be slow, but sudden change of configuration is usually reflected in sudden ecological change.

In mid-Europe, the total flora usually shows distinct diminution in any case at say 1500 feet (500 m.), regardless of ecological relations. There has not yet been time enough for all the species to climb so high, and to overcome the barriers of climatic change, &c. The latter includes many features, like increasing insolation, lower temperature, greater moisture or less, more wind, shorter season, and so on; besides the probably increasing steepness. On the whole the conditions require more drought-resistance, as do those of the seabeach, and one actually finds a few plants like *Rhodomyrtus tomentosa* (CEYLON, MALAYA) or *Plantago maritima* (SCOTLAND) living in both places.

We have been accustomed to put down to the climate the differences in the composition of the mountain flora. But this no longer explains everything, and our new conception of evolution, which involves adaptation at birth to the conditions of a limited area, with *isolation from crossing* (due to the specific changes), makes a different outlook needful. Age, which gives time for readjustment to changing conditions, is extremely important. The latter fulfil the negative part of barriers, and are no longer to be regarded as causal. Given time enough any ordinary barrier may be overcome by gradual physiological adaptation to the new conditions, with an occasional specific change, but one which will not show, as a rule, any structural adaptation to the new conditions. Great energy and much speculation, for example, has been expended on the question of the lower heights reached by trees in BRITAIN compared to those of the Continent, and no notice has been taken of the fact that they are usually much younger of establishment.

Not only do the mountains owe their flora to ascent from below, but after a certain height endemic forms, species or genera, tend to appear, suited to the local conditions, and thus able to ascend to greater heights as a rule, without suffering so much strain, and the process may be repeated. It is perhaps thus that we may imagine a *Ranunculus* of the plains setting out upon the course which will ultimately lead to *R. glacialis* of the heights (p. 12).

Most of the mountain endemics tend to belong to the same genera and tribes as those of the plains, to which they are evidently related, while high up we may get endemics related to species of cooler climates, like *Ranunculus* in

Ceylon, and many more. These have travelled a long time ago, and become changed *en route*. It is in a high degree unlikely that they are relics of past vegetation, as used to be supposed. We have already said much upon the subject of supposed relicdom (see Index of *AA* and *Evol.*, and pp. 63, 69, &c, &c above). Every species, as far as we can see, is at first specially adapted only to the spot of its birth, and as its first spread must be very slow, the theory of specialisation and localisation, which must be true for every species at its birth, has grown up. But unless it is prevented by barriers that are quite impassable, the species will in time grow beyond them, becoming adapted to other places. Each individual plant must in general be adapted to the particular place in which it is growing. It will on the whole be the oldest and largest genera of the plains that will first reach the hills and begin to ascend, and whose offspring will ultimately reach the highest elevations. To take some examples, in Britain the mountains are not very high, and their flora is recent, so there are no endemics of note. Tansley (122) gives 88 mountain genera, of which no fewer than 21 are *Compositae* or *Gramineae*; 20 more belong to *Legum.*, *Caryo.*, *Eric.*, and *Scroph.*, and another 8 to *Ranunc.* and *Ros.*, so that 49 genera, or well over half, belong to this familiar list of large families, while 17 more belong to *Crucif.*, *Cyper.*, *Junc.*, *Lili.*, *Polygon.*, *Saxifr.*, and *Umbell.*, so that 75% of the genera occur in 15 families. The average size of a genus in Britain is 4.3, while that of a genus of the hills is 10.9. The selection of the mountain flora is obviously due mainly to the laws of ASA.

In Schröter's small flora of the Alps (113), the average world size of its 105 genera is 156 species, well above the average for western Europe. But above 3000 m. (10,000 feet), there are only 43 genera left, in 19 families :

Boraginaceae	1 genus	Gramineae	1	Rosaceae	2
Campanulaceae	2	Leguminosae	2	Salicaceae	1
Caryophyllaceae	4	Liliaceae	1	Saxifragac.	1
Compositae	8	Plantaginac.	1	Scrophular.	4
Cruciferae	6	Polygonaceae	1	Violaceae	1
Ericaceae	2	Primulaceae	3		
Gentianaceae	1	Ranunculaceae	1		

The average size of these genera is 217, or much above that of all the alpine genera (156). Families 1, 3, 4, 7, 10, 11, 19 of the list on p. 173 contain 24 of these genera, and only five families above do not appear in that list. If we arrange the families in parallel rows by size, we get

High Alps	1179	675	548	344	259	259	142	122	and 11 below
Alps	726	334	111	66	47	37	34	24	and 9 below

Again the Monocots are of interest. In the Alps as a whole they are only 14 genera, or 13.2% against 20% for the world, while in the High Alps they are only two (*Poa* and *Lloydia*) out of 43, or just over 4%. Again the facts indicate that they were rather late in arrival in Europe.

Chenevard's results on heights reached in Canton Ticino on the south side of the Alps are also of great interest (24).

At 3000 m. one finds

Genus	World size	Disp.	Genus	World size	Disp.
Agrostis	125	Cosmop.	Androsace	80	N. temp.
Poa (2 spp.)	200	Cosmop.	Artemisia	280	N. hemisphere
Carex	900	Cosmop.	Eritrichium	50	Temp.
			Veronica	250	Extra-trop.
Salix (2)	160	Cosmop.	Pedicularis	275	N. temp., S. Am.
Cardamine	130	Cosmop.	Phyteuma	45	Temp.
Draba (3)	270	Cosmop.	Gnaphalium	150	Cosmop.
Silene (2)	400	N. temp.	Achillea	115	N. temp.
Sedum	450	N. temp., S.Am.	Chrysanthemum	180	Eur., As, Afr.
Saxifraga (5)	325	N. temp., S.Am.			
Potentilla	300	Cosmop.	Average size of all, 236		
Sieversia	40	Temp., arct.			

A rather striking example of age and wide dispersal as the "selection agents". All but three are British.

Going down 500 m. we find 16 new Monocots (Dicots too numerous), including 10 genera with 18 species of grasses, 2/7 sedges, *Juncus* (3), *Luzula* (3), and *Chamaeorchis* and *Nigritella*, Scandinavian, but not British, orchids, 1 each.

Another 500 m. lower, the new Monocots are 6 grasses, 4 sedges, 10 *Liliaceae*, 3 orchids, *Triglochin* and *Crocus*. Again the supposition of late arrival of Monocots, other than grasses and sedges, is supported. Of the 44 Monocot genera above 2000 m., 33/52 are British, and 11/12 non-British; and Ticino is a long way off, and on the other side of the Alps.

Whymper (165) gives lists of the plants that he found in the High Andes, over 4000 m. Of 46 genera, only 14 are below 100 in world size. In order of size, those over 300 are :

Senecio
Astragalus
Solanum
Carex
Salvia
Gentiana
Cassia
Cyperus
Baccharis
Hypericum
Ranunculus
Geranium

Genera in italics not British

Far away as this region is, only 20 of the 46 genera are non-British, and the average world size is 269, or higher than in the High Alps. The bulk of a mountain flora is made up of the genera that were old enough to reach the base in time, but the bulk of their species are endemic. Another High Andes flora is that of Fries (160). He found 180 genera in the mountains of N. Argentina, of which 66 are British. At 4000 m. 22 out of 55 are British, but have more species than the other 33. It is also of interest to find that the Monocots have nearly a quarter of all the genera.

A rough list, made up from my *Dict.*, of all genera confined to mountains, or nearly so, shows that nearly half of them have one species only, and that the larger ones are in great ranges like the Himalaya or the Andes, where they can spread more easily above the tree level. As the Himalaya passes to the north into a great plateau (Tibet), which loses in height northwards, one will expect, and one finds, that a good many of the larger genera also occur in China and Japan, while in the Andes this is less marked, except at the south end. Most endemic genera occur in the large ranges, a fact difficult to explain upon an adaptational basis. The families with at least ten are *Asclep.*, *Borag.*, *Comp.*, *Cruc.*, *Eric.*, *Gram.*, *Legum.*, *Lili.*, *Orch.*, *Rubi.*, *Scroph.*, and *Umbel.*, obviously a list of very large families; they are in fact families 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 21, 23, of the list of the largest families, on p. 173.

Endemics localised to the mountains and the immediately surrounding mountainous country are roughly:

Himal. 92/1, 30/2, 17/3, 8/4, 8/5, 2/6, 2/7, 2/8, 1/10, 3/12, 1/15, 2/18, 2/20, 25, 30 Total 172, average 2.9
Andes 51/1, 19/2, 14/3, 10/4, 11/5, 2/6, 4/7, 7/8, 11/10, 4/12, 3/15, 4/20, 3/25, 40, 50, 60, 100, 115, 140 Total 149, average 7.9

In spite of the probably seriously incorrect figures, there can be little doubt that the small genera figure to a greater extent in the HIMALAYA than in the ANDES, a fact hardly to be explained upon any adaptational ground. The average size of a Himalayan genus is roughly 3, of an Andean 8, and 7 even if we leave out the two large orchids at the top. Plants reaching BOLIVIA only are nearly all ones.

This list also shows how much depends upon mere size and space. Of the 24 families that have at least five mountain endemics, 22 have them both in the HIMALAYA and the ANDES.

The fact that one finds endemic species at a higher level than endemic genera tempts one to suppose that the species may be a stage on the way to a genus. We have already considered this conception, and found it to be improbable, and as a rule there is little sign of any species from which the genus may have come.

It is fairly clear that the invasion and peopling of the mountains by plants has in general followed the same rules as that of the plains, but in the vertical, not the horizontal, direction, which has made the process much slower by increasing the difficulty of barriers, but encouraging the formation of endemics.

Structurally there are few special characters about mountain plants, and all of them, like dwarfness, reduction of leaf-surface, crowding of leaves, thick cuticle, hairiness, etc., may be found in xerophytic plants of the plains.

21. *The floras of islands.* Islands are very numerous, and vary in size to whatever one may consider a maximum. After AUSTRALIA, important islands are NEW GUINEA (330,000 sq. m.), MADAGASCAR (230,000), NEW ZEALAND (104,000), GREAT BRITAIN (88,000), JAVA (44,000), CUBA (do), CEYLON (25,000), the HAWAIIANS (6,500, but very isolated, with a very remarkable flora), JAMAICA (4450), the SEYCHELLES (156). The total area, without AUSTRALIA,

is perhaps about two million square miles, and evidently most of them must at some time have been part of the mainland.

Even though the separation be small, the flora differs from that of the mainland, for the sea acts as a barrier, and prevents younger and smaller things from arriving. Palmgren (**100**) has shown that the smaller an island is, in an archipelago, the fewer the species. Sea makes the most formidable barrier, for it is not open to conquest by gradual adaptation. Here Ceylon is of special interest, for botanically it is two islands, a dry to the north and east, separated from dry South India by a narrow and shallow strait, and a wet to the southwest, cut off by a broad stretch of deep water. Dry Ceylon shows the flora of dry India, reduced in size, and with few endemics, while wet (and mountainous) Ceylon shows more of some things than wet India, less of others, and has many endemics in a richer flora.

The effects of the breaking off of islands, and the proof of former land connection, may be well seen in such a flora as that of Stewart Island, cut off from the south end of the South Island of New Zealand by 16 miles of shallow water (**140**, **33** p. 23).

Genera locally	N. Z. proper	Stewart	%	Not in Stewart
of 1 sp.	155	32	20%	123
2	54	22	40	32
3	29	20	68	9
4-5	29	23	79	6
6-10	36	32	88	4
11-20	16	15	93	1
Over	10	10	100%	—
	329	154		
Average size	3.8 spp.	7.6 spp.		

More than half the Stewart flora belongs to genera that have at least four species each in New Zealand proper, and that range from end to end of it.

If we take the Chatham Is., 300 m. east of New Zealand, we get the following result (*cf.* also pp. 17-18).

5 wides have ranges in New Zealand of 60, 180, 440, 570, 580 miles
3 wides have ranges between 761 & 880
9 wides have ranges between 881 & 1000
49 wides have ranges between 1001 & 1080

This dropping out in going to islands of the smaller and less distributed genera of the mainland destroys the value of the current supposition that distribution depends mainly on degree of adaptation, other than in the temporary ecological communities that are continually forming and changing. This is also shown by the remarkable agreement between the floras of the SCILLY Is. in the warmer southwest of BRITAIN, the SHETLAND Is. in the colder north of SCOTLAND, and CLARE I. in the windy and rainy west of IRELAND, islands which differ very much in climatic and geological characters (and *cf. AA*, p. 70). All these results, and a great number of those given above, violently contradict the explanation of these things in terms of natural selection. Any local adaptation, enough for survival, must have been brought to an island with the species from some part of the mainland close by, where the local adaptation would be essentially the same.

The flora of an island thus depends chiefly upon the age of its members, which are on the whole the older of those of the relative mainland. In this connection, the following quotation is of interest. With regard to a review of THWAITES' *Flora of Ceylon*, and GRISEBACH's *West Indies*, DARWIN, in a letter to HOOKER in 1865 (30, I, p. 260) says: « more than half the flowering plants belong to eleven orders (families) in the case of the WEST INDIES, and to ten in that of CEYLON, while with but one exception the Ceylon orders are the same as the West Indian. How extremely curious is the fact of similarity of orders in the tropics. I feel a conviction that it is somehow connected with glacial destruction, but I cannot " wriggle " comfortably at all upon the subject. " We have elsewhere explained this similarity as due to the fact that these island families are all very old, and the largest on the whole the oldest. We have already seen that the British *Cruciferae* are simply the larger or older of those in FRANCE (p. 51), and if we take the *Araceae* as an illustration for the WEST INDIES, and divide the mainland genera into two lots, those that do, and do not, reach the WEST INDIES, we find their sizes to be

W. I. 500, 240, 40, 30, 30, 18, 15, 2, 1, 1 Average 87
Not 100, 80, 30, 25, 12, 12, 12, 10, 3/6, 5, 2/3, 3/2
16/1 Average 10

Other families show the same, and it is clear that the island flora was mainly selected by size (age) across a land union. The wides that reach the islands belong on the whole to larger families and genera the further out that the islands lie, and at the same time, endemics are more common, a fact that does not fit with the conception that they are relics.

The greater youth of the endemics, even on such isolated islands as the HAWAIIANS, is also shown by comparing sizes of wide and endemic genera. Of the 258 species there in Dicot wide genera, only 105 are confined to one island, and the average dispersal is to 2.6 islands, while of the 227 in Dicot endemic genera, 126 are confined to one island, and the average dispersal is only 2.

The following quotations from HOOKER and from GUPPY are of interest as showing how little importance is to be attached to adaptation in this connection and in the long run : " Of the *Compositae* common to LORD AUCKLAND'S group, FUEGIA, and KERGUELEN'S Land, none have any pappus at all ! Of the many species with pappus, none are common to two." (*AA*, p. 55.) " *Phyllanthus* shows by its distribution in the Pacific that dry-fruited *Euphorbiaceae* are as widely distributed, and as much at home, as the fleshy-fruited ones (Pacif., p. 325)."

In the HAWAIIANS the proportion of endemic genera is 7% for families of one genus, 13% for those of two or three, 18% for four or five, and 30% for more. In CEYLON the proportion of endemic species varies from 12% for genera with one to 40% for genera with more than five. About 150 families, rather less than half the total, have no island endemics, but are definitely much the smaller families, with only a few, like the *Betulaceae*, *Capparidaceae*, or *Chenopodiaceae*, of any serious importance.

So common upon islands are genera with all (usually only one) of their species endemic, that one gathers a definite suggestion that with mere passage of time, and isolation, a species may become changed (*cf.* HARLAND, p. 62, *Evol.*).

It is not improbable that such changes as those in the species of *Stratiotes* observed by Miss CHANDLER in different geological horizons, come in here (*AA*, p. 143).

Endemics, as we have seen, mark invasions, and there are many instances among the islands. Thus the southern invasion of NEW ZEALAND (fig. at p. 407) seems to point to a southern source upon the supposed ANTARCTIC continent, and if this be so, there were probably connections to JUAN FERNANDEZ, 400 m. off the coast of CHILE, and to NEW ZEALAND, &c. Of the 15 genera that show endemics in JUAN FERNANDEZ (*Cardamine*, *Carex*, *Chenopodium*, *Cladium*, *Coprosma*, *Drimys*, *Gunnera*, *Libertia*, *Loranthus*, *Pernettya*, *Plantago*, *Trisetum*, *Uncinia*, *Urtica*, *Wahlenbergia*, all show endemics in NEW ZEALAND also, but only *Cardamine*, *Carex*, *Coprosma*, *Gunnera*, *Plantago*, and *Wahlenbergia* in TASMANIA. There is great probability that there was connection by way of the south between all these southern lands.

There are interesting things to be made out about islands by a study of the behaviour of individual families. Let us begin with the very ancient family of the *Rubiaceae*, giving the usual list.

Rubiaceae in order of size in the world

Genus	World spp.	Tribe		Seychelles endc. spp.	Madag. endc. gen
1. Psychotria	500	Heading II. 5	*Psychotrieae*	S (5)	M (2)
2. Galium	250	Heading II. 11	*Galieae*	—	—
3. Oldenlandia	225	Heading I. 2	*Oldenlandieae*	S (1)	M (2)
4. Ixora	200	Heading II. 4	*Ixoreae*	S (1)	M (2)
5. Uragoga	150	2nd Psych.		—	—
6. Randia	125	Heading I. 8	*Gardenieae*	S (1)	M (4)
7. Palicourea	120	3rd Psych.		—	—
8. Borreria	100	Heading II. 10	*Spermacoceae*	—	M (1)
9. Canthium*	100	Heading II. 1	*Vanguerieae*	S (2)	M (2)
10. Faramea	100	Heading II. 8	*Coussareae*	—	—
11. Gardenia	100	2nd Garden.		S (1)	—
12. Lasianthus	100	4th Psych.		—	—
13. Pavetta	100	2nd Ixor.		—	—
14. Rondeletia	100	Heading I. 3	*Rondeletieae*	—	—
15. Rudgea	100	5th Psych.		—	—

*Plectronia.

I, II, are Sub-families *Cinchonoideae*, *Coffeoideae*.

There are ten other heads of tribes below these, but they only contain 375 species among them, against 1700 for the first nine. The 19 heads contain 2075 species out of the

6070 in the family. Many things can be learnt from the study of floras or families made up like this by sizes, and the *Rubiaceae* is one of the most interesting families that the writer has studied, but space will not allow of any treatment.

A very interesting fact about the *Rubiaceae*, which goes to show their great age, is their commonness upon the islands of the warm countries to which they are mainly confined. This shows that they must have been very early upon the ground, so that when an island was detached, they formed a part of its flora, and would often be old enough themselves to give rise to endemics there. They show the third largest number of island endemics of any family (*Orchid.* 166, *Comp.* 155, *Rubi.* 147, *Legum.* 109, *Palm.* 100). This goes to show that they go back in the tropics to an extremely ancient date, if indeed they are not the oldest tropical family of all, for the orchids and the composites have means of dispersal that would help them better across a narrow strait. The breaking off of an island makes a good absolute date for any particular neighbourhood.

If now we look at the flora of the SEYCHELLES, we soon see (**163**) that a great deal of it is made up of the common tropical weeds, but the endemics, marking the older portion of it, are of great interest. There are 71 endemic species, 51 of them Dicots, and no fewer than 14 endemic genera, on a small area of 156 sq. m., six Dicots, six palms, and one each in *Araceae* and *Triuridaceae*, so that here the Monocots are the more numerous in endemic genera, though not in endemic species. The two most important families for endemics are the *Rubiaceae* and the *Palmaceae*, about which we must say a little. In the former there are nine genera with, and only four without, endemics. But if we make a list of the SEYCHELLES *Rubiaceae* by size and rank (cf. pp. 424-5, 443-6) we discover some very interesting facts :

Genus	Spp. in world	Tribe	Spp. in Seych.		Endemics	
Psychotria	500	Leader of Family and of *Psychotrieae*	5		5	
Oldenlandia	225	Leader of *Oldenlandieae*	2		1	
Ixora	200	Leader of *Ixoreae*	3	15	1	10
Randia	125	Leader of *Gardenieae*	2		1	
Canthium	100	Leader of *Vanguerieae*	3		2	

Genus	Spp. in world	Tribe	Spp. in Seych.		Endemics	
Guettarda	60	Leader of *Guettardeae*	1	8	—	4
Morinda	50	Leader of *Morindeae*	1		—	
Gardenia	100	2nd Garden.	1		1	
Tarenna	30	4th Garden.	1		1	
Vangueria	40	2nd Vanguer.	1		—	
Craterispermum	10	4th Vanguer.	1		1	
Timonius	30	2nd Guettard.	1		1	
Amaracarpus	7	low in Psychotr.	1		—	

These are all the *Rubiaceae* of the Seychelles, and they form a most remarkable list, which alone is almost enough to prove our contention of downward evolution. It is absolutely inconceivable that such a choice should have been made by any kind of accident, or by sea carriage. All but the last species, which is a native of the Malay Archipelago and was evidently accidentally brought to the Seychelles, are leaders in seven cases and the rest are not lower than fourth in their tribes; and the largest number of species, all endemic, belongs to the leader of the whole family, and therefore the oldest genus in it. They must have come to the Seychelles in very early days, when land carriage was still possible; and they must have come from some early home of the family, where the leading tribes were well represented. In the list on p. 468 the leaders of tribes 1, 3, 4, 6, and 9 are all in the Seychelles. *Galieae*, the second tribe, is at least wrongly placed so high, and we imagine may not even be a member of *Rubiaceae*.

Incidentally, *Guettarda*, one of the leaders, is represented by the common coast plant of the Indian Ocean, *G. speciosa*, and it is very noticeable how many small genera of coast plants have been evolved in the *Rubiaceae*, for the simple reason, apparently, that the family reached the coast long ago, in good time to make the necessary adaptations to coast life. In the Malayan region, they have been early enough to make myrmecophilous adaptations in a number of smaller genera.

Good evidence for these conceptions is also given by the number of other leaders, or nearly leaders, that also show endemism. These, including one second and two thirds, and *Vernonia*, head of the tropical tribe of *Compositae*, amount to 16, *Pandanus* with 4 species, *Mimusops* with 3, all species endemic, three twos, and the rest ones. It is noteworthy that among the Seychelles genera one finds 12 of the largest in the world (p. 448), almost the same proportion as in Britain, but on an area of only 156 sq. miles (40,335 ha.), equal to Rutland, the smallest county in Britain. Further confirmatory evidence may be obtained from the *Araliaceae* and the *Sapotaceae*, both admittedly old families.

Other good evidence may be derived from the flora of Madagascar, where the *Rubiaceae* show many endemic *genera* in most of the tribes found in the Seychelles.

Psychotrieae	endemic	genera of	2, 1
Oldenlandieae	—	—	1, 1
Ixoreae	—	—	1, 1, 1
Gardenieae	—	—	3, 1, 2, 1, 1, 1
Spermacoceae	—	—	1
Vanguerieae	—	—	1
Paederieae	—	—	2
Cinchoneae	—	—	1
Naucleae	—	—	1
Mussaendeae	—	—	1, 1

It is definitely noticeable in both the Seychelles and Madagascar how far ahead of the *Psychotrieae* the *Gardenieae* seem to have gone. The latter have an immensely long tail of small genera following a rather small head, which may be due to an extra capacity for production of new genera, but which is rather puzzling.

We have now seen that *Rubiaceae*, with which probably go its old and large allies like *Araliaceae*, *Compositae*, and *Campanulaceae*, show signs of being among the very first families to appear in the tropical and sub-tropical countries. It showed clearly in the Seychelles, and it is worth while to look at some of the other islands, beginning with the Bahamas, which are among the younger. They contain the following *Rubiaceae* (x, a small genus):

	Spp.	Endc.			Other genera
Psychotria	3	—	Leader of	*Psychotrieae*	
Galium	1	—	Leader of	*Galieae*	
Oldenlandia	1	—	Leader of	*Oldenlandieae*	
Randia	1	—	Leader of	*Gardenieae*	3x
Borreria	8	6	Leader of	*Spermacoceae*	2x
Guettarda	6	3	Leader of	*Guettardeae*	3,
Morinda	1	—	Leader of	*Morindeae*	
Chiococca	2	—	Leader of	*Chiococceae*	2, 2, 5
Exostema	1	—	2nd	*Cinchoneae*	
Strumpfia	1	1	small	*Ixoreae* (W. I. endemic)	
Rachicallis	1	1	small	*Rondeletieae* (do)	

Another remarkable list, which fully supports that of the SEYCHELLES. CEYLON, an island with more endemism, shows

	Spp.	Endc.			Other genera
Psychotria	13	9	Leader of	*Psychotrieae*	4, 9, 5x
Galium	1	—	Leader of	*Galieae*	4
Oldenlandia	32	18	Leader of	*Oldenlandieae*	3, 2x
Ixora	5	2	Leader of	*Ixoreae*	2, 3
Randia	5	1	Leader of	*Gardenieae*	2, 3, 5, 4x
Borreria	3	—	Leader of	*Spermacoceae*	x
Canthium	7	5	Leader of	*Vanguerieae*	7
Guettarda	1	—	Leader of	*Guettardeae*	2,x
Mussaenda	1	—	Leader of	*Mussaendeae*	2, 4, 2x
Morinda	3	—	Leader of	*Morindeae*	x
Nauclea	1	1	Leader of	*Naucleae*	2, 3, 4, 5, 8
Wendlandia	1	—	2nd	*Rondeletieae*	—

Twelve tribes are thus represented, eleven by their leaders; nearly all have some smaller ones also. Note that some have consecutive numbers, like *Cichorieae* in BRITAIN, indicating that they were fairly near to their source. Let us now try the GALAPAGOS.

	Spp.	Endc.		Others
Psychotria	2	2	Leader of *Psychotrieae*	—
Borreria	14	14	Leader of *Spermacoceae*	2, x
Chiococca	1	—	Leader of *Chiococceae*	
Relbunium	1	—	3rd *Galieae*	

NEW ZEALAND shows (leaders only) :

Galium	2	2	Leader of *Galieae*	3
Coprosma	39	39	Leader of *Anthospermeae*	4

Let us finally take the HAWAIIAN Is., which have been isolated for an immensely long time.

Genus	Spp.	Endc.		Tribe
Psychotria	2	2	Leader of	*Psychotrieae*
Straussia	5	5	Endc. genus	*Psychotrieae*
Kadua	16	16	Endc. genus	*Oldenlandieae*
Gardenia	2	2	2nd	*Gardenieae*
Canthium	1	—	Leader of	*Vanguerieae*
Gouldia	5	5	Endc. genus	*Mussaendeae*
Bobea	5	5	Endc. genus	*Guettardeae*
Morinda	1	—	Leader of	*Morindeae*
Coprosma	9	9	Leader of	*Anthospermeae*
Nertera	1	—	4th	Anthosp.

Eight different tribes are represented, in these ten genera, and four of them by their leaders, one by its second genus, and the other three by endemic genera of some size. Nearly all the species of all the genera are endemic, a phenomenon which is so frequent and so widespread that it requires an explanation. No efforts of the writer have educed any general law that seems to direct or control it, and it looks as if something genetical were probably its explanation. We shall refer to this again below, under "Swamping".

Turning to the Monocots of the SEYCHELLES, great interest centres in the palms, where all six endemic genera have one species each. At first one wonders whether one has at last come across real relics in a warm country, but this notion is soon destroyed when one finds that five of them belong to the largest tribe of palms, *Ceroxyloideae-Areceae*. Let us begin with our usual list :

Palmaceae by order of size in the world

1.	Calamus	325	Heading	*Lepidocaryoid-Metroxyleae-Calaminae*
2.	Bactris	100	Heading	*Ceroxyloid.-Cocoeae-Bactridinae*
3.	Geonoma	85	Heading	*Ceroxyloid.-Areceae-Geonominae*
4.	Daemonorops	75	2nd	Lepido-Metrox-Calamin.
5.	Cocos	60	Heading	*Ceroxyloid.-Cocoeae-Attaleinae*
6.	Chamaedorea	60	Heading	*Ceroxyloid.-Areceae-Moreneinae*

About 46% of the genera are endemic to islands in the warmer parts of the world, and about three quarters of these belong to the largest tribe of all, the *Areceae*. Five of the six endemic genera of the SEYCHELLES belong to this tribe, so that it is evident that they are the descendants of some early arrival(s) of it, though we cannot as yet tell what was the parent. The tribe in question is very widespread, with endemics on at least the following islands: AUSTRALIA, BONINS, BORNEO, CAROLINES, CEYLON, COMOROS, CUBA, FIJI, LORD HOWE, MADAGASCAR, MALAY ARCHIPELAGO, MASCARENES, MOLUCCAS, NEW CALEDONIA, NEW GUINEA, NEW HEBRIDES, NORFOLK, PELEWS, PORTO RICO, SAMOA, SEYCHELLES, &c. The group must have been very old to reach so many, even if some could be carried by water like the coconut, which belongs to a different group.

The sixth palm endemic to the SEYCHELLES is the well known double coconut or coco de mer, *Lodoicea*, now flowering, I am told, in the CEYLON Botanic Gardens. It is a member of the small tribe *Borasseae*, to which belongs the well-known Palmyra palm of SOUTH INDIA and CEYLON.

The distribution of the endemics in the SEYCHELLES is as follows

In genera that are leaders of their families	23
locally endemic (one a leader)	14
In other genera	48
	85

Ten of these last are in small genera of MADAGASCAR, the MASCARENES, or E. AFRICA. A good many others are heads of tribes.

There are a number of unusual phenomena in islands that are worth mention, but all need much more investigation, for which the writer, at nearly 80, is growing too old.

A very remarkable feature about the GALAPAGOS is their number of *Amarantaceae*, without, curiously enough, having any endemic genera. All three tribes are represented, while the genera are (1) *Alternanthera*, the leader, with 3 species, all endemic, (2) *Amaranthus* (6, 2 endemic), (3) *Froelichia* (4, all endc.), *Iresine* (1,? endc.), *Pleuropetalum* (1 endc.), *Telanthera* (now looked upon as *Alternanthera* pp., 11, 9 endc.). One endemic *Telanthera* reaches ten islands, one endemic *Amaranthus* seven; ten endemics are confined to one island each.

If one look at a Mediterranean island like SARDINIA (6), one may see other points brought out by taking all the endemics. *Iberis* heads the list of Dicots, with one endemic only, or an endemic percentage of 100%. It is followed by 31 others, of which 19 are *Sympetalae*, all above the average of representation of 15.4%. Below that there are 6 *Archichlamydeae* and 5 *Sympetalae*, so that the representation of the latter is much above its proportion in the world, suggesting that in the early days of the European flora, at least so far as SARDINIA is concerned, the *Sympetalae* were well in front. They have a considerable preponderance, both in number and position, which one would not expect from their much smaller numbers. On the other hand, only five Monocots enter the list at all, and then at a much lower percentage of endemism. Three are grasses, *Trisetum*, the top Monocot at 33% endemism, *Poa*, and *Festuca*, the others *Asphodelus* and *Allium*, both *Liliaceae*, and the percentage of endemism for the whole is only 11%. One gets always an impression that the Dicots are older in EUROPE than the Monocots and occasionally one that the *Sympetalae* are older than the *Archichlamydeae*, confirming the notion one gets that perhaps the *Rubiaceae* are the oldest family of the Dicots, at any rate in the tropics.

In JUAN FERNANDEZ, there are 72 genera of one species only, of which 31 show endemism, 41 not. Of the former 6 are British, of the latter 19, giving the impression that the British things were mostly too young to have formed endemics in the time available. Those with endemics are *Apium*, *Berberis*, *Carex*, *Cladium*, *Chenopodium*, and *Plantago*, while in those without are many familiar genera, about a third of which occur in NEW ZEALAND, making one wonder, as do a good many of the things that we have brought up in this chapter, whether there was ever any very open road from north to south in very early times. But we must leave it at that, for the evidence is very slight as yet.

A genus with only one species rarely occurs on more than one island, so that an archipelago does not often show a high proportion of ones. If one make a rough comparison of the MALAY ARCHIPELAGO with some of its constituent islands, one gets

Size of genus Islands	1	2	3	4	5	6	7	8	9	10	More	
Bali, near Java	1	—	—	—	—	—	—	—	—	—	—	
Timor	8	—	—	—	—	—	—	—	—	—	—	
Java	50	3	—	—	—	—	—	—	—	—	—	—
Borneo	61	7	1	3	—	1	—	—	—	—	—	—
New Guinea	125	23	14	5	1	2	—	1	—	2	15, 18	
Archipelago	8	15	15	5	4	2	3	1	—	5	12,3/15, 50	

The same thing is shown in the WEST INDIES. As we have been contending for a lifetime, the ones are evidently the youngest genera, and the more genera that reach the islands, the greater the number of endemics. In the case of such very widely separated islands as the Hawaiians, there are many large endemic genera; one finds there about 227 species in 47 genera (62), making the high average of about 5. Even in MADAGASCAR, with its much larger flora, and many endemic genera (more parents) there are not so many very large endemic genera, but a great number of small ones; old figures give 191/1, 37/2, 10/3, and so on to 12, 18, 20.

So many conclusions have been based upon island floras that it is important to get as clear an understanding as one may. To take a simple case, a tertiary flora is supposed to have survived in the CANARIES &c, because the island conditions were more favourable to it, when it was killed out by the cold in EUROPE. There is nothing against this so long as one remembers that the killing out was due to a great change for the worse in the European conditions, a change which would have killed out most things. There is no evidence that the tertiary things were less efficient, except that being largely of tree nature, their growth, reproduction, and movement were not well suited to the new conditions, when migration was required in some cases. Nor is there evidence that they were *driven* to the islands as a refuge, the islands being then continuous with the mainland. They must have been there before the breakage of communications, and they occur upon many more of the islands than do the Mediterranean things that came later (51) and must therefore be older than these. There is no evidence that they are dying out in the islands, other than the fact that a woody flora like this is usually at a serious disadvantage when cultivation begins, especially with goats or other destructive animals. Though the species of this tertiary flora are now endemic, some of them may have been found upon the mainland in former days. It is by no means impossible too that frequent small mutations may go on in any species, which may in time add up to specific value. Darwinism of course had to assume that very local things had at one time been more widely dispersed, so that these locals in the islands would be relics. The idea of relicdom for endemics like the CANARY tertiaries is largely based upon the endemic genera. But the islands are very old as such, so that there has probably been plenty of time for the genera to grow to their present size, and all the endemics are not tertiary, while they often belong to the same tribes as other genera.

In islands that are very far out, like the HAWAIIANS, the flora may have come from different directions, and at different times; though even in the geologically recent BRITISH Is., one finds species, chiefly in the hills, that speak of a northern, rather than of a southern origin. They are not, however, numerous enough to upset any of the figures that show that the general source was southern. In some cases one can trace more than one invasion. In NEW ZEALAND, for example, there seems to have been an invasion from the north when the climate was getting warmer in the south, and one from the south when the reverse was happening. Each was accompanied by formation of endemics (plates at p. 407-8) and if one plan the rate at which wides and endemics fall off in going one way or the other, one can see a much more rapid decrease in the southern invasion. If we note the numbers that occur in each zone of the islands of equal length from north to south, we get :

Direction of Invasion, from						Cook's Strait						Foveaux Strait
North. Wides	10	13	11	12	10		8	8	7	6	5	3
Endcs	84	89	87	78	64		62	50	40	35	32	14
South. Wides	83	87	100	97	101		105	104	102	100	91	51
Endcs												
to N. Z. & Is.	16	17	19	21	24		27	28	28	29	29	18
to N. Z. only	33	55	76	95	115		189	205	220	228	166	46

The last column is mostly the plants of Stewart I. It will be noticed that there is no serious difference between the numbers on either side of Cook's Strait in the first four rows. All these plants, including the endemics that reached the Chathams or other outlying islands (fourth row) were in general in time to pass at the centre of New Zealand before the formation of any serious width of strait there, while the last row, the endemics confined to New Zealand, were often so young that they were unable to pass. All the rows, but especially the last, drop markedly at Foveaux Strait in the far south.

It is clear from what we have seen in this section that the floras of islands will lend very useful assistance in determining the relative ages of families in their neighbourhood, and in other points upon which we much need information.

22. *Endemic representation only, in non-endemic genera (Swamping).* This subject, known as swamping 25 years ago, a name proposed by Prof. Sinnott, and a phenomenon described in *AA*, pp. 95-98, was a great bone of contention at the time of publication of *AA* (1922), and my replies to critics are there given. It still awaits a satisfactory explanation, which might throw much light upon evolution and dispersal. The writer has a portfolio some inches thick containing work that he has done in trying to find some general laws running through it, but he has had no success. It seems to occur in islands or on the mainland, on mountains or on the plains, in such small genera as are common in Ceylon, or in such large as are frequent in the Hawaiians, like *Senecio* or *Ranunculus*, but nowhere, so far as he can trace, with any definite rules behind it.

Many different explanations have been proposed. The " swamped " genera were often supposed to be relics dying out, an idea that would hardly fit *Ranunculus* or *Senecio*, or local adaptations, an explanation that does not hold water very well in view of the little evidence in favour of it, except that for such adaptation in the newly born species. These genera behave like any others, as a very little study of such a list as that of the CEYLON flora on p. 109 will show. One of the characteristic features of the genera with mixed wides and endemics is the progression upwards from many genera with WE (one wide, one endemic) through many fewer with WEE to genera with still more Es. The swamped genera show exactly the same, without any wides.

One is tempted to think that age has something to do with it, till one finds that in CEYLON a great many of the genera are the comparatively small endemics, not of CEYLON but of INDOMALAYA whereas in the HAWAIIANS they are such large genera as *Ranunculus*, *Viola*, *Silene*, *Senecio*. The author, though with but little evidence to go upon, is inclined to suppose that swamping is due to rare *arrival* in the country where it shows, so that there will be very little likelihood of crossing, and it may be that as HARLAND suggests, long continued gene separation may lead to gene change, which in its turn might involve mutation. In the present state of our knowledge, there seems nothing to be gained by bringing forward the great amount of work that the writer has done in his (fruitless) attempts to supply an explanation.

23. *Fossils* have been asked to bear a greater load of evidence in favour of " Darwinism " than it is reasonable to demand. Now that we know that the characters of tribes and subtribes come by divergent mutation from those of the head of the family, it is evident that a fossil that shows them must probably be a more recent growth than the original head, so that it is not safe to base evidence upon it.

Imperfection of the geological record is often brought forward as an explanation of the difficulty of tracing ancestry, even of a family in the orders. But if we remember that we have gone back into a period of wide divergences, we can get a more satisfactory explanation. There may not be, or have been, any geological record, now that we have seen how marked divergences may be. It would even seem by no means impossible that the whole step from one class to another might be taken at one operation.

We have also seen that a monotypic genus, beginning its life, is necessarily suited to the place where it grows, and did not begin by killing out some less suitable species or ancestral form. It is more probable that the average localised fossil simply represents a sideline of evolution that was killed out by some catastrophe (cf. **158**, p. 23). In looking through lists of fossils, one is rather struck by the number that seem to be monospecific, which goes to indicate that they were probably young beginners. A fossil is a relic of old times, but rarely belongs to an extinct line of plants like the *Psilophytales*; it is more probably due to some catastrophe, even so simple a one as a rapid change of conditions.

Old floras tend to show a number of genera in common, and various speculative conclusions have been based upon this fact. It is more probable that the genera in common were simply early genera of the different families, which had had time and opportunity to spread more rapidly in the comparatively uniform conditions then supposed to have been ruling. The generic separation of so many fossils may be due simply to their age, they perhaps dating back to a period when divergence at birth was generally larger than it now is.

24. *The laws of geographical distribution.* It is now clear that signs of the universal rule of law are beginning to show themselves here, as elsewhere. The writer has studied this subject for many years, searching for what he knew must be there. The first clue came from noting the regular way in which a flora was graduated, from a few large genera in each family of any size, which were usually well separated from one another in number of species, at the top, down to a great many small ones, overlapping in size, at the foot. This one may see in many distributions, like the farmers' names in a Swiss canton (*Evol.*, pp. 35-8, and 40), or in an English county (**162**), or the names in a telephone directory, often quoted by opponents as a proof of "accidental" distribution. But there are laws even at the back of accidents, and we are trying to trace those that lie at the back of distribution, as TYNDALL has so well described (p. 266) for glaciers.

A few years of work in the tropics were enough to convince the writer of the unsatisfactory nature of the theory of progress by trial and error with selection. No proof could be obtained that adaptation had much hand in the matter, nor that the structural differences in plants had anything adaptational about them, except in the more extreme cases like waterplants. In reality they appeared to be quite neutral. The writer's first large bit of research work was a study of the *Podostemaceae* of INDIA and CEYLON (*Evol.*, pp. 8 seq.), then supposed to be the last word in adaptation. This, together with his botanical and agricultural experiences, showed him clearly how unsatisfactory selection was, and made him one of the early converts to de VRIES' theory of mutation. But realising that one thus lost the supposed gradual urge of adaptational improvement, he stipulated in 1907 for the possibility of complete specific mutation at one operation. Working from this basis, on the hypothesis given on p. 96, he gradually deduced many of the laws that seem to govern dispersal.

After a number of papers from 1907 onwards, the writer published his first book upon this subject, *Age and Area*, in 1922. With its appearance, it soon became evident to him, and to his friend Dr. H. B. GUPPY (*cf.* his article there on p. 101) that this was a very promising line, and he has steadily followed it for 42 years in all. It was clear that the first law of dispersal was (1) that *distribution was a dynamic subject*, not a static, as was so commonly supposed. Each species, when it got the chance, was increasing its area of dispersal, but usually only with extreme slowness, though sometimes getting the opportunity of pioneering (*cf. Lantana* and *Mikania*, pp. 406-9).

This was followed by law (2), that of *age and area* (*AA*), the conception that all through the phenomena of distribution there showed a general and well marked tendency for the area occupied to be determined by the age of the genera in the world, and local area by local age. To allow for variation between one and another, one should take species in groups of say ten allies, comparing only with other tens allied to the first. Single cases usually showed well enough, but it was better to argue from groups.

This led by analogy to law (3), *size* and *space* (*AA*, p. 113) that taking genera as before, in allied groups, the area that they occupied went with their size in the world, and this was followed by the obvious further law of (4) *age and size*. The laws of ASA, as we have called them, were thus complete (p. 23). They have proved to be of very great importance in the study of dispersal, for most of whose phenomena they are almost sufficient explanation.

The writer continually improved his way of using subconscious deduction, with the laborious subsequent verification from the facts. As these deductions, when they came up, were extremely fugitive, and had usually nothing whatever to do with the work that was in hand at the time, the writer has used them as predictions. The surprising thing was that all proved correct to an extent as great as one has any right to expect in biological matters with their complex interweavings, and in this way the author obtained a great part of the matter in this book. The success of these predictions thus seemed to indicate that the premises, including the laws already given, were correct and fairly complete. This was also indicated by the fact that the subconscious refused to have anything to do with " swamping " (p. 478). The writer has taken this as an indication that he has missed something essential to the argument, but what it may be he has not found out. Probably the question is one for genetic investigation.

An early deduction of this kind gave him what was later found to have been published a few months earlier by his friend Dr. GUPPY, whom he then knew only by correspondence over great distances. This was law (5), really a law of evolution, but of very great importance in distribution also, that *evolution* must have gone from the larger divisions like families and genera *downwards* to species and other small divisions, and not in the reverse way, as stipulated under " Darwinism ". That this conception fits the facts much better than the previous one is abundantly shown by such facts as are given in the numerous tables of leaders published above (list under Leaders, in Index), tables which seem only explicable upon the new conception.

From the single genus that began a family, save in cases of polyphyly, all the members of the family were thus formed by the continual production of new genera and species. Some of the new genera, especially, were very divergent from the original parent, like for example *Ruellia* from *Justicia* (p. 195), and we now regard them as the heads of sub-families or tribes, just as from Jacob as parent there came the tribes of Reuben, Judah, Simeon, and so on, which together made up the super-family of Jacob. All the plants that had not, in the course of their mutations, lost so many of what we call the family characters that they could not longer with any certainty be regarded as members of that family, made portions of it. The family characters were in fact those that had best survived the mutations. In any family of more than a very few genera, one rarely finds all of the important family characters in any one genus, though always a sufficient majority to prove structural relationship. It is for this reason that the words usually, frequently, often, or, and the like, are in such continual use in taxonomic descriptions. For example, opening ENGLER-DIELS at random at p. 234, we find such words employed 22 times in the few lines of description of the *Leguminosae.* The larger the family, the more they are used like this. The same rule applies equally well to genera and species, and is covered by the writer's suggestion of *kaleidoscopic mutation* (**155**). This also is a law of evolution, but we may count it, by reason of its great importance to dispersal, as law (6).

A necessary consequence of this law was (7), that *at a mutation the parent also survived,* the offspring only occupying a very small area in or near to that of the parent.

Mutations thus happened dichotomously, usually showing marked divergence in one or more, commonly more, characters at each mutation. This is what we have termed law (8) DDM, or *dichotomous divergent mutation.* Probably the parent was one or few individuals that somewhere came under some unusual strain of conditions, causing a rearrangement of the genes and chromosomes, thus automatically producing a new structural form.

These last laws got rid of the difficulty hitherto always felt with adaptation, as to how it was acquired. If a new species was born like this, as a few individuals only, it was evident that unless its members had inherited from their parent, already living somewhere not very far away, enough adaptation to survive to the stage of reproduction, they would almost at once die out.

This change in the direction attributed to the process of evolution means a considerable change in our way of looking at the whole subject, which we have now, in a sense, to view from the opposite direction. Law (9) evidently is that *adaptation is automatic,* for a birth of a few individuals not properly suited to the conditions at that time and place could not be expected to produce anything likely to survive and reproduce.

Law (10) is described in *AA*, p. 34. *As a species extends its numbers* by new births, *its rate of progress will increase* also, though the species will have to become locally adapted to each place in turn, probably simply through adaptability based on the conditions under which it was born. And when a little extra strain arises anywhere, it will probably give rise to another new species, suited to the conditions that then obtain there. Hence the great numbers of endemics that form in a much broken region (*cf*. map of *Siparuna*, p. 224).

Evolution and dispersal thus become once more closely associated. They are both working upon laws that are largely mechanical, so that they can be well studied together, and also studied in connection with the dispersal of animals and of man, with questions of changes and movements of human population, and the like. They will also help in their turn to throw some light upon these subjects. The old conceptions of trial and error must yield room for the incoming of law.

With the reversal of the supposed direction of evolution the very important law of (11) *leaders and sub-leaders* comes in. The first genus or leader of any family, so soon as it begins to mutate, tends to give rise to leaders of the next lower rank—sub-families or tribes—and these to leaders of the rank below them—sub-tribes—and so on downwards even to sub-species. All this we have abundantly seen in the many tables of leaders of families, genera, and so on, given above (list under Leaders in the Index). This at once gives rise to other questions that cannot yet be answered, such as why all the offspring do not behave like this, but only about 60-80% of the topmost.

Law (12) is that an endemic species or genus of great localisation is, in the great majority of cases, a new species or genus which is just commencing to spread, but given time and opportunity will at some future time occupy a much larger area. *Endemism, taken as a whole, simply represents the earlier stages of distribution.*

The next law, (13) is that *divergence* at a mutation is not only the rule, but *seems to become the more marked*, on the whole, *the nearer* one goes *to the starting point* of the family, genus, &c. The further one goes, the larger the divergences that one occasionally finds, like that between mosses and liverworts, mosses and ferns, ferns and gymnosperms, &c. But however great the divergence may be between any two individual members, one must remember that sooner or later, as one goes back through the ancestry, one comes to the place of coalescence, beyond which only one of the two is to be seen. The first appearance of characters like this reminds one forcibly of appearances under the laws of Mendelism, and it is probable that there are some rules of what we may call a super-Mendelism at work.

Another important law is (14) that as soon as a species tries to move from its birthplace, it comes up against *barriers* of the most various kinds, even if at first only so slight as differences in soil, in water-supply, in insolation &c. Thus dispersal is largely a matter of overcoming barriers, and rate of dispersal depends largely upon how many of these there are, how formidable in each case, and so on. Yet another extremely important law is (15), that of "to him that hath shall be given", "first come, first served", or "the early bird gets the worm". The first arrivals practically always get the best of everything in the way of success or progress, even if not permanently so.

The numbered laws that we have so far given are fairly well established, but there are other principles, still under investigation, that it will be well to mention. Let us begin with endemism, which is a very loosely employed term, and could hardly be otherwise, since with the exception of the few proved relics, it evidently represents the earlier stages of growth and dispersal. There is much said about it in *AA*, chaps. XV, XVI, especially pp. 166-7, which may be used to illustrate and co-ordinate the fragmentary articles above.

Endemics are in general young beginners as species or genera in their early very localised condition (pp. 66-96, 139), which later would extend their areas as far as the barriers around them and the slowness of local adaptation allow. They are apt to produce new species at times and places of greater stress, such as often happens in broken country, where conditions change quickly from place to place. Their area is small simply and usually because they are young, or because the barriers have been unusually formidable. Only rarely are they real relics, and that especially within the range of the ice of the glacial periods. In fact, with the new light now thrown upon the subject, it seems unlikely that a widespread species could be reduced to a very small area, except by some agency that killed everything out, as did the ice, and was not selective.

One can see the history of the growth of a few endemics, derived from the first invading genera, into a flora, in the Australian *Inuleae* (p. 444) or the Mediterranean *Cynareae* (p. 445). In the whole 54 Australian *Inuleae*, there are only *Helichrysum*, *Helipterum*, and perhaps *Cassinia*, *Gnaphalium*, and *Blumea*, that are outside genera probably large enough to have given rise to one, or possibly more, endemics in the great list of them. Many of the small endemics are probably descendants of the larger endemics, while the two large outside genera at the top have probably most descendants of all. But all are evidently their offspring, direct or indirect, except those that may have come from *Cassinia* &c, though even these probably trace back to *Helichrysum*, the leader of *Inuleae*, in the end. The flora thus made up shows the same composition, numerically considered, as one that contains no endemics. There is no difference, except in numbers of genera, between the *Compositae* and any other family.

Endemics are thus fully comparable to new arrivals from other countries. Both will have a struggle to get themselves fully established, and will afterwards spread, more and more quickly, as far as possible in the time available. The number of species in a genus will thus tend to increase, in the world towards the original place of birth, in any one country towards the original place of invasion. They thus tend to make a pattern of wheels within wheels, like the works of a watch, and as those of smallest areas will be the most numerous, they form a hollow curve. The larger and more "successful" genera show most of the endemics (*cf. Ranunculus* in NEW ZEALAND, p. 65).

Inasmuch as subgroups are formed from above downwards, they will be very old, and will therefore appear to a great extent, even among the local endemics. For example, in the CEYLON *Rubiaceae* one finds endemic genera in two tribes, and endemic species in eight. The endemic flora of one country bears a definite relation to that of its neighbours (pp. 69-83), being governed by these definite laws.

Endemism shows better the older the genus or family (pp. 68-9, 140, &c). The more outlying the country, in the warmer regions at any rate, the greater its proportion of endemics. In the cool temperate zones the flora may be quite recent, as in BRITAIN, showing few or no endemics. They tend especially to form in broken country, and here isolation tends to be much more marked, so that in mountains or in islands the endemics may still be only comparatively local, even though old.

Leaving out of consideration those genera that are only represented by one or more endemic species (E, EE, &c), though themselves found in other countries (p. 478), the most usual representation is one wide and one endemic, WE, the next most common WEE, and so on. We have seen that it is very probable that both are descended from the W (Chap. VI), a fact which goes with the way in which the leader of a family seems at first mainly to mutate into other tribes (*cf. Senecio*, p. 176). Isolation probably helps in the formation of endemics, but this question needs genetic investigation (p. 316).

Endemism in one country tends to bear a definite relation to that of its neighbours, as was shown in SPAIN and the BALKANS in Chap. III, or in CEYLON and MADRAS (p. 74). It is evidently governed by the same laws, which have produced similar results. Small genera, confined to small areas as a rule except in cases of very uniform conditions like waterplants, but very numerous (58% of all genera in the world are of three species or less) are just like any other endemics, whether the name be given to them or not.

The divergences between two endemics formed from any one genus seem to be as great as their differences from the parent. Cf. Chap. VI, and the case of *Rhamnus*, p. 107.

Land transport is the way in which most things get about; when it is not possible to move beyond a certain point, as in SHETLAND Is. (p. 23), there tends to be an accumulation of species there. The tracing of migrations is mentioned on p. 75.

Representation also requires a few words. In a family, as a necessary consequence of DDM, there will tend to be a few larger genera at the top, well separated in size, but with the separation diminishing downwards till presently one comes to an overlap of two genera of the same size, after which the duplication will in general increase downwards to a considerable number at the foot, where on the average there will be about 38% of ones (*cf.* Yule for law of compound interest, and pp. 303-4). Somewhat the same thing will happen with the areas occupied by the species of a genus—a few large areas at the top, many small ones at the bottom (*cf.* *Ranunculus* in New Zealand, p. 65).

The central part of the area occupied by a family, where the original parent was born, will be the region in which most of its genera will tend to occur; but as the oldest genera will have gone furthest out, the average size of a genus will increase as one goes outwards. The smallest or most recent genera will be found over practically the whole range of the family, except where it is too young to have produced any, as in Britain. The most frequent genus to be found at the extreme margin of the distribution will on the whole be the actual leader of the family, especially in the northern hemisphere. The distribution of a genus by areas will tend to form contour lines (p. 58).

The first species of a genus to appear in a country will usually be that which is the oldest in the country from which the plants are coming. In migration and invasion it is the youngest and most local species that tend to be left behind. Small dispersal in a country usually means late arrival there.

Early comers at first tend to gain an advantage everywhere (first come, first served) by finding less opposition, and by having more time to suit themselves to the local conditions (*cf.* *Lantana* and *Tithonia*, p. 408), from which they can go on to suit themselves to others round about, but are liable to comparative suppression when something comes along which happens to be better suited to the conditions at that place and time (*cf.* *Mikania*, pp. 408-10).

CHAPTER XIV

General conclusions

As these three books, *Age and Area*, *The Course of Evolution*, and *Birth and Spread of Plants*, form a more or less connected whole, representing much of a lifetime's work, we have given here a general connected account of our final conclusions, which are at least the result of over 40 years of work, devoted to finding out the laws that govern evolution and distribution, two subjects that are inextricably bound together; and they are arranged in sequence.

Evolution (1)

1. Evolution has not proceeded from below upwards in the way formerly supposed, except in the general way that the more complicated things are the more recent.

2. In its detail, it appears to have gone the other way, from larger down to smaller divisions of the vegetable kingdom, as first suggested by my friend Dr H. B. Guppy, F. R. S. The work here described, especially that dealing with leaders of the various groups, seems to afford a very good proof of this contention.

3. It is working upon definite laws, which appear to have a largely mathematical basis, and is probably largely dependent upon chemical and electrical phenomena. It is thus coming into line with other mathematically based work.

4. It seems to have been a necessary consequence of the appearance of life upon the globe, which has been able to produce, by chemical and other reactions that do no harm to the living plant, all the variety shown.

5. It is now our task to find out how this has been done, to turn our activities into the most promising directions to quicken the process, and perhaps to learn to guide evolution to some extent.

6. We do not know whither nature by evolution is leading us, nor even if she has any definite aim in view. The former notion of "nature red in tooth and claw" is undoubtedly on the wane, and may perhaps be replaced by something of a more co-operative nature, as proposed by my friend Dr WHEELER (128), but evidence is not yet sufficient to decide so large a question.

7. Evolution did not go on by the casual picking up of new characters on the way by the selection of improvement in adaptation. The new characters were furnished according to law, probably the acquisition of one character making possible that of another on a later occasion.

8. YULE's work showed that the growth of a family or other group must be by divergent mutation with the *survival* of the parent, not its destruction, as formerly supposed. Hence our theory of dichotomous divergent mutation (DDM), whose essential features are given on p. 99.

9. The new form thus born was probably only a very few individuals, born from one or few parents. It would occupy but a small area, within or close to that of the parent (*cf. Ranunculus*, p. 65).

10. As the parent thus occupies much more area than the offspring, it will rarely if ever be killed out by any superiority that the latter may happen to possess.

11. The diminution of the emphasis and divergence of mutation as one comes downwards from family to species seems to suggest some kind of decrease in the energy available. It is perhaps best shown in large families, where the mutations have been more numerous. As my friend the late Dr Charles Balfour STEWART suggested, there may be some transfer of energy at every mutation, resulting in a small loss. This may have some bearing on Small's work on senescence and death of a species.

12. This type of evolution is so common and so well marked in all but a very few families (*cf. Monim.* or *Arac.*) that when it does not occur, one feels that there may be some simple explanation like polyphyly.

Divergence

13. The first feature to show in evolution is divergence (p. 263). It is in fact one of the great marks of evolution. It often implies the acquisition of new characters in the child, seems to be automatic, and is probably electrically controlled.

14. Divergence shows right down to the smallest forms. We have seen it especially in Chaps. V, VI, and it shows in all characters, even in the most important (*cf.* fruit in *Ericaceae* pp. 368-9). It seems to become larger the further back into the past one goes. Above family level it seems to affect more characters at once, and it is very difficult to place a large family in its proper relationship to other large families.

15. The great differences of early days are more easily explained by large mutations. Natural selection could not make them larger upwards. Divergence was always one of DARWIN's great difficulties (p. 252).

16. On the other hand, the variety of divergence seems to increase downwards with the increasing number of characters. It is possible that each divergence makes others feasible.

17. Transition stages are few and far between. What are usually called such, like *Henriquezia*, are more correctly interminglings of complete characters, some of A and some of B, not intermediate stages between A and B in character. An alternate leaf seems usually to mutate directly to an opposite.

18. Mutations may be of any taxonomic rank.

19. The divergent features shown at mutation, like leaf alt./opp., anther extrorse/introrse, ovary superior/inferior, capsule/berry, and so on, *must* coalesce somewhere if one go far enough back into the ancestry (pp. 164-5). This means that the ancestor must have been carrying both the characters, or more probably, their potentialities.

20. Divergence is excellently well shown in the leading families, as is clearly to be seen from the lists of leading genera above. It also shows very well in the tables of endemics, WE in Chap. V, and WEE in Chap. VI.

21. Many divergences are so marked that they could only be formed by sudden mutation (pp. 105-7).

22. When a new divergence is added to preceding ones, it becomes of necessity one in a crowd that is continually on the increase, and so it is usually comparatively unimportant, like a single voter. But old characters that have been long handed down seem to become less liable to change with the passage of time, and become more important.

23. But any character is liable, so far as we can see, whether a family character or not, to change at any mutation, so that in a large family, one will hardly find any character that will certainly occur everywhere. Hence the constant use of such terms as usually, frequently, often, or, and so on, in taxonomic descriptions of families (p. 128).

24. The characters in use in small genera, not usually considered endemic unless their country of habitation is somewhat clearly marked off, are similar to those found in cases always admitted as endemic (pp. 129-32).

25. A divergence almost necessarily brings in a character not actually shown in the parent.

26. Every new genus, by reason of the divergence that occurs, is liable to need a new group for itself, but this is commoner in early genera than in late.

27. Divergent mutation is treated in more detail on pp. 164-194.

28. As a genus grows, therefore, it acquires a tail of satellites more or less resembling itself (p. 35).

29. We seem to have been trying to work evolution in a wrong direction.

30. The general relationship between members of the family at the same stage becomes closer the further back that one goes, though of course that between parent and child is the same everywhere.

31. The new form, by its divergence, will often be so structurally isolated from its parent that there will be no risk of loss by crossing, and it inherits local adaptation, so that it stands a very fair chance of survival.

32. On the whole, the largest divisions are the most ancient, being the first formed, and the smaller are the more recent.

33. Every firstborn representative of a family may be regarded as a genus, or a species, or both, at will.

Selection and adaptation

34. Too much was left to chance in selection with adaptation. Evolution seems to be, not a matter of chance, but the result of a great thought or principle, which has worked itself out by law upon a definite plan like physics or chemistry.

35. Adaptation, advantage, and selection are discussed on pp. 317-22 more especially, and in many places elsewhere. Adaptation is born with a species (pp. 11-16) and improves later (pp. 13-14), and is primarily functional.

36. Selective adaptation has been made to explain everything, and has been worked too hard (p. 115).

37. The older theory now leads to little but speculation, and many difficulties are arising in its path (p. 42).

38. Adaptation and selection must now take a rather less important place than formerly.

39. Isolation becomes of more importance than hitherto, but at the same time the species begins with it.

40. Similar causes, acting upon similar plants, in similar surroundings, may produce similar results, as one may see in the cases of xerophytes or water plants.

41. Natural selection will not explain "success" or dispersal (pp. 11-14). The Mediterranean floras offer a formidable problem (p. 44), and it is very difficult under it to account for family or generic differences. It is primarily an individual problem; all As do not defeat all Bs (pp. 27-28). Gradual transition is needed with it (p. 98); it does not select species (p. 99), and could hardly produce the connections of characters seen (pp. 128-9).

Struggle for existence

42. This is inevitable, by reason of excess of births.

43. It is not specific, and all As do not defeat all Bs, unless one species is composed, as in the case of a newcomer or a new species, of a very few individuals (p. 298).

44. A pioneer may gain a great advantage at the start, yet lose it again if something else turns up with a serious advantage (pp. 406-9).

45. One genus has little or no advantage over another, when they are taken in groups. Some may gain, or lose, by one quality, others by others.

46. Specific characters have evolved as a rule without relation to their possible value in the struggle for existence (de Vries, pp. 254-5).

Destruction

47. We have fought for a lifetime against the almost universal conception of wholesale destruction of transitions or intermediate types, which hardly seem to exist at all in the form of things showing intermediates in *characters* between two extremes.

48. The destruction of unnecessary individuals is one of a different kind, due to the inevitable struggle for existence, itself caused by the excess of births.

49. It is not a specific, but an individual struggle.

50. There is little evidence for dying out of species till they reach a great age, or are killed out by some catastrophe (pp. 35, 340).

51. Destruction cannot be called in in so light-hearted a way as used to be the case (pp. 231, 253).

52. There is, if anything, still less evidence for the extermination of genera, other than the very local ones that are the most common as fossils.

53. Destruction has usually been called in to account for the increased divergence at higher levels, but there is no good evidence for this. The great destruction is in the young species, before they have covered an area sufficiently large to make them fairly safe, and in the young of every species.

Fossils

54. Fossils are dealt with on pp. 35-7, 57, 99, 169, 479.

55. Unless they are common and widespread, they cannot be considered as more than side-lines of evolution.

56. There is a remarkable absence among them of the innumerable transitions demanded under the conception of Darwinism.

Evolution contd. (2)

57. One must remember now to reverse many of the directions in which we have been accustomed to look at the work of evolution. *Hieracium* and *Rubus*, for example, are not an exhibition of early stages in species formation, but the latest stages in it.

58. Evolution seems to go straight forward, but the vital and other factors cause deviations this way and that. It has no immediate adaptational basis (p. 109). Adaptation is by simple inheritance at birth, and not very different from that of the parent (p. 109). Once born, the new form slowly adapts itself to any necessary changes.

59. The appearance of characters is not a guiding cause of evolution, but a by-product (p. 131).

60. Mutation can cover any existing difference between parent and child.

61. Though evolution goes on as before after a mutation, it is not necessarily the same in detail after some deviation from the track caused by a vital or other factor.

62. There is no *necessary* reason that we can see why for example *Resedaceae* should be produced in a given line of descent, and if slight changes had been made in the ancestral processes by some outside influence, some now quite unknown family, the *Dubitaceae,* might have been evolved.

63. My working hypothesis, used successfully for 40 years, is given on pp. 96 (parent survives), 99, 310.

64. Selection is largely eliminated as a factor; it has never proved satisfactory.

65. The new form will often be so structurally isolated from its parent that there will be no risk of loss by crossing, and it inherits the local adaptation of its parent very closely.

66. The real evolution that is going on seems to be a case of internal rather than external reconstruction.

67. The latter is more of the nature of a compulsory change due to the former.

68. Each stage is a logical development of the preceding one.

69. The structural evidence for close relationship now loses some of its potency.

70. Each divergence seems to add new directions in which further divergences are possible, so that the number of possibilities is always increasing.

71. Evolution works by laws as yet not properly understood.

72. It is evident that formerly we have tried to a large extent to work evolution backwards, and we must now remember to look in a different direction at its work.

73. One must not yet expect to be able to predict the course of evolution, even in broad outline. One cannot even predict what will anywhere be the next mutation to appear. Cf. 62 above.

Leaders and subleaders

74. We have pointed out in *Evol.*, Testcase XX, p. 134, that the largest genera tend to separate at the head of a family by an important divergence, and to go into different tribes. This has proved to be a practically universal rule.

75. The first mutation of the leader of a family usually produces a sub-leader, head of one of the sub-families or tribes. The early mutations of this tend to produce the leaders of sub-tribes, and so on right down to sub-species.

76. Each family, genus, or species, of more than very small size is generally broken up into sub-groups by structural, usually markedly divergent, characters, each group of course being led by its largest member.

77. A tribe or genus, therefore, begins with A, whose immediate progeny B more often than not belongs to another sub-group.

78. The formation of these sub-heads is usually an event that follows the formation of the heads as closely as may be, as may be seen in the many lists that we have given of the top-most parts of families and genera (list in Index under Leaders), like the *Compositae* on pp. 173-82, or the *Saxifragas* on p. 428. In the case of species, we must take the area covered as an equivalent for the size.

79. This fact is shown for all the larger families in the table on p. 173, which shows clearly that all the big early genera tend to be well separated, and so to give the characters to the sub-groups, as the parent did to the whole family.

Each tribe takes for itself some of the characters with which the parent began.

80. This system of the formation of sub-leaders from the early descendants of a leader is so universal that it may be called a law of evolution (p. 331).

81. It is incompatible with the view of evolution "Darwinism" that has been so long accepted, but harmonises well with the "downward" theory of evolutionary development that the author has put forward in his writings for many years.

82. The way in which tribes &c are headed by their earliest born in this divergent way is a convincing proof of the writer's deductions on the subject of evolution; *cf. Evol.*, p. 134 (Testcase XX).

83. The effect of this early formation of sub-leaders is seen in the widespread fact that in nearly all cases we find a great representation of these leaders (p. 173). In BRITAIN, for instance, we find eight tribes of the thirteen in the *Gramineae*, and in CEYLON twelve. The flora of any one country tends to show many of the subdivisions of families and of genera (p. 172). The newer genera tend to fall away from the standard type of the leader (p. 173).

84. Such dispersal, in the writer's opinion, *cannot* be determined by selection or by adaptation, but must be due to subdivision by divergence at the earliest opportunity, so that most sub-groups had the time necessary for wide dispersal.

85. The younger genera, being formed by early divergence from the leader, tend to fall away from the type set up by it, and to become less closely related to it, structurally, genetically, and geographically, the younger and smaller that they are (p. 175).

86. The marking of a large group, to which we often give a special name like *Cynareae* or *Eu-galium*, is usually due to the formation at a far back period of some combination of characters that has since remained to a reasonable extent unbroken, and has thus formed the characters of a family, &c.

87. The oldest tribes, especially in large (old) families, do not show numbers and sizes of smaller genera to suit the leader, the suggestion being that this is due to many of these smaller genera having in their turn become the leaders of other and smaller groups (pp. 187-8).

88. If the family spreads into many and different types of country and conditions, as do *Compositae* or *Gramineae*, the real leader (the largest genus) is often left behind in various places, especially in markedly warmer or colder climates (pp. 192-3).

89. The leading families show very wide divergences from one another (pp. 330, 428-9).

90. The British families that lack their real leader are very largely tropical in origin (p. 193).

91. No selection or adaptation that one can conceive, it seems to the writer, could make the species of a genus behave as we have shown that they do on pp. 427-8, with the leaders of the sub-genera so closely following one another.

Taxonomy

92. Classification of plants is dealt with on p. 322.

93. For practical purposes we must make some kind of grouping of the members of the vast dichotomous branching that has gone on, which is combined with the transmission of characters in such a way that the parental characters are the most likely to appear, though mixed with the divergences.

94. A really natural, genetic, structural, and geographic system of classification would be of much value, like a chromosome map, were we able to construct it, but we must remember that we need, for purposes of identification, the most convenient, practical, and easily handled system that can be devised, whether it be natural or not. The general principles that guide our present system are well described by HITCHCOCK (cf. p. 309).

95. The rules of taxonomy are of necessity different from those of descent (p. 308).

96. Much of our taxonomic classification is necessarily artificial, whenever a certain character or characters depart from the direct hereditary line, putting in an appearance somewhere else. It must also necessarily be artificial when it has to group together, as agreeing structurally, things that are really only horizontally and not vertically related, by the appearance of the same or very similar characters in both. A natural classification obviously cannot be constructed upon a structural basis alone (pp. 141-5).

97. Classification is based upon divergences within divergences. The first thing that nature does is to provide the divergences, the oldest being the most comprehensive and widespread, the youngest the least so (*cf.* Leaders). But the geographical divergences do not agree of necessity with the structural, nor either with the genetic, though it is becoming clear that all are of great importance.

98. Descent is vertical, and each genus in turn heads all its own descendants, though not, of course, those of its parent, which also survives, and has its own line of descendants. We divide all the descendants somewhat artificially by certain characters that appear with varying degrees of emphasis, of persistence, and dispersal. Classification, which to be natural should follow the natural genetic lines, is often compelled to follow horizontal lines of structural relationship. It cannot depend only on structure (p. 217), but must take note of geography, genetics, and divergence.

99. Structural alliance may completely ignore geographical difficulties, and very often the sub-divisions of families cannot be made to agree with their dispersal (pp. 339-40).

100. In spite of great splitting, no proper harmony can be made between structure and geography; it would need destruction inconceivably extensive and selectively efficient (pp. 150-1, 193, 272).

101. Arithmetic regularity (hollow curves) tends to disappear when a large group is taxonomically split up. *Cf.* p. 215 with the taxonomic division of *Acanthaceae*, and *cf.* also *Monimiaceae* and *Araceae*. The two leading *Monimiaceae* are widely separated structurally, but agree very well geographically. The discrepancy is often considerable in such cases; *cf.* *Rhamnus* and *Siparuna*, p. 353.

102. Taxonomy based solely upon structural relationships cannot be generally reconciled with DDM or with dispersal (pp. 150-1, 339).

103. It is of interest to look at the different groupings of the *Monimiaceae* (pp. 228-31 &c).

104. It is becoming clear that geographical and genetic relationships are as important as structural (p. 205).

105. There is no special relationship in the ecological communities (p. 7).

106. Classification is most natural in small groups like

the *Hieracia* or the *Rubi*, though even there we are no longer sure of our position (p. 264).

107. Relationship gets closer as one follows a family or a genus back to its head, much upon the same lines as in human descent, so that a natural classification would be too complicated for practical use.

108. The large families cover the taxonomic field very well by themselves alone, while the smaller, largely satellites of the large, squeeze in between them (p. 330).

109. The earliest genera trace out the lines of the taxonomic division of the family.

110. Above the family level the difficulty of making a natural classification of the families (into orders) increases, and shuffling is always going on (pp. 323-36).

111. The difficulty of placing a family increases with the size of the head (p. 357).

112. The history and taxonomy of a family is largely determined by the few genera at its head (p. 358 seq.).

113. The combinations of characters that mark families are largely " chance ", though probably governed by a complex system of laws. Permutations and combinations of characters, polyphyly and other phenomena probably interfere largely with the simplicity of the matter, and the formation of complexes in the larger genera is another source of confusion (pp. 211, 299, 369, &c.).

114. There is now no special reason why the whole tree of a family should not exist upon the earth at the present moment (AA, 240).

115. There is no longer the need that existed formerly, to search for transitions (pp. 169, 298, 314, 332-3, &c.).

116. There is no need to call in geographical destruction as formerly (p. 118).

Characters

117. The behaviour of specific and generic characters, about which so little is known, needs early investigation in detail.

118. Evolution seems to have been a vast dichotomy, with the characters either handed right down, or acquired on the way, largely as divergences, perhaps some by selection.

119. They seem to obey the rules of what may be a super-Mendelism (p. 134).

120. Until we can trace some laws, we are working in the dark (pp. 190, 355 seq.).

121. It is becoming clear that the acquisition of new characters was not casual by selection, but genetically, by law, from above (p. 263).

122. The incidence of character was governed by what at present we can only call chance, but which has law behind it (pp. 361-5); acquisition by selection was probably rare (pp. 298-9).

123. The characters of a family seem at present a chance lot determined by previous changes in the ancestral history, and that remained comparatively fixed in the heredity (p. 299-300).

124. The potentialities of all characters are handed down by heredity.

125. They are apparently developed by the action of conditions, probably mostly external, upon certain internal characters.

126. The distribution of characters at birth is evidently not unlike that at the birth of human individuals, and similar rules probably apply to animals.

127. The early mutations produce the most " important " characters (p. 336).

128. The larger a genus, the greater the range of its characters (p. 364).

129. Geographical separation also occurs with the same character (p. 209), and is frequently due to the presence of a linking overrider (cf. p. 232).

130. Species are more numerous than " important " characters, so that permutations and combinations of the latter are needed (pp. 189).

131. In larger families especially, one often finds unexpected characters turning up. Often they come from other families, date far back, and must have been carried as recessives.

132. Most characters found in a family may appear anywhere in it, and sometimes elsewhere, and at any time (pp. 131-6, 211-13), but most commonly in related forms.

133. Characters of one family may appear in another, though usually with less frequency. All, or their potentialities, are probably present in the leader (pp. 143-151, 367).

134. The first characters of division of *Acanthaceae* and others occur in other families, but with varying degrees of importance, due to different age, in each (pp. 193-5).

135. The larger the family, the greater the probability of exceptions among the younger members (p. 311).

136. There is a great lack of transitions between characters and often the differences are such that they could only have come by divergence (p. 367).

137. The value of a character depends upon its absolute age from its first appearance, and also even more upon the number of descendants that show it (pp. 128, 222-5). It is often confined to the family or group where it first appears.

138. It seems not unlikely that the increasing number and dispersal of characters is a law of the continual production of new characters, and the continually extending use of permutations and combinations of them, used kaleidoscopically.

139. The importance of a character in one family is no guide whatever to its age or importance in another, unless in a few cases where the families are closely related; and not necessarily even then.

140. Teratology (pp. 100-05), which brings up awkward difficulties for selectionists, seems to prove that any species may be carrying a great number of "recessive" characters, which may at any time appear unexpectedly in that family.

141. It is also a proof that a character, though not visible in the parent, may be given complete and perfect to the child (p. 104).

Size in the world

142. The law of size and space is described on p. 19; its operations are shown on p. 201. Size in the world is a character of very great importance (p. 190). The system upon which the sizes in my *Dictionary* were prepared is described on p. 190.

143. The range of dispersal in BRITAIN goes largely with the size of the genera in the world. A comparison of the

sizes of *Cruciferae* and *Umbelliferae* in BRITAIN and in FRANCE, which shows features of interest, is upon pp. 50-51.

144. The first genus in the world in a family is on the whole about twice the size of the second (p. 191). Generic sizes are considered on pp. 333-6, 350.

145. The law of "to him that hath" is of importance in this connection.

146. Duplicates in size tend to run in different lines of descent (pp. 191, 219-20).

147. Very old families may be smaller by reason of lack of characters upon which to draw (pp. 336, 344). This may also account for the shrinkage in sizes sometimes seen as one gets near the top (p. 327-8).

140. Size of a genus has been completely neglected as a generic character, yet is proving (as marking age) to be one of the most important.

Mutations

149. The mutation that is going on seems, so far as we can see at present, to be a casual choice of characters (p. 324).

150. There is probably some general law at the back of incidence of mutations (p. 226).

151. Early mutations in a family &c seem to be of higher rank, or at least they have more descendants, and so are of more "importance", than the later (p. 170-1).

152. The mutation division of the cell is probably electrically controlled (C. Balfour STEWART), p. 164.

153. Mutation is easier (more change), apparently, in water plants, saprophytes, and other such things as have a more plastic consistency (p. 240).

154. Larger size of a genus offers more opportunity for change (p. 302).

155. Usually the result of a mutation appears to be neutral as regards its reactions to the outside world, but if the change of conditions is going on in a definite direction there is usually a definite tendency in the mutations to be in directions favourable to that, but whether this is due to compulsion, to encouragement of favourable mutations, or to the killing off of unfavourable, we do not know (p. 302).

156. Kaleidoscopic mutation is considered at p. 376 and elsewhere.

157. What seems to go on in mutation at birth of a new form seems suggested by the phenomena of a kaleidoscope. The differently coloured pieces of glass continually take up different relative positions, as if it simply happened so.

158. A very slight accidental change in the formation of A might result in a more different B, and so on. Except that some character is furnished to every organ, the characters of a species seem a casual assortment, except when under certain stresses of conditions, such as increasing dryness, evolution is going in a certain direction.

Hollow curves

159. Hollow curves are formed, both for number of species and for area occupied. They appear to increase by compound interest, inasmuch as the parent survives, as well as the offspring (p. 192). This is the necessary result of DDM, as Yule showed (158). *Cf.* also pp. 305-9.

160. An accumulation of young genera forms at the foot, by reason of the continually increasing number of possible parents.

161. As the family grows in size, the curve lengthens at both ends (p. 34). The great bulk of the species are in the large genera at the top, and there are wide gaps between the top genera, increasing with the age of the family. A good example may be seen in the *Podostemaceae* (*Evol.* p. 19) where the local genera must be the younger, and are most dorsiventral; plagiotropism is always hard at work, and its results show best in the youngest genera.

162. See also Testcases I-VIII in *Evol.* and Chaps. XII, XIII.

Genetics

163. The rules of genetic descent are necessarily different from those of taxonomy (p. 322).

164. The closest genetic relationship is at the top of a family, where the structural divergence is the greatest (pp. 188, 206-7).

165. So long as taxonomy tries to be genetic, it lays itself open to criticism that is extremely difficult to meet (p. 341).

166. A genetic system of classification would be too complicated for practical use (p. 175).

167. Something of a "super-Mendelian" nature is indicated as a probable line for a discovery of the laws of incidence of characters (p. 134). Pollen patterns (p. 210) suggest themselves as useful material for such a study.

168. Old ideas of relationship based solely upon structure will have to be revised.

Polyphyly

169. Now that the former facile explanation of so many features of evolution, that they were due to destruction of intermediate or transition forms, seems no longer to be available for universal use in difficulty, polyphyly, or development from different, though usually allied, ancestors, is the most feasible.

170. But it is very important that this explanation should not be used until all others possible have been tried, and inductively tested, otherwise it will soon fall to the same level of disrepute as its much overworked predecessor.

171. Possible cases are given on pp. 41, 151, 157, 196-7, 354, 369 seq. &c. And it is very probable that both *Monocots* and *Sympetalae* are made up of two or more groups each of different ancestry.

172. Some characters of allied families may appear at times in other families, but are less frequent and perhaps less important than the appearance of the same character in different places in the same family.

173. If mutation be kaleidoscopic, one will expect fairly frequent polyphyly.

174. Overriding genera probably produce many cases.

Distribution

175. Distribution is a dynamic subject, and is always going on. There is no proof that leaders missing in BRITAIN, like *Hibiscus* for example, cannot reach there in time (p. 49).

176. Time, or age, is the essential feature of distribution.

177. The laws of geographical distribution, and some of its general features, are discussed on pp. 480 seq.

178. The subject must now be treated in consonance with the newer conception of evolution that we have brought up.

179. Dispersal is much more mechanical than has hitherto been supposed. Evolution and dispersal seem to proceed in a simple arithmetical way by law.

180. The vital factors make continual deviations in the straight line of evolution, but their action is much more local and variable than that of the mechanical factors.

181. Spread is largely mechanical, depending upon how rapidly each species can overcome the barriers that hinder its dispersal; and it becomes more rapid as time goes on (*AA*, p. 34).

182. Dispersal is largely governed by the laws of ASA (pp. 23, 50, 87, 303).

183. Age is largely accompanied by size in the world (pp. 25, 85). It is a factor of very great importance (p. 321), as it allows the time necessary for any change. It makes real as opposed to structural discontinuity. It makes the importance of a character. It allows increase of area occupied. It provides more choice of characters. Age in the family is dealt with on p. 218 seq.

184. Younger genera follow the laws of ASA most closely, as in their case there has not been time for the effects of great geological and other changes to show to their full extent (p. 256-7).

185. Dispersal of a new form will in general be regulated by the laws of ASA, but it is safer to take several species together, to cancel out the effects of local factors.

186. There is no question that the simple mechanical explanation provided by the laws of ASA does much more to explain the facts of dispersal in long time on large areas than any vital cause.

187. Plant dispersal is coming into line with human, and they should be studied side by side (cf. GUPPY in **162**, WILLIS on names in Canton VAUD (**153**, p. 35 foot), and the work especially of PEARL and others in AMERICA).

188. Discontinuous dispersal, real and structural, is dealt with on pp. 89-94; also 66. Some may be due to polyphyly.

189. Barriers are among the most important factors to be reckoned with in distribution. Though negative, they have very great influence upon the rate at which plants travel and they tend to have a different effect in each case (p. 45, and *AA* espec. Ch. V).

190. The things left behind at a barrier are the smaller and more local things (p. 46).

191. The British flora is mainly a reduced French flora, the Irish a reduced British, and so on (p. 48).

192. It is clear that delay, and not acceleration, of spread has been the general rule (*AA*, p. 53).

193. Migration to and fro in regions towards the poles probably killed out many smaller things that could not move quickly enough, or that had very limited areas (p. 36), Mrs. REID's Pliocene flora gives an idea of some of the replacements effected (p. 36).

194. If we take things by geographical relationship, we get a good deal of taxonomic scattering, if by taxonomic of geographical. Roughly speaking there is little or no selection of one character as against another, so that geographical propinquity with close structural similarity commonly means real relationship, though overriding genera may bring in some confusion.

195. Taxonomic relationship, on the other hand, depends upon structure, which may be divergently changed at any single mutation, so that it must remain, almost of necessity, more or less artificial in various places, while to bring in all geographical and genetic characters would make it too cumbrous for practical use.

196. The effect that may be produced by an overriding genus is described on p. 147 seq.

197. The facts of distribution clash violently with the Darwinian explanation (p. 28).

198. Large genera tend in any country to overlap the smaller in area of distribution, whether in large or in small size of area, *e.g.* in *Arac.* pp. 267-72.

199. Outlying genera tend to be the largest, because the oldest (pp. 29, 45-6).

200. The bulk of the species of small dispersal occur in the larger genera (pp. 21-2).

201. Small dispersal usually means late arrival, or recent birth (pp. 11, 21-2).

202. YULE's description of a geological " cataclysm ", which is referred to on p. 219, should be read.

203. A genus usually thins out to a leader, not necessarily *the* leader, at the edge (p. 45-6).

204. Examples are given under *Acanthaceae* (p. 198), and on pp. 444-6 of the way in which we have treated families under the new rule of ASA.

205. Migration from one country to another is generally by means of land transport. Water transport is almost negligible (*AA* pp. 14, 17, 36).

206. British species are usually very widely distributed, BRITAIN being an outlying and also young island in which there has been no time for the formation of local endemics, so that it is mainly populated by the oldest species of any genus except those of warm climates. The dispersal of the British flora is mainly regulated by the laws of ASA.

207. The British flora includes numerous leaders, and shows a high average of size, while the floras of FRANCE and SPAIN are definitely lower in average size, with many more small genera (pp. 51-2).

208. Distribution in BRITAIN goes largely with the size in the world of the genera concerned (pp. 83-5).

209. The dispersal of the British flora is largely mechanical (p. 38).

210. BRITAIN, FRANCE, SPAIN and the BALKANS are compared on p. 47.

211. A number of interesting facts are brought out about islands, on pp. 464-78.

212. One of the most interesting is the proof of how largely the SEYCHELLES flora (p. 469) shows leaders, especially in *Rubiaceae*, one of the oldest families, if not the oldest, present.

213. Mountains (pp. 458 seq.) also show many interesting features. The ascent of a high mountain, with its rapid alteration of the flora, gives a picture of the rapidly increasing and changing stress of the changing conditions. The climb to the summit reminds one of what one sees on a journey very far north.

214. Owing to the possibility of further transport being destroyed, there tends to be an accumulation of species at the top of the list of the flora of a country (pp. 23-4).

Endemism

215. No explanation of distribution that does not explain endemism is of value (p. 63).

216. Endemism is not a casual phenomenon, but obeys definite laws, and is open to inductive study (p. 76).

217. We have now studied endemism for 50 years, and have no doubt whatever that in the great majority of cases endemics are simply the early stages of dispersal of species that as yet have not had the time or the opportunity to spread far. They are simply young beginners as species or genera (p. 64).

218. They are discussed in Chaps. V, VI, p. 95, and the genera in Chap. VII, p. 137. These follow the same rules as species.

219. The characters of an endemic must have come from its parent, whether there shown *or not* (p. 106). The divergences between the wide and the endemic offspring are well shown in CEYLON in the contrasts given in the lists on pp. 111-113 and 121-7.

220. No two people agree as to what shall be the upward limit of size for an endemic.

221. No line can be drawn to separate a " wide " from an " endemic " (p. 139). The tables of *Acanthaceae* show how difficult it is to do so, and the table of *Cynareae* shows how the wide genera at the top pass gradually into the endemic genera at the foot (p. 445).

222. Endemics show no inferiority whatever to other species, whether of small or of large genera. They occupy smaller areas on the whole because they have had no time, or sometimes no opportunity, to spread further. They are more common in the large and widely distributed families (p. 75), and are much more common in mountainous or broken areas, where conditions readily differ from point to point.

223. A plant newly arrived in a country will behave there like an endemic, with slow establishment and dispersal.

224. Small genera everywhere usually agree with endemics in all respects, except in such special cases as water-

plants, where the uniformity of conditions allows of very wide spread with very few species.

225. Endemism in the old world largely ends at the great mountain boundary from the PYRENEES to the mountains of CHINA. The boundary is much less marked in the new world and in the southern hemisphere. North of the great transcontinental range the floras are in general too young to have had the time for development of endemism.

226. Real relics are rare, and are mostly in places that were sufficiently near to the ice of the glacial period for the cold to kill out some species and to leave others untouched. They are discussed upon pp. 106, 114, 129, 254, 257-8, 318.

227. There is a definite relationship between one Mediterranean country and another, or between CEYLON and MADRAS, or other places not too far apart (pp. 64-87).

228. Relationships between southern endemism and the composition of the British flora are well marked (pp. 82-3).

Chemistry and economic botany

229. Chemical analogies, which are very suggestive, are dealt with (with the assistance of my cousin the Comte de CHANAZ) on p. 372. The laws that seem to do much of the government of matters are so simple that one might expect that they originated in laws of the chemical and other phenomena going on prior to the advent of life, that were modified to suit the new conditions.

230. There are certain parallelisms with what goes on in chemistry (p. 374).

231. A good deal of importance in regard to the much neglected subject of economic botany seems to attach to the reversal of the direction of evolution. If we can get an approximate idea of the course followed by the evolution of any plant producing something economically valuable, like rubber for example, we can begin to study the chemical evolution of it, and trace out ways of making it artificially. We have already brought this subject up in *Evol.*, pp. 8, 89, 169 (top), 177 (middle).

Final

232. We have, we think, now shown the value which inductive study may have when applied to geographical distribution, which has for so long been simply a happy hunting ground for the speculatively inclined.

233. We are also inclined to think that our study of this subject, together with its associated subject, evolution, has not been altogether fruitless, but has shown many promising paths in which useful work may be done, as well as placing geographical botany upon a path in which progress seems possible without speculation.

234. Our theories, now well supported by facts, explain easily many of the difficulties whose pressure has been increasing, like the apparently purposeless nature of many differences, the wide structural discontinuities often seen between species living near together, the increase of divergence as one goes upwards, and so on.

235. Our work proves the general truth of *AA* and of *Evol.*, and of the laws of ASA and of DDM, which prove to be the chief laws that govern the whole subject, and whose acceptance brings about a very noteworthy change in our ways of viewing it. Other laws are also added to them, but they seem to be the chief laws of dispersal and of evolution.

236. The success of all the predictions made by the aid of the sub-conscious mind (pp. 97, 248-9, 482), at least a thousand in number, has added enormously to our confidence that in this work we have been working upon sound lines, and this confidence has also been added to by the fact that illustrations of anything under discussion could always be obtained from any book that happened to be lying upon the table (pp. 97-8), without any need to search for examples.

Appendix I

LIST OF THE SIX LEADING GENERA IN EACH FAMILY MENTIONED ON P. 173

1.	Comp.	Senecio	Hieracium	Centaurea
		Vernonia	Aster	Eupatorium
2.	Orch.	Dendrobium	Pleurothallis	Bulbophyllum
		Epidendrum	Habenaria	Oncidium
3.	Legu.	Astragalus	Acacia	Cassia
		Mimosa	Crotalaria	Indigofera
4.	Gram.	Panicum	Andropogon	Paspalum
		Poa	Eragrostis	Festuca
5.	Rubi.	Psychotria	Galium	Oldenlandia
		Ixora	Uragoga	Randia
6.	Ascl.	Cynanchum	Asclepias	Ceropegia
		Stapelia	Gonolobus	Hoya
7.	Cruc.	Draba	Cardamine	Lepidium
		Arabis	Alyssum	Heliophila
8.	Umb.	Eryngium	Peucedanum	Pimpinella
		Bupleurum	Azorella	Hydrocotyle
9.	Acan.	Justicia	Ruellia	Strobilanthes
		Barleria	Thunbergia	Dicliptera
10.	Lili.	Asparagus	Smilax	Allium
		Aloe	Ornithogalum	Anthericum
11.	Scrp.	Pedicularis	Verbascum	Veronica
		Calceolaria	Scrophularia	Euphrasia
12.	Euph.	Euphorbia	Croton	Phyllanthus
		Acalypha	Macaranga	Glochidion
13.	Palm.	Calamus	Bactris	Geonoma
		Daemonorops	Cocos	Chamaedorea
14.	Apoc.	Tabernaemontana	Gynopogon	Rauwolfia
		Aspidosperma	Strophanthus	Echites
15.	Labi.	Salvia	Hyptis	Stachys
		Scutellaria	Plectranthus	Nepeta
16.	Mel.	Miconia	Leandra	Tibouchina
		Medinilla	Memecylon	Microlicia
17.	Sapd.	Serjania	Allophylus	Paullinia
		Dodonaea	Guioa	Matayba

18. Rut.	Fagara	Agathosma	Evodia
	Boronia	Ruta	Cusparia
19. Ros.	Potentilla	Rubus	Rosa
	Acaena	Prunus	Crataegus
20. Gesn.	Cyrtandra	Didymocarpus	Aeschynanthus
	Columnea	Besleria	Corytholoma
21. Eric	Rhododendron	Erica	Vaccinium
	Gaultheria	Thibaudia	Gaylussacia
22. Bign.	Tecoma	Arrabidaea	Adenocalymna
	Jacaranda	Anemopaegma	Tabebuia
23. Borr.	Cordia	Heliotropium	Tournefortia
	Onosma	Cryptantha	Cynoglossum
24. Anno.	Uvaria	Xylopia	Polyalthia
	Annona	Unona	Guatteria
25. Cyp.	Carex	Cyperus	Scirpus
	Fimbristylis	Rhyncospora	Heleocharis
26. Arac.	Anthurium	Philodendron	Arisaema
	Amorphophallus	Homalomena	Schismatoglottis
27. Flac.	Homalium	Casearia	Xylosma
	Hydnocarpus	Scolopia	Dovyalis
28. Chen.	Atriplex	Salsola	Chenopodium
	Suaeda	Obione	Kochia
29. Sol.	Solanum	Cestrum	Lycium
	Physalis	Nicotiana	Cyphomandra
30. Verb.	Lippia	Clerodendron	Verbena
	Vitex	Lantana	Premna
31. Myrt.	Eugenia	Myrcia	Eucalyptus
	Syzygium	Jambosa	Melaleuca
32. Meni.	Stephania	Tinospora	Cissampelos
	Cyclea	Pycnarrhena	Sciadotaenia
33. Sapo.	Mimusops	Sideroxylon	Chrysophyllum
	Palaquium	Illipe	Bumelia
34. Anac.	Rhus	Semecarpus	Terebinthus
	Toxicodendron	Mangifera	Lannea
35. Malv.	Hibiscus	Abutilon	Sida
	Malvastrum	Pavonia	Sphaeralcea
36. Gent.	Gentiana	Swertia	Sebaea
	Chironia	Halenia	Exacum
37. Aral.	Schefflera	Oreopanax	Polyscias
	Aralia	Cussonia	Dendropanax
38. Am'l.	Agave	Crinum	Bomarea
	Hypoxis	Hippeastrum	Haemanthus
39. Saxi.	Saxifraga	Ribes	Hydrangea
	Chrysosplenium	Philadelphus	Escallonia
40. Cary.	Silene	Dianthus	Arenaria
	Cerastium	Stellaria	Alsine
41. Mor.	Ficus	Dorstenia	Artocarpus
	Cecropia	Pourouma	Conocephalus
42. Camp.	Campanula	Lobelia	Siphocampylus
	Centropogon	Wahlenbergia	Phyteuma
43. Malp.	Byrsonima	Heteropteris	Banisteria
	Tetrapteris	Stigmatophyllum	Mascagnia

44.	Cuc.	Melothria	Gurania	Cayaponia
		Trichosanthes	Sicyos	Cyclanthera
45.	Ster.	Hermannia	Sterculia	Dombeya
		Melochia	Buettneria	Cola
46.	Icac.	Stemonurus	Apodytes	Pyrenacantha
		Villaresia	Iodes	Mappia
47.	Meli.	Aglaia	Trichilia	Dysoxylum
		Guarea	Chisocheton	Turraea
48.	Brom.	Tillandsia	Pitcairnia	Aechmea
		Vriesia	Puya	Dyckia
49.	Irid.	Gladiolus	Iris	Moraea
		Crocus	Romulea	Sisyrinchium
50.	Am't.	Alternanthera	Gomphrena	Ptilotus
		Iresine	Celosia	Amarantus
51.	Cel.	Gymnosporia	Euonymus	Maytenus
		Celastrus	Cassine	Myginda
52.	Zing.	Alpinia	Costus	Globba
		Amomum	Zingiber	Renealmia
53.	Laur.	Ocotea	Litsea	Cinnamomum
		Nectandra	Lindera	Cryptocarya
54.	Rham.	Rhamnus	Phylica	Gouania
		Zizyphus	Ceanothus	Cryptandra
55.	Ran.	Ranunculus	Clematis	Delphinium
		Anemone	Aconitum	Thalictrum
56.	Prot.	Grevillea	Hakea	Protea
		Leucadendron	Persoonia	Dryandra
57.	Gutt.	Hypericum	Garcinia	Clusia
		Calophyllum	Psorospermum	Tovomita
58.	Tili.	Grewia	Triumfetta	Corchorus
		Tilia	Luehea	Columbia
59.	Conv.	Ipomoea	Convolvulus	Cuscuta
		Evolvulus	Pharbitis	Jacquemontia
60.	Onag.	Epilobium	Oenothera	Fuchsia
		Jussieua	Godetia	Ludwigia
61.	Urti.	Pilea	Elatostema	Boehmeria
		Pouzolzia	Urtica	Laportea

Appendix II

LIST OF MOST IMPORTANT LITERATURE USED

(to be added to lists in AA and Evol.)

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Index

in two portions, Latin Names, and General

Abbreviations used : *AA (Age and Area,* 1922), alp(ine), *BH* (Bentham and Hooker), *BSP* (*Birth and Spread of Plants,* 1949), caulifl(oral), char(acter), cont(our), *Dict(ionary)* disc(ontinuous), disp(ersal), distr(ibution), div(ergent), end(emic), E (endemic species), e. g. (endemic genus), *EP* (Engler and Prantl), *Evol.* (The Course of Evolution, 1940), gen(us, era), *Gen. Pl. (Genera Plantarum),* intr(oduction), isl(ands), l(eaf), *LC (London Catalogue of British Plants,* 11th ed.), *NP*/1 or *NP*/2 (*Die Natürlichen Pflanzenfamilien*) polyphyl(etic), *PR (Das Pflanzenreich),* sim(ilarity at a serious distance apart), seq. (and following pages), terat(ology), unexp(ected), unus(ual), W(ide), WE, WEE (wide and one, or two, endemics).

Families are given under their latin names only in the general Index, where also some of the most frequently used genera or tribes are given a second time. All of rank below fam. are given in the latin Index.

The heading of an article in the Index is supposed repeated with each subordinate entry. For example, under Britain, British, read in line 7 there *British families,* in line 14 *British flora,* and so on. But sometimes an addition to the heading is taken up, and may have one or more subordinate entries. *e. g.* in line 16 read *British flora mostly from France.* Usually the subordinate entry is not in its proper alphabetical order.

Index of Latin Names

SUPPLEMENT

Index General