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 avalanthes (*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 insurmount-

able 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 complete-
ness 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, inciden-
tally, 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 *A A* 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 (*A A*, 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 indi-
viduals 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 disper-
sal, 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 GALA-
PAGOS, 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 *A A*, *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

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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
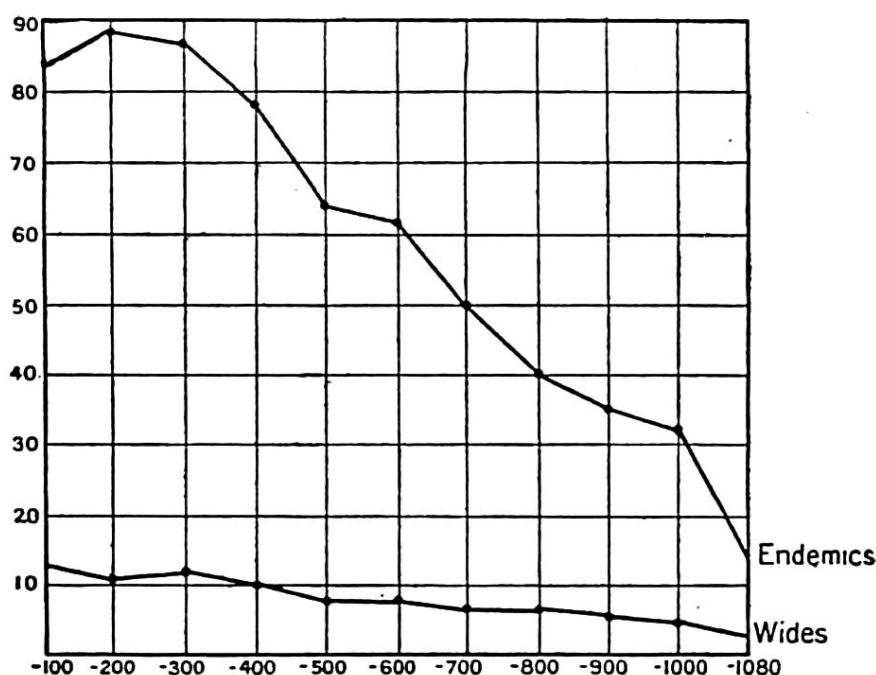
NORTHERN INVASION OF NEW ZEALAND

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.

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 intro-duction 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 emigra-tion. 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 fur her 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 *Archichlamy-deae*, 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. *Mono-
porandra (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 condi-
tions, 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 descrip-
tion 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.

a	Species (b) evidently began somewhere there, in rather
a	drier conditions than (a) (OREGON is a very wet country),
a	and went ahead of it to the south.
a	
ab	*Cymopterus*, described as to dispersal in (93) is the
abc	third American genus of *Peucedaneae (Umbell.)*. The
ab	map given by its author shows that *C. acaulis* was pro-
ab	bably the original parent, which appears to have arisen
b	somewhere in the region of DENVER, COLORADO, at a
b	height of say 5000 feet (1500 m.). From there it spread
b	into the region of the MISSISSIPPI, into the SW corner of
b	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 *Cichorieae*, 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	10 P	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

	Spp. World	Spp. Brit.	Max. Disp.
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

	World	N.Z.	Endc.
1) *Senecioneae*			
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		

	World	N.Z.	Endc.
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.		Spp. World	Spp. N.Z.	Endc.
5) *Astereae*				9) *Heliantheae*			
5. Olearia	100	35	35	1. Bidens (weed)			1 —
7. Brachycome	60	5	5	10) *Arctotideae*	Nil		
x. Celmisia	50	43	42	11) *Mutisieae*	Nil		
x. Lagenophora	15	6	6	12) *Helenieae*	Nil		
x. Vittadinia	8	1	—	13) *Calenduleae*	Nil		
Haastia	4	4	4				
Pleurophyllum	3	3	3				

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 che-

mical combinations with the formation of new ones, a pheno-menon 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 cha-racters, 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 explan-ation 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 "domi-nant" 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 import-
ance 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 cate-
gorical 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 loga-
rithmic 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 al ow 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 :

	Ones	Twos	Threes	Total
Crucif.	18	7	4	29
Umbell.	21	10	10	41

Found only in America and the West Indies :

	Ones	Twos	Threes	Total
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.	Chrysanthe-		
Saxifraga (5)	325	N. temp., S.Am.	mum	180	Eur., As, Afr.
Potentilla	300	Cosmop.	Average size		
Sieversia	40	Temp., arct.	of all, 236		

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	Carex	*Cassia*	Hypericum
Astragalus	Salvia	Cyperus	Ranunculus
Solanum	Gentiana	*Baccharis*	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 :

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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 moun-
tain 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 increas-
ing the difficulty of barriers, but encouraging the formation
of endemics.

Structurally there are few special characters about moun-
tain 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	

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Genus	Spp. in world	Tribe	Spp. in Seych.		Endemics	
Guettarda	60	Leader of *Guettardeae*	1		—	
Morinda	50	Leader of *Morindeae*	1		—	
Gardenia	100	2nd Garden.	1		1	
Tarenna	30	4th Garden.	1	8	1	4
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	1	2	3	4	5	6	7	8	9	10	More
Islands											
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 *A A*, 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 *A A*, 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).