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## CHAPTER XII

### General Considerations

Evolution by divergence, downwards; classification;  
incidence of character; chemical analogies;  
permutations and combinations;  
kaleidoscopic mutation

In this chapter we have attempted to draw together some of the threads that run through the whole of this work, and it may be well to give an index of them.

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1. *Introductory*. So many changes in outlook are suggested that a further review seems advisable. We have seen how age and area led to size and space, with the complementary



law of size and age. By way of the hollow curve discoveries, these led in turn to dichotomous divergent mutation, with its corollary that evolution went towards the species, not conversely, and this led to further deductions, which are continually increasing. We have also seen how large and how divergent a mutation can be, not only in single species, but in the large families, tribes, genera, and other divisions. We have given many examples of these, showing how the descendants tend to go into other divisions than does the parent, and that automatically. The phenomenon, in fact, is completely general, and is a law of evolution. The turning of the evolutionary process back to front clears up at one stroke many difficulties that have long beset us, and makes the whole process much simpler and clearer.

Evidently species and genera began as very local endemics, gradually increasing in number, and spreading further afield, and that with increasing rapidity ("to him that hath") as time went on (*AA*, p. 34), so long as not interfered with by other agencies or barriers. Evolution worked downwards towards the species, not away from it (*cf. Evol.*), in discontinuous mutation that covered a varying number of characters; and according to the size, number, and "importance" of the divergences, we have been accustomed to judge the rank of the newcomer, which has, however, not usually been recognised as such.

Perhaps the greatest difficulty that has always troubled the theory of evolution by selection of advantageous variations first presented in a very rudimentary condition, has been the considerable and discontinuous, often incompatible variation between one species and another. Many of the characters in common use show such incompatibility that one cannot trace them back to a common source, even in such simple cases as leaf glabrous/hairy, or ovule erect/pendulous. In nearly all cases, there is divergence somewhere, that cannot be made gradually to merge in some ancestor, selection or no selection. Such union, which must occur somewhere, is only possible if the joint ancestor was carrying the potentialities of both characters, but could only display one. Some kind of super-Mendelism is evidently at work. The first plant of the family, of course, was not necessarily carrying all the characters, afterwards displayed, in a ready-made condition. The possibilities were there if

certain things were put together in certain ways. Each new divergence makes other ones possible, as the formation of a new compound in organic chemistry makes further combinations possible.

The mere fact that however far back one may trace angiosperms, one finds no sign of new families, goes to show that the upward direction of evolution from species, demanded by the older school, cannot be upheld. And the final proof that it must have been the other way seems to be given by the table on p. 173, which cannot be explained except by downward evolution, and the tables of leaders (cf. Index).

We have shown that mutation covers the whole divergence between two species at one operation, and selection is not valid in dealing with such. At most a choice may be made between the two *faits accomplis* of parent and child. As the latter must, when it survives, have inherited enough of adaptation to do so, and this, unlike that of the parent, centred upon the local conditions, the child will probably be at no disadvantage, unless by its small numbers. Its divergence will isolate it from loss by crossing with the parent.

Selection being thus eliminated as a leading urge in evolution, we no longer need to find the supposed great numbers of intermediates, whether as relics or as fossils. Many years ago, HOOKER said (*AA*, p. 205) "the advocate of creation by variation may have to stretch his imagination to account for such gaps in a homogeneous system as will resolve its members into genera, classes, and orders...". For a long time we have been accustomed to believe that this could be done upon a system of gradual progressive development, though the thought of the discontinuities was always disturbing, and this was more clearly realised with the work of BATESON, DE VRIES, WENT, and others. The difficulty disappears with the acceptance of divergent mutation, which turns some of the evolutionary process back to front (not upside down), taking away the need for destruction of intermediates. There is now no reason for the death of the parent, so that the number of species and genera tends to increase upon the principle of compound interest, the logarithmic straight line. In this connection, one may look at DARWIN's diagram of evolution in the *Origin*, p. 91, with an actual decrease at first, followed by an increase at a far future date.

Characters, it would seem, are not usually acquired for

adaptational value by selection along the road, but by some much more definite method, with a law behind it, which, as WENT said in 1907, had no adaptational aim, that indeed seems almost impossible under divergent mutation. Development of characters seems to be by the action of conditions, probably mainly external, upon certain internal characters. As none of them is likely to repeat itself exactly, the way is thus open for an enormous variety in evolution, as the number of characters increases, from which permutations and combinations can be formed. Upon the whole, the selection of the best individuals that is always going on will keep things always near the highest possible pitch of efficiency for the conditions met with at any particular place and time. But there will be no further progress in efficiency till possibly, though not necessarily, a new mutation may bring in a more efficient variety or species. And we must never forget that a plant depends upon the total efficiency of all its characters, any improvement probably costing material which will have to be made up elsewhere. Any mutation that lessens the total efficiency will be punished, probably by extermination.

Though the possibility of occasional acquisition of a character by selection cannot be excluded, it is probably rare. In the writer's early days, desperate efforts, in which he took a small part, were made to find adaptation in everything, with the result of almost complete failure. A much more probable view is that potentialities of all or nearly all characters are handed down from above by heredity, so that at any time, as far as we can see, any character found in a family, or more rarely outside of it, like the superior ovary in a few *Rubiaceae*, may appear. In the changes or divergences that this is liable to bring about at any mutation, it reminds us of the behaviour seen in inheritance by the laws of Mendelism. This does not in any way mean that in an early protophyte there *are* the characters of say the *Labiatae*, but that there are certain potentialities that if they go through certain changes in the future may result in *Labiatae*, but if they do not, no *Labiatae* will appear, or a family *Dubitaceae* may appear in their stead. The characters of *Labiatae*, or any other family, are, it would seem, a kind of chance lot that happened to come together in a way dictated by previous changes in the first ancestor of the family, and

with no mutual correlation that we can yet perceive except that they generally cover all parts of the plant. For some reason unknown, they remained very constant in the heredity, and formed the family characters. But a very small change anywhere in the processes that went on would have produced a different result after a few mutations more, and would perhaps have given us a new family or families now quite unknown. These suggestions seem to get over the former difficulties about divergence and transitions, to a very fair extent.

One must not forget the possibilities in HARLAND's suggestion (*Evol.*, p. 62) of selection of slight genic changes. These might be added up till the strain upon the nucleus produced a divergent mutation, probably electrically controlled (*Evol.*, pp. 182, 47). But we do not know that such changes are actually adaptive, so that selection can hardly be expected to do much, and in a case like the pollen patterns of *Acanthaceae*, it would seem powerless. If two species meet with close similarity of stress, there seems no reason why they may not mutate upon more or less parallel lines, but that is about as far as we can go at present.

Without doubt, selection has proved itself an unsatisfactory explanation. Even without much other contradictory evidence, it is helpless to explain all the arithmetical results brought up in the establishment of the laws of ASA, the hollow curves, the dichotomous divergent mutation, the early production by the leader of the leaders of tribes, sub-tribes, and so on. The whole process of evolution and dispersal seems to be following arithmetical rules, and bearing out what YULE and the writer said in 1922, that evolution is unfolding itself by mathematical law, while the vital and other factors only cause temporary deviations from the dominant plan (and *cf.* summary in *Evol.*, p. 191). Beyond this statement the writer's lack of mathematical training will not allow him to go, but YULE (158) worked out a mathematical theory of evolution based upon our joint discoveries.

Under the conceptions that we have brought up, evolution seems to run with comparative simplicity and smoothness, and we have given above, and have in reserve, a formidable mass of favourable evidence. The kaleidoscope, which we have used as an illustration for 40 years, gives fair suggestions



of what seems to be happening. The theories here put forward seem to explain with simplicity the difficulties whose pressure has long been increasing, such as the apparently casual and purposeless nature of the differences between species &c, the wide structural discontinuities so often seen between species of the same genus living near together, and the narrow ones sometimes seen when they are far apart. Destruction of transitions has been too much called upon, especially when it is often impossible to have a transition. Some may be explained by the writer's conception of an overriding genus or species (147).

One may see this impossibility of transition by looking at the list of CEYLON WEs on p. 111, and there is evidently no conceivable use-value in such divergences. They are evidently incidental results of the mutation, which readjusted the equilibrium of the nucleus, and may be compared to the chemical changes that so often occur when one brings together two bodies like chalk and an acid. The substances after the reaction are quite different from those before it; their atomic content is the same, but put together in a different way. There has been no destruction, but only a permutation to a new combination of the units. Sometimes the pressure of the surrounding conditions exercises a definite pressure in one direction, and there seems a tendency to produce mutations that show movement also in that direction, which one may, if one please, regard as "adaptation". Like causes tend to produce like results upon material that is not too dissimilar. Many xerophytes show such phenomena, which we may see in a small family like the *Penaeaceae*, which are localised in CAPE COLONY with five genera, *Penaea* (12 spp.) *Brachysiphon*, 5, *Sarcocolla* 4, *Endonema* 2, and *Glischrocolla* 1. Yet, as so commonly occurs, there are two tribes, showing once more that the direction of evolution must have been downwards.

All show ericoid habit with crowded evergreen opposite leaves, xerophytic characters which must have appeared in the first species of *Penaea*, probably *P. mucronata* the most widely dispersed. Their appearance was in some kind of response to the dryness of the country. The characters of this first species have been handed down, and as the family is evidently recent, it has not yet had time or opportunity for much variety. But young and small as it is, there is

already an indication of the behaviour which in larger genera produces complexes, where the same character may appear unexpectedly in more than one place, and in different genera, for *Sarcocolla* has sometimes one, and *Glischrocolla* with its solitary species always one ovule, so that there are signs of intermingling. This kind of thing, upon a large scale, is frequent in large genera.

Even in so small a family as this, we have to use such words as usually, or sometimes, for the characters tend to alter, even the family characters, to some extent at every mutation. Larger size offers more opportunity for change, as one may see in *Violaceae*, where *Rinorea* with 260 species in the *Violeae* has sometimes an appendage at the back of the stamen, but shares the useless character with *Gloeospermum* in its own tribe, and *Amphirrhox* in *Paypayroleae*; sometimes it has not the appendage, and shares that divergence with *Melicytus* and *Hymenanthera* in its own tribe, and *Paypayrola* and *Isodendrion* in *Paypayroleae*. A still more complicated phenomenon of this kind is described in *Evol.*, p. 139, where the same divergence occurs in three separate but related families. It is in something of the same kind of way, rather than the trial and error once so much appealed to, that what we usually call adaptation has been brought about.

Evolution must apparently go on, though but slowly in such cases of uniform conditions as *Hippuris*. It is more rapid in *Podostemaceae*, though the conditions are perhaps even more uniform, for there is a constant pressure of plagiotropism, and a whole lot of useless modifications seem to have been brought about in response to that. Even in such plants as the more or less internal fungi, like the *Puccinias* (700 spp.) or the *Polypori* (500) there are many species, in spite of the apparent uniformity of the conditions. This may be due to the greater plasticity of the body of the plant, or more probably perhaps to the variety in chemical composition of different hosts.

As yet we cannot say whether outside pressure *compels* mutation in any given direction, *encourages* it by the gain that may result, or perhaps most probably *kills off* those mutations that go too far in any other direction. The known facts show that under the normal conditions of mesophytic life on land, for example, the mutations may affect any of the features of the plant, but especially, as is well known,

those of the vegetative rather than the reproductive organs. It is even possible that some of the changes in the latter are correlated with those of the former.

But to the results of these periodical mutations, it is usually quite impossible to attach any adaptational value. In practically the whole list of divergences in CEYLON endemics on p. 111, the characters are neutral or indifferent. As we said in 1907 (131), one of these endemics, *Acrotrema lyratum*, "only occurs on the summit of Nillowekanda, an isolated precipitous rock in the Hinidum pattu. Is it to be supposed that the long peduncles that characterise this species are a special adaptation to the conditions on the very small area of the top of the rock?"

It was also pointed out in that paper how much simpler the tracing of descent becomes upon the theory of mutation with large divergences, and that unless these are actually harmful in the struggle for existence, there is no reason why "the whole tree of a family should not actually exist upon the earth at the present moment". In a following paper, suggestions (very crude, for lack of more detailed knowledge) were made for a tree of *Dilleniaceae*, and many suggestions are made in this book.

2. *The laws of ASA.* We have already said so much about these, for example upon pp. 16-23, and in the two preceding books of this trilogy, that there is little to add. Age and area, the law from which all the rest of my work has logically followed, is described on pp. 16-19, and was the main subject of the first book, in which the law itself is dealt with on pp. 54-83, answers to objections on pp. 84-100, and a review by Dr GUPPY, the coauthor of much that is here brought up, upon p. 101. The law of size and space, deduced from age and area, is dealt with on pp. 113-8. In this book it is described on pp. 19-22, and illustrations are given. The third law, of age and size, necessarily follows from these two, and the laws of ASA (p. 23) are complete. They have proved to be universal in distribution, and by their application, apart from subsequent deduction, a good deal of the incoherent mass of facts that have so far constituted the subject of geographical distribution, may be reduced to order. Special instances of their applicability will be found, not only in the latter half of *Age and Area*, but also in *Evol.*,

pp. 27-32, where there is a brief summary of the whole position, in Testcase III, p. 69, and several other testcases, especially XXV, p. 140, and XXVI, p. 146. In this book, besides the description on pp. 16-23, there are references on pp. 26, 30-34, 38, 45, 50-58, and so on nearly all through.

3. *Competition individual, not specific.* In 1867 FLEEMING JENKIN made what DARWIN considered the best criticism made of his ideas, changing them to suit it. JENKIN showed that evolution could only work with very small variations if the competition was between considerable areas of the new and the old, or any improvement would soon be lost by crossing. This, by making a new species begin upon a considerable area, caused the growth of the ideas of relicdom for species or genera of very small area. For many years we have been trying to show that there is no reason to suspect relicdom, except near the coming of the ice, or in other exceptional places, and indeed a glance at the map of the New Zealand *Ranunculi* on p. 65, or the S. American *Siparunas* on p. 224, makes the idea seem somewhat absurd. Even in *Ranunculus* itself, a bare 25 of its 300 species are really widely distributed. The distribution of the genera in BRITAIN goes largely with their size in the world, much more so than with any vital factor.

Part of the legacy involved in these conceptions of DARWIN and JENKIN was the idea that species competed as units, and that the competition reduced the older one to a relic, or killed it completely out. But with what we have now seen of the operation of the laws of ASA and of dichotomous divergent mutation, it is very evident that that idea must be discarded. Competition is a law of life, but it is not the controlling force of evolution.

We have referred to this matter at various places, notably on pp. 27-8, 88-9, 208-9, and many others. If competition is specific, or in other words if relicdom be the general rule, then we are on the way, as the writer has often pointed out, to a wholesale extinction of genera and species, so that ultimately only a very few will be the survivors, even in *Ranunculus*, old and large genus though it is. But there is nothing whatever to show any superiority of one species over another; the larger area occupied by some species is simply the result of their greater age, as has now been abundantly proved.



It is also, perhaps, not fully recognised that the competition that is really going on is much more complicated than a mere struggle between two species as to which shall win when one, for example, has ten stamens, the other only five, or one a superior, the other an inferior ovary. It depends in any single case upon the efficiency of the whole outfit of the one individual as against the other, and also upon whatever may happen to be, at that particular time and place, the whole pressure of the local external conditions upon the two competitors, which may and usually will differ at every time and place, and may even differ for the two competitors themselves, whose surroundings will be different. It is a competition restricted almost entirely to individuals; very rarely indeed, if ever, will a whole species take part in it, unless in the case of a new species beginning as a few individuals at a definite place.

Such competition as that described by CROMBIE in (28) is quite a different matter, for there it is a competition of two species of different genera, in one particular locality and set of conditions, but not over the whole range of these already established species. A comparison of the divergences given in the tables on pp. 111, 132, 165, &c above will show this clearly. All Smiths are not competing with all Browns, though John Smith and William Brown may be desperate rivals. Thomas Smith will win in one place, in one set of conditions, James Brown in another.

4. *The hollow curve.* Our work upon this subject has aroused even greater opposition than that upon age and area. Opponents have insisted that it is accidental, not realising, perhaps, that an accidental, but regular, occurrence is one that must have behind it some law or laws. Besides a good deal in *AA* (especially Chap. XVIII, p. 195) and in *Evol.* (especially Chap. IV, p. 33, pp. 96-7, Testcase V, p. 99, and on pp. 164 and 173), there are many references in the present book, of which we may just mention those on pp. 18-19, 30-35, 67, 124, 170, 185, 190-93, 204, 219, 258-9 (and curves).

YULE showed that the curve was just the *necessary* result of dichotomous mutation with survival of the parent. Some people think that the law of compound interest, which we have followed here, and which certainly gives a very close

approximation, is too simple. It is for example, not improbable that the formation of new species does not exactly follow this law. But in dealing with such matters one must remember that nature was not out to create new species and genera, which are more or less artificial conceptions that deal with nature's divergences by making them into groups, which we regard as greater in standing (genera), or less (species). One cannot define these, but only describe them, and largely by mutual comparison. Not being a mathematician, the writer can only refer the makers of such objections to the paper by YULE, formerly President of the Statistical Society (158), and to our joint paper in (159). When a family is young, it follows very closely, as we have seen, the chief laws that we have brought out, those of ASA, of the hollow curve, and of dichotomous divergent mutation. But as it grows older, and especially as its leading genera begin to exceed about 20 species, other factors, whose gradual results only show themselves after long periods of action, begin to make their effects visible. Such factors are changes of climate, the effects of irruptions of the sea, of the formation or disappearance of mountains and other barriers, and so on.

There can be no doubt that the formation of the hollow curve is due to the action of a general law, and we owe this discovery to YULE, who showed that what the writer had suspected was due to the continual operation of dichotomous mutation with survival of the parent. In this connection, the first 12 pages of YULE's paper, which require no mathematical knowledge, should be read, as well as our joint paper in (159).

The 15 largest families of all show beautiful parallel hollow curves (fig. at p. 260) which by logarithms plot out into sloping straight lines (p. 262). Down to families of say 100 genera, the curves are good, but lower down, below say 20, they begin to become very irregular, so much so in many cases that one does not feel sure that they are really the early stages of the good curves shown higher up. Yet there cannot be one law for large and another for small, and the suggestion obviously is that some of the very small families, of which great numbers have been made in recent years (p. 341) upon structural considerations only, are not strictly genetic, as under the circumstances one might expect. But as we have shown that this is inevitable, it does not matter

(now) from the taxonomic point of view, and the breaking up into separate families will probably be better for identification purposes. Now that we have seen that as one goes upward in a family from the small genera to the large, genetic relationship increases in closeness, while the divergences become more distinct, we can no longer take structural resemblance as the only, if even the chief, test of genetic relationship. Size of a genus, or area covered by a species, is of equal or greater importance. The largest genera in a family are the most closely related that is possible, though of course all over the family there are groups of genera that are equally closely related, formed in the same way by the descendants of a single mutation at the top, like the mutation that formed the head of the family.

One must not forget that the great bulk of genera and species are contained in the larger families at the top. Those with more than 100 genera are (*cf.* p. 173) only 28 in number out of 309, but they contain 8005 genera out of 12,516, or nearly 64% of the grand total. That the rule of "to him that hath shall be given" holds here as everywhere may easily be seen by noting that new genera are added in greater proportion to the large families. In the last issue of the Supplements to the *Index Kewensis*, there were 406 genera added to the 28 large families, and only 370 to the small 281.

The great irregularities shown by the smaller families, *e. g.* *Aceraceae* (*Sapindaceae*, genera of 110, 1), *Achariaceae* (*Passifloraceae*, 1, 1, 1), *Actinidiaceae* (*Dilleniaceae*, 250, 25, 12, 1), *Alangiaceae* (*Cornaceae*, 30, 20), *Aquifoliaceae* (180, 12, 3, 2, 1), and so on, show that there are probably several disturbing causes at work. But the grand total of all these very irregular families is so small that it is clear that if they were genetic they would be obeying the same laws as the large. Their formation has much in common with that of such a group as the sub-family *Thunbergioideae* in *Acanthaceae* (details on p. 216), which is founded on structural characters only, showing the somewhat marked divergence of papilla- rather than hook-shaped retinacula. This is shown in the large and widely dispersed *Thunbergia* itself with its 150 palaeotropical species, mostly African, but outside this genus is only shown in *Pseudocalyx* with one species in MADAGASCAR, and *Meyenia* with one in the EAST INDIES (these two evidently originating from different species of

*Thunbergia* at different places). It is evident therefore that the two or three intermediate genera, if there were any, must have mutated back to the group that contained the original parent of *Thunbergia* itself.

The divergence producing *Thunbergia* could evidently only be a mutation, and the genus has no genetic right to a special sub-family on that account. Probably the same thing may be said of many of the little families, especially those made during this century (the name of the family from which they were split off is given in the first four above). They are very convenient for purposes of systematic classification, but probably often have no right to be considered permanent genetic groups. We may almost look upon some of them as what we may perhaps call temporary extrusions from some other sub-group. They have been given their rank for structural reasons only, and we have now seen that the rules of taxonomy are necessarily different from those of genetic descent. We have not fully understood that incidence of character seems always to be determined by law, and have therefore had to work by "valuation", which is well known to differ in almost every case, the real and only connecting link being that of age. Probably some of the direct descendants that ought to fill in the unexpected gaps, such as are found in *Thunbergioideae* or *Aquifoliaceae*, have reversed or altered the particular mutation that gave rise to their group.

Having regard to the rule of dichotomous divergent mutation, it is not easy to believe, for instance, that *Piper* and *Peperomia* (cf. p. 289), or such genera from small families as *Acer*, *Begonia*, *Canna*, *Dichapetalum*, *Dioscorea*, *Erythroxylum*, *Nepenthes*, *Oxalis*, *Plantago*, *Salix*, *Saurauja*, or *Xyris*, have a real right to their positions as supposed heads of genetic families.

On the theories that we have adopted here, it is clear that on any one continent, the members of a family should be fairly closely related, arising as they do from one or more of the now large genera that have led the family or its sub-groups from the commencement, and that in a large family tend to occur in many, or even all, of the continents. For example, taking the first five families by size from p. 173, and looking at their leaders, we find *Senecio* and *Panicum* in all five large areas in the world, *Astragalus* and *Psychotria* in four each, and *Dendrobium* only in two, though all the



families occur in all five. In the single case of the *Compositae* we find the leaders down to 150 all more or less cosmopolitan, while the smaller leaders of the last four, none larger than 80 species, are all confined to one continent each. In such cases one must not forget the law of "to him that hath".

If the laws that we have suggested hold, therefore, we shall expect that upon each continent each genus that reaches it, of over say ten species, will form a hollow curve in proportion to its size. The result of all this should be the formation of a combined hollow curve for each large division of the world. We have seen how this is the case in *Acanthaceae*, and in large divisions on pp. 180-1 in *AA*.

The hollow curve is a regularly recurring feature of the growth of a family, and may be added to the very many simple arithmetical demonstrations that show how mechanically followed out are the processes concerned in evolution and in geographical distribution, though they are interfered with in their regularity by the intervention of barriers, and other factors that cannot be easily foreseen, or discovered to have been intervening in the past, such as changes of climate, and other things. See diagrams at pp. 260-2.

5. *Divergent mutation*. We have already said much about this in Chap. V, especially on pp. 99, 100, and the description of teratology on pp. 100-105, and again in Chapter VIII, but there are still points of interest that must be clearly brought out. HITCHCOCK (63, pp. 4-5) says that "the generally accepted classification in use... is based upon genetic relationships. The theory of organic evolution assumes that the organisms of to-day are descended from similar, though slightly different organisms of the past, and that all organisms are genetically related... The modern classification of animals and plants is an attempt to arrange the groups of individuals in a system which shall represent their genetic relationships."

It would seem that a somewhat different point of view will now have to be taken, as nature seems to lay great stress upon creating marked differences, to a greater or less extent, at every mutation, and we have been accustomed to lay too much stress upon close structural relationship in as many details as possible. We have considered as awkward difficulties those divergences, such as ovary superior/inferior,

which appear to be part of nature's scheme. What the writer proposes in place of the older conceptions is what he has called dichotomous divergent mutation, whose essential features are pointed out upon p. 99. They include dichotomous mutation, survival of the parent, automatic isolation of the new form, well marked divergence in one or more characters, less in others, acquisition of the needful local adaptation by simple heredity, and no necessary improvement, though any deterioration is at once punished by natural selection, usually with prompt death. A new form is thus produced at one operation, ready to begin to spread with no risk of loss by crossing, if it can survive to the stage of reproduction.

The great tendency seems to be for the earliest mutations, whatever the character of the differences, to head the taxonomic divisions into which we split the family. These earliest mutations will be the most obvious, distinct, and "important in that family" because they are the oldest there, appearing before so many other mutational changes have come to (perhaps) obscure the first, though as a matter of fact they usually show clearly enough; and still more because, being the oldest, they can pass on some at least of their peculiarities to a great many descendants if the family be of any size. Though all these will probably inherit most of their peculiarities, there is no guarantee, nor indeed upon our theories any expectation, that they will inherit all, or nearly all, inasmuch as every mutation seems to change, more or less, more than one single character, in a divergent way. At present we know no laws governing the matter of the changes, which seem to come by mere chance.

The exhibition first of all of the leaders of tribes, subtribes, &c, working downwards to genera in these groups, and only rarely with a further break into something markedly divergent and new, shows that the greatest divergence of character is at the top, and that it diminishes downwards, though at times we may get a more "important" divergence than usual, producing even the head of a new genus, subtribe, or other group. At present we are quite in the dark as to why, when, where, and how these things happen, and it is one of the many new tasks brought up by all this work, to find answers to these questions. There seems no appreciable difference in divergence between the first two genera

in a large, and the first two in a small family, but there is a fairly definite one between the divergences which on the whole are near to the head of a family, and those which are near to the foot. This difference, easily seen, but not so easily defined, though appearing on the whole to be marked by divergence in more characters, seems to the writer one of the most important points needing consideration in connection with the incidence of characters.

There is, as we have said, probably some systematic and perhaps arithmetical distribution of characters going on, upon what we have called super-Mendelian lines, which may need some work to elucidate. The characters are evidently handed down in such a way that every organ that existed in the parent is again provided with some character in its offspring, sometimes by a definitely divergent mutation, sometimes by a change of size which is more like a fluctuation, except that it has a new mean. At other times, and especially in the case of flower or fruit characters, the change is less noticeable, and the ovary may remain inferior, for example, changing only in minor features, which make no difference to its essential character.

As HITCHCOCK says on p. 5, "fundamental or inherent characters are inherited with certainty (the writer would add a proviso that any one might change at any time)... superficial are easily modified... inherited in a less certain or less definite manner." This is largely the problem that lies before us. Why are there these differences in inheritance? Why do the family characters remain almost unaltered through a series of mutations? What selects certain characters for "inherence" in one group, while in another they may be rare, or variable? That at any one mutation any one character should remain unaltered is not surprising, but that two should do so, and remain in the same mutual relation is much less common, and that several, like the family characters, should do so, even though only to a great extent, is much rarer.

The larger the family, the greater the probability of exceptions among the smaller members, and of complexes among the larger. If all the unexpected characters that may appear in a large genus were to do so *together*, we might get a completely new family or genus, as we illustrated in (146). Or let us take *Psychotria*, the head of *Rubiaceae*, and put

together all its unusual or "abnormal" characters, when we should get an almost herbaceous undershrub, 50 cm. high, with large dark-coloured four-pointed stipules united into a cup, heads of 4-merous flowers, 2-3 cm. long with very small bract and bracteoles; calyx oblique at mouth, corolla with circle of hairs at base, teeth horned as in *Rudgea*; ovary 5-locular, fruit with broad wings. All taken together, these characters would fully justify a new genus, but that they should all happen together is practically excluded by the ordinary laws of chance.

The heads of tribes are mostly in the largest (oldest) genera of a family, and tend to be the first to reach a given country, as we have seen in BRITAIN, so that as a rule a family with only two British genera shows a marked divergence between them. A genus A heads a family, and splits off B, which in three cases out of four heads a new tribe. It is by no means unlikely that the next two or three mutations may all be from A, which has a long start while B is getting established. A careful study of the genetics of the large genera might be profitable. For example *Begonia*, which has a very large series of chromosome numbers, has but very few and very small descendants that show its own main characters; most of the even numbers of the grasses occur in *Carex*, and so on.

The species behave in the same way as the genera, taking space rather than size. The British genera in A with only two species each, but with these accepted by all workers, show :

Achillea	{ L. linear, serrate; heads few, hemispherical L. much divided; heads many, small, ovoid	
Althaea	Perenn., with velvety down Annual, with long hair	
Anemone	L. ternate	L. bipinnate
Anthriscus	Umbels terminal	Umbels lateral
Arctostaphylos	{ L. evergreen, shining, box-like L. strongly veined, withering at end of year	
Asperula	L. about 8 in whorl	Opp., or 4 in whorl
Aster	Invol. bracts few, oblong	Many, narrow-linear

This bears out what we predicted above.



At the beginning of a family, the child is three quarters sure of being in a different group from the parent, but this rapidly diminishes in later stages. It is clear that rank goes mainly with the comparative age of the parent. This, in fact, is the principle which GUPPY named rank and range (*cf. Evol.*, p. 100). The effect of mere age has been quite ignored in taxonomy, to say nothing of the geometrical increase of numbers.

More than one character seems to change at each mutation, some more than others, while they are practically all unsuited to selection, and many to transitions. Some of the smaller changes may probably be attributed to the principle of compensation, a loss in one place being made good by a saving in another. This may be the reason why, for example, some species of *Krascheninikovia* (*Stellaria* p. p.) show dimorphic flowers, the sterile with petals, the fertile without. There are many such cases.

Divergences may occur in any character, and each new one may open the way to the possibility of yet others, so that on the whole, though some may be lost, the available total will increase, like the numbers of chimes that can be rung upon larger and larger sets of bells, so well described in *The Nine Tailors* of Miss Dorothy Sayers. We have seen how large and how divergent a mutation may be, in endemics in Chap. V, small genera on pp. 130-31, small families in *Evol.*, p. 199, genera that head tribes on p. 173 *et seq.*, and in species on pp. 182-3. In the early division of a family or genus, *no matter what the characters of divergence may be*, the offspring show a strong tendency to go into a different group from the parent.

As soon as it has become reasonably established, B tends to repeat the procedure of A, its early descendants including most of the heads of sub-tribes, and so on downwards, upon what we must regard as a diminishing scale of operation, from family through tribe to genus, species, and sub-species, where we have to use area of occupation as an index of age. If one follow the mutations of A, or B, and not those of their offspring, we seem to keep to "larger" mutations. But there seems little or no difference in rank of the first mutation shown by a large, or by a small family. The whole subject needs much intensive study.

What are often called transitions to other families or genera are in my conception simply appearances by divergent mutation of characters that more distinctly mark other families or genera. Such are, for example in *Rubiaceae*, the whorled leaves of some *Argostemmas*, *Limnosipaneas*, &c, the sometimes winged seeds in *Anotis*, *Kadua*, or *Sickingia*, no endosperm in *Henriquezia*, and so on. The last named, with its zygomorphic flowers and other peculiarities (for *Rubiaceae*) is often called a transition to *Bignoniaceae*, but now that we know that the whole step may probably be accomplished at one operation, it is no longer necessary to look for transitions. There are no transitions in single characters, except very rarely. What such things as *Henriquezia* represent is really a mixture of characters, of the one side or the other, but just as finished as usual.

In the case of large families, it is necessary for reasons of convenience to break them up into more subheads than in the case of small ones, where two lines in the key will often suffice. The larger number of subgroups in a big family (*cf.* table, p. 173) is thus partly due to such needs, and they are not always so well distinguished as in small.

We have dealt with evolution in many places above, in the whole book *Evol.*, and in places in *AA*, and we shall carry it further in the section upon the Orders, upon p. 323. Selection and adaptation being now excluded as important agents in urging it on, though they cause "deviations this way and that from the dominant plan", the latter becomes a good deal more mechanical. The size of a divergence matters less than its age, and the isolation that age gives to it. The principle of "to him that hath shall be given" thus assumes very great importance as a law of distribution. Even in the details of ecological distribution, as we have seen on pp. 24-8, 38-9, and 42, the most widely dispersed species of a country include most of the dominant species of its associations, which were simply among the first to arrive there, so that they have become specially well adapted to the local conditions, and that in a variety of places.

Under "Darwinism" such things as the innumerable sub-species of *Rubus* or *Hieracium* had to be regarded as incipient species, but, as we have pointed out on p. 184, this is no longer necessary. They are later ripples of the evolutionary wave which is dying out, and not the first ripples that

come with the onset of the wind, and gradually unite and develope into larger waves.

In the lifetime of the flowering plants, with which we are mainly concerned, it is not yet possible to say with certainty that mutation is decreasing in emphasis from above downwards, so long as one keeps to the line of the families, for one can see no difference between bi-generic (*Evol.*, p. 199) and large. But in an individual family, it seems to diminish from family through genus to species and variety, and the divergences are better marked and in more characters, perhaps, at the top. In any case, the taxonomic scheme which will be employed in dealing with any group soon reveals itself, and this is a very important law which seems to run throughout. In this connection, we may refer especially to pp. 168-77, 181-84, 188, 206-10.

When life first appeared, perhaps in the form of something like a schizophytic alga, there would be so little complication of structure that possible divergences would be few and simple in most cases. A hydrophytic alga might modify for life on land, probably in different places, and a few changes of form would occur, each one perhaps making others open to its descendants, while with increasing possibilities, the time between changes might be lessened, so that the next big change, to a moss or a pteridophyte, might not need so long a wait, and so on.

In fact, we would suggest that the list of heads of these great groups might be like that of the leading genera of a family, chiefly formed among the earlier mutations, even though these were few and far between. Further possibilities would tend to open out upon an increasing (hollow curve) scale. This description fits better with the line of attack upon the whole question that was taken by my friend Dr GUPPY, and which caused him to give to the whole theory the title of Evolution by Differentiation, which seems to the writer less descriptive than Divergent Mutation.

The acceptance of the laws of ASA and of dichotomous divergent mutation thus brings comparative order out of what has hitherto been rather chaotic, the understanding of distribution. The laws of ASA are evidently of supreme importance in this respect, and age, size, and area are among the characters that are of most importance. But we are still almost ignorant of the laws that govern the incidence of

characters, and when we begin to gain an insight into that problem, we shall be upon the way, with the help of Mendelism and of that insight, to obtaining some control of evolution. One must be careful not to suggest that the structural result of any evolution might be predicted. The plan upon which it works appears to be always the same, but a very trifling difference in the earliest stages might ultimately lead to totally different final results, so that instead of getting *Compositae*, for example, we might get some family quite unknown, by some other combination of characters than any that exists, or has existed.

6. *Isolation*. In our two earlier books we have said a good deal about this subject, whose increasing importance we have long realised. When we adopted the theory of mutation in the early years of the century, it was clear that its logical conclusion was that it must very probably produce a new species at a single operation, not, as was so frequently supposed, by a series of small mutations that gradually added up to a specific distinction. The supposed driving force of selection was necessarily abandoned if one took up mutation, and what was to ensure that one small mutation should be followed by another which would help towards the formation of a new species? Where and when, for instance, was the boundary that commonly exists, that of mutual sterility, crossed? It was much simpler, as we gradually left behind us, with the new century, the period of the boom in adaptation, to imagine the new form, specific or generic, formed at a single mutation. This, incidentally, would make it quite possible for the new species, now really isolated, to commence its existence, and to begin to spread, among a number of individuals of the parent species, without any risk of loss by crossing. Had this been earlier thought of, there need not have been so great a boom in relicdom as occurred. This isolation, which would not in any way involve the death of the parent form, thus becomes a very important factor in evolution.

The writer's working hypothesis (p. 96), used since 1907, of sudden specific or generic mutation under a strain of outside conditions, has of course always included the notion of the isolation thus brought about, and the subject has been brought up in many places. We may refer especially to *AA*,



chaps. XV, XVI, to *Evol.* pp. 57, 92, 24-30, and the chapter there on isolation on p. 61, and to various references above, in the present book.

HARLAND's work, referred to in *Evol.*, p. 62, adds considerable importance to this matter, by suggesting that long continued gene separation may lead to gene change, and this in turn might cause the necessary pressure to ensure specific or varietal mutation. The work of STEBBINS may also be referred to (121). There is a fair chance, especially when the land is not too closely occupied, that a seed may be carried further than usual, and start life in a geographically isolated position, when, if some gene change had occurred, it might even be able to commence a new form. The gradual succession of forms that we have described in some *Podostemaceae* (129) at different cataracts in the same river goes to indicate that the outfit of potentialities of character may differ between two individuals. The seeds having no adaptation for clinging to the rock (except in *Farmeria*) are usually washed away and lost, so that it is not an easy matter to colonise a new cataract.

If the individual possessor of some gene difference remain isolated, its later mutations will tend to differ from those of a normal plant, but there would be no reason to look upon it as a relic, as would formerly have tended to be the case. The process of formation of new forms seems to have considerable resemblance to the formation of new individuals in man, with the generations at great distances apart.

The writer's observations over many years, with those of HARLAND added, have suggested that it is not impossible that no two individuals of any species may be exactly alike in the make-up of the genes, chromosomes, and other features, to say nothing of any possible effect that might be due to simple fluctuation in the characters. If this be so, isolation may automatically tend towards increasing difference, followed by sudden mutation when the pressure reaches a certain point. The fact is evident, that isolation and its effects are worth much more of careful study.

7. *Adaptation, advantage, and selection.* The writer spent some years in the arcana of natural selection, in the palmy days of that theory, and began his investigations at the period when all efforts were devoted to finding adaptation

in everything structural. This was clearly necessary if advantage in the struggle for existence was to be kept upon its pinnacle as the moving force in the evolution and distribution of living things. It was taken for granted at that time that as evolution was only visibly shown by structural differences, it was these same differences which represented the advantages that had led to the survival and to the relative success and wider distribution of the species that showed the most efficient of them.

Thanks largely to the criticism of FLEEMING JENKIN (74) it was assumed that a new species must begin upon a comparatively large area in order to have any chance of survival and success. This of course meant that the great numbers of species occurring only on very small areas, as do, for example, about a couple of hundred CEYLON endemics, must be relics of previously existing vegetation that were slowly diminishing their areas of occupation. The writer has devoted a great deal of work to combating this strongly held opinion. For example he showed that on RITIGALA summit in CEYLON (130) the local endemic *Coleus*, confined to that summit, was accompanied by the most widely spread species of the genus, but showed no sign whatever of any inferiority, or of dying out, and the same proved to be the case with practically all endemics, wherever they were found. Not only so, but the endemics existed in great numbers, especially those of the smallest areas of occupation. For example, dividing them into five groups from small areas to large, they showed in

Ceylon	233	192	136	139	90
New Zealand	296	190	184	120	112

(*AA*, pp. 60-4)

A state of relicdom caused by selection could not graduate the numbers like this, and this discovery, borne out by similar ones in many other places, was a blow to the conception of relicdom. A long list of queries made to its supporters, which seem in general to have been found unanswerable, and have been entirely ignored, is given in *AA*, pp. 90-92, and to them we may just add a few others :

(1) The larger (more "successful") genera are marked by close genetic relationship, which seems to the writer the only possible explanation of all the tables that we have given

of the genera at the heads of many families. As the "relics" among the small genera show the same tribal characters as some of these large ones, and in a general way form groups of satellites round the latter, we have now to support relicdom explaining how all this came about with inheritance *from above*. Surely if the relics were older than the successful genera, they would not show the tribal characters of the latter, in a family where the latter were formed by divergence from the head of the family.

(2) How did epiphytic things like *Rhipsalis*, in what must be a lesser competition for lack of numbers of individuals upon a given space, come to evolve so many local, endemic, species?

(3) Why do the endemics of NEW ZEALAND, which is much older as an island than CEYLON, occupy in general so much larger a space than those of CEYLON?

(4) Why do the wides and endemics of NEW ZEALAND appear in the different zones of 100 miles in length, from north to south of NEW ZEALAND, in the following numbers?

Zones	0-100	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
Wides	208	207	235	234	234	239	233	224	213	202	110
Endemics	234	280	330	368	386	537	532	527	516	414	137
						Cook's Strait			Foveaux Strait		

The wides take no notice whatever of COOK'S STRAIT at the middle of NEW ZEALAND, and a smaller one than the endemics of FOVEAUX STRAIT at the south end, where 54% of them cross, as against 33% of the latter. The endemics suddenly increase from 386 to 537 at COOK'S STRAIT. This seems a practically conclusive proof of the writer's theory of the greater youth of the endemics, which are beginners, not relics. As we saw with *Ranunculus* at p. 65, many of the endemics tend to begin in the south, and this is enough to account for their comparatively good showing at FOVEAUX STRAIT. But it is clear in any case that the wides are much older than the endemics, and therefore that the latter are not relics.

The writer's work upon age and area and the hollow curve led to a very long series of deductions, in number about a thousand, mostly by aid of the sub-conscious (p. 249), which have proved correct when tested by the facts, and have

provided the material for *Evol.* and for the present book. It is this testing which has involved the great amount of labour spent upon this work in the last fifty years. Its uniformly successful result has made him believe strongly in its premises, the probable general truth of the laws of ASA and of dichotomous divergent mutation, working downwards.

It further proved to be the case that the larger, *i. e.* upon the old conceptions the more successful, and the more widely distributed that a genus was, the more "relics" did it show, upon the average. Even in so old and so large a genus as *Ranunculus* only about 25 of its 325 species are really very widely distributed, *i. e.* found in the whole north temperate, or at least the north palaeotemperate zone, and very few other genera can rival this.

Almost everywhere one may find a few wides, one or other or more of them usually going to the extreme edge of the distribution of the genus, at least if the locality were not so geographically isolated as to prevent this. Except in cases like this, the endemics did not generally reach the edge, and in a long isolated island like NEW ZEALAND, where the time had been available, they often formed the characteristic pattern of distribution that one may see in the species of *Ranunculus* in that island (p. 65). The map shows the local dispersal of the genus as proceeding from the southern half of the SOUTH ISLAND, while three of the four wides cover the whole of both islands, as well as the CHATHAMS, 375 miles to the east, thus showing how much older the wides are than the endemics.

Endemics, in fact, are evidently the offspring of the wides among which they usually occur. There are exceptions to which we shall refer in the next chapter, but in *Ranunculus*, for example, they are not very numerous. The older theories of relicdom cannot hold their ground against such arithmetical methods of distribution, especially since the many proofs that have been given (*cf. Evol.*, especially Testcases, and the tables in this book, especially that on p. 173) that evolution has proceeded by dichotomous divergent mutation, *downwards* towards species, not upwards as hitherto supposed.

It is now becoming fairly certain that this was the course of evolution, and if this be the case, it is also clear that adaptation and advantage can have but little influence upon that course, as YULE and the writer said in 1922 (159).



There is little for selection to act upon, and the great structural divergences everywhere shown seem almost never to have adaptational value. The simple and automatic way in which evolution and distribution seem to proceed makes a great obstacle to any belief in the efficacy of selection when one has to deal with large spaces (larger than those occupied by single plant societies) and long time (longer than the life of a society or two). General conditions may favour growth of forest rather than prairie, but our work seems to show that it is in general rather the earliest arrivals of the species of the preferred kind that will become the leaders. The first arrivals will get a good start in becoming well adapted in detail to local conditions, which will always be changing a little.

The former conception that large groups, whether families, genera, or species, were the "successful" ones, is true enough if one look at number, or great dispersal, as signs of success, but they go, as we have now abundantly shown, principally with age, and progress is largely operated by the somewhat cynical law of "first come first served", or "to him that hath shall be given". Age is everywhere proving to be a factor of very great importance. The writer has been preaching this doctrine ever since the publication of *Age and Area* in 1922.

The *Anemoneae* (pp. 30-1) are evidently not demonstrably superior to the *Helleboreae*, both showing similar curves, and being distributed side by side. But the uppermost *Anemoneae*, like *Ranunculus*, *i. e.* the oldest, are older than any *Helleboreae*, and show both greater numbers of species and greater dispersal. Even in a little country like BRITAIN, the difference can be seen, the local distribution of the top four being

of all <i>Anemoneae</i>	112 (a)	109	76	49	Total	346
of all <i>Helleboreae</i>	112 (b)	66	65	33		276
of <i>Anemoneae</i> without <i>Ranunculus</i>	109	76	49	46		280

a) reached by six *Ranunculi*, b) reached by one *Caltha*.

Even without *Ranunculus* the *Anemoneae* are equal to *Helleboreae*.

On p. 278 we have given an instance of specific distribution in *Chrysosplenium*, and on p. 11 have shown that there is nothing to choose between large and small families. There is no inferiority in the latter but greater youth.

8. *Classification of plants*, like any other, depends for its keys upon finding characters that exist in many, in few, in two, or in one only, of the objects to be grouped. Evolution seems to be a great series of divergent dichotomies, and while nature is evolving the plants, and probably the animals too, she is also providing a system upon which they can be grouped. This is evidently largely dependent upon their mere age. But without perhaps realising this fully, we are continually trying to make our classifications more "natural", by which we mean following more closely the genetic lines of development. We have not fully realised that genetic and structural resemblances do not necessarily go together in detail, and that things with the closest genetic affinity may structurally be widely separated, and be placed in different tribes &c. This procedure especially characterises the genera at the top of a family, where they are the most closely related that is possible. *The first dozen or so of genera have already traced out the taxonomic lines of descent of the family, the tribes, the genera and the species.*

Our present classification depends entirely upon structural resemblances, which we call affinities, taking notice of divergences only to use them for keys, for their proper explanation has escaped notice. Taxonomy and genetic development, therefore, are not capable of the agreement into which we try to force them, and time and labour might be saved by a frank recognition of this fact, while at the same time the actual classifications might be simplified. It is generally recognised that since the fashion for attempted reconciliation has come in, our groupings have become more complicated and more difficult to use for their primary purposes, while people are tending to go back to the earlier system of BENTHAM and HOOKER.

A classification that follows nature's divergences is as natural as any other, but the term is not used in the same exact sense everywhere. However we classify plants by structural characters, the largest genera are so divergent that they must be at the tops of any divisions that we make.

This is for the simple reason that they were first formed in the genetic descent from the head of the family, and that this divergence is greatest among the oldest genera, whose descendants therefore form the great divisions of the family, though they themselves belong to a small and closely related group. To make a really correct genetic classification will probably prove to be as difficult and complicated a process as to make a chromosome map, another very desirable thing, and it should not be allowed to interfere with the making of a taxonomic classification, by structural characters only, unless some helpful feature can be brought in from elsewhere. Such a classification should be in international use, and should be adopted at a botanical congress, and only altered by the vote of subsequent congresses, for which long notice should be given.

9. *Classification contd. The orders or cohorts.* In families and genera there are many characters with which one can work that are common to many of them, while the divergences are seldom so great or so numerous as to make one feel uncertain about broad genetic connections. But as we go upward towards their origin, whether it be from one or from many points, the divergences become more numerous, and at times perhaps greater, making it more difficult to trace probable relationship, as one will soon find in dealing with orders, next above families. Among other things, this is shown by the great shuffling and rearrangement that is made in each new system. It is here that our classification is most unsatisfactory, especially when we try to make it genetic. As we have seen at a lower stage in the *Araceae*, there is a tendency to put the most difficult families, singly or in small groups, into orders of their own, thus temporarily shelving the difficulty. It is also shown by the increasing number of orders, and by the various ways in which the families in BENTHAM and HOOKER's *Incompletae* are dealt with. The same difficulties were evidently felt by these authors long ago, when they placed most of the difficult families there.

Looking closely at these difficult families, it seems fairly evident that much of the trouble arises from the fact that in the formation of the various combinations of characters that mark what we call families more of those characters

usually considered "important" have been changed than usual, and importance largely rests upon mere age. In a large family, as we have seen in (146), or on pp. 311, 312, all kinds of changes may occur, but usually the most marked happen at different mutations, while if all occurred at once, the result might be impossible to place in any present family (cf. p. 312). Fortunately this kind of thing rarely happens, but it is not improbably to occurrences like this that we owe the existence of the *Incompletae* (see below).

The list on p. 173, supported by subsequent lists, indicates that the genera at the top of any family show, in about three quarters of the cases, such structural divergences from the immediate parent, which must usually be close above, that we have to place them in different sub-families or tribes. This of course is partly due to the fact that coming as they do so near the very top of a family, they have the best possible chance of leaving a large number of descendants visibly carrying their own chief characters, and thus forming a tribe of some importance. The same tendencies are shown in their own proper descendants, which tend to break up into heads of sub-tribes, and so on right down to what we have seen with species and sub-species upon pp. 182-4. As there are but few genera in the family at this period, any divergence tends to assume importance, which is continually made more and more valid as the descendants that show it increase in number. We know so little as yet about the possible electro-chemical syntheses and changes that may go on in living beings, that it is usually impossible to make any predictions, and everything tends to look as if it were simply a matter of chance. There are certain cases where the same chemical compound appears to be made in unrelated plants that might perhaps afford a path of approach to this question.

The phenomena seen again suggest forcibly that the mutation that is going on is, to a greater or less extent, a matter of what appears usually to be a casual choice of characters in which divergence is to be effected. And when this choice happens to include two or three characters that were of great importance in the parent, the result may be so different that we find it very difficult to place the family in its proper genetic position. This kind of difficulty, however, need not affect our classification, as we have pointed out. Discussions as to genetic position should be kept



separate from taxonomy, until results commonly accepted are reached, and those such as may be inserted in taxonomic works without making them more cumbrous and difficult to use.

*Leguminosae* or *Orchidaceae*, for example, are well defined groups of plants. If we take the former, and begin with the monotypes we find (figures some years old) 240/1, that we may in general regard as beginners as *Leguminosae*. They form well over a third of the whole family's 675 genera, though their species are a mere 240. Being the youngest, they had the largest possible number of potential parents available, but beginning in a very small way, they will require a very long period of time to reach the stage of two species, after which they will expand with increasing rapidity (AA, p. 34). There is rapid decrease in number of larger genera, there being only 70/2, 42/3, 33/4, and 22/5. These are older genera, or most of them are, born when the family was smaller. After 5 we get the genera separating more and more rapidly from one another by size (pp. 30-33), and the hollow curve shows clearly, plotting logarithmically into a close approach to a straight line p. 262.

*Leguminosae by sizes of genera in the World*

Genus	Spp. (world)	Sub-family	Tribe
1. Astragalus	1600	Heading <i>Papilionatae</i>	<i>Galegeae</i>
2. Acacia	550	Heading <i>Mimosoideae</i>	<i>Acacieae</i>
3. Cassia	450	Heading <i>Caesalpinioideae</i>	<i>Cassieae</i>
4. Mimosa	400	2nd <i>Mimosoid.</i>	<i>Eumimoseae</i>
5. Crotalaria	350	2nd <i>Papil.</i>	<i>Genisteae</i>
6. Indigofera	350	3rd <i>Papil.</i>	2nd <i>Galeg.</i>
7. Trifolium	300	4th <i>Papil.</i>	<i>Trifolieae</i>
8. Bauhinia	250	2nd <i>Caesalpin.</i>	<i>Bauhinieae</i>
9. Desmodium	180	5th <i>Papil.</i>	<i>Hedysareae</i>
10. Aspalathus	175	6th <i>Papil.</i>	2nd <i>Genist.</i>
11. Lupinus	175	7th <i>Papil.</i>	3rd <i>Genist.</i>
12. Phaseolus	160	8th <i>Papil.</i>	<i>Phaseoleae</i>
13. Vicia	160	9th <i>Papil.</i>	<i>Vicieae</i>
14. Dalea	150	10th <i>Papil.</i>	3rd <i>Galeg.</i>
15. Inga	150	3rd <i>Mimosoid.</i>	<i>Ingeae</i>
16. Tephrosia	150	11th <i>Papil.</i>	4th <i>Galeg.</i>

The figures of size of genera given in ENGLER-DIELS, 11th ed., though slightly different from mine and often a trifle lesss, how the first seven in exactly the same order, and in the others, *Lupinus*, *Dalea*, and *Vicia* are displaced by *Oxytropis*, *Psoralea*, and *Rhynchosia*, with a result hardly different. This is the rule for every family. *Compositae* is the first in matter of size, and we have given a table of its leaders on p. 176; *Leguminosae* is the third (in genera, but second in species), and as we have had few Monocots, it will be well to give a table for the *Orchidaceae*, the second family.

*Orchidaceae by world sizes of genera (tribes from NP/1)*

1. Dendrobium	750	Heading <i>Dendrobieae</i>
2. Pleurothallis	550	Heading <i>Pleurothallideae</i>
3. Bulbophyllum	450	Heading <i>Bulbophylleae</i>
4. Epidendrum	425	Heading <i>Laelieae</i>
5. Habenaria	400	Heading <i>Ophrydeae</i>
6. Oncidium	350	Heading <i>Oncidieae</i>
7. Eria	325	2nd Dendrob.
8. Eulophia	200	Heading <i>Cyrtopodieae</i>
9. Stelis	175	2nd Pleurothallid.
10. Microstylis	150	Heading <i>Liparideae</i>
11. Angraecum	120	Heading <i>Sarcantheae</i>
12. Calanthe	120	Heading <i>Phajeae</i>
13. Coelogyne	120	Heading <i>Coelogyneae</i>
14. Liparis	120	2nd Liparid.
15. Masdevallia	120	3rd Pleurothallid.
16. Maxillaria	120	Heading <i>Maxillarieae</i>
17. Cyrtorchilum	115	2nd Oncid.
18. Disa	110	2nd Ophryd.
19. Chloraea	100	Heading <i>Neottieae</i>
20. Oberonia	100	3rd Liparid.
21. Odontoglossum	100	3rd Oncid.
22. Polystachya	100	Heading <i>Polystachyeae</i> .

Thus in the first sixteen, there are 12 heads of tribes, but all in the sub-family *Monandreae*. It is clear that here, as in the other two very large families, there is a great deal of well marked divergence at the top. In ENGLER-DIELS the classification of MANSFELD is used, but there are only small

differences, the chief being that the tribes of PFITZER are reduced to sub-tribes, so that *Dendrobieae* becomes *Dendrobiinae*, and so on.

Thus these first three families, heading all the rest by a large margin, are not only as divergent from one another as it is possible to be in the flowering plants (*Gamopetalae-Inferae*, *Monocotyledones*, *Archichlamydeae*), but show, among their largest genera, the heads of six out of seven sub-families, and of 32 tribes out of 60, including nearly all the most important.

Taking the tribes headed by any of the genera in the first sixteen of each family there are

in the first three tribes of each, together, about 280 genera	
second	560
third	800

This tendency to increase in size from the very early tribes is well marked at the top of many families, and we are not yet clear as to its meaning; more work is needed, and time is insufficient. Two other features that we have mentioned are evidently associated with it in some way; (1) the way in which the offspring of the leader of a family tend to go automatically into other tribes (pp. 173-8) and (2) the great differences that show between the upper and the lower tribes in some large families (figures for *Compositae* on pp. 187-8).

It is not of course impossible, or even improbable, that some flowering plants were in existence before any of these big families. The earliest families of all might be things like *Magnoliaceae*, which are woody, would probably be of slow growth, while the divergences open to them would probably be but few. The family is usually looked upon now as one of the oldest of all, and if we remember that in any case its early members would belong to the period of marked divergence, it is probable that such a group as *Schizandraceae*, often regarded as a separate family, should really be considered as a sub-family only. Cf. also notes about *Magnoliaceae* on pp. 338-9.

The same rules of behaviour apply to all families of moderate or large size, and as we said in *Evol.*, p. 76, "the first mutation, in a family newly formed by a large change from some ancestral form, may be in turn large". *Evol.* is really a first volume to the present one, and the whole chapter

may be read in the present connection, especially the letter from HOOKER to HUXLEY on p. 74, and p. 85, where we have said "It is clear that if we suppose the big genera of a family to be the first formed, and that by the most divergent mutation that on the whole occurs in the family, whilst the intermediate and smaller genera are younger, we can get a satisfactory picture of what seems to have gone on."

We have now added greatly to the proof that this is in general correct. The convincing evidence given by the table on p. 173, and the following tables of the leading genera of families, had not been fully collected in 1940. But while this theory of evolution that we are now putting forward diverges from that previously held, there is no doubt that the evidence in its favour is very strong. Evolution and distribution seem to proceed in a simple and arithmetical way as if directed by simple law like other scientific disciplines, and this seems to fit on naturally to such sciences as chemistry and physics (*cf. Evol.*, p. 175, noting also the paragraph about Dr GUPPY at the top of the page). Later in this chapter we shall point out the chemical analogy.

Of course, going so far back into the past as we are now doing, we cannot be sure that the three gigantic families mentioned above are really the oldest of all. It is quite likely that *Rubiaceae*, which is largely a forest family of damp and warm conditions, was really earlier than *Compositae*. This is more suited to drier and more open situations, where, incidentally, evolution and distribution might be much more rapid. Somewhat similar objections might be urged against *Orchidaceae*. But in the list of the 45 largest families just below, there can be little doubt that most of the oldest are included. It is clear that they are well and divergently separated, none of them giving any suggestion of relicdom, and they are well scattered in the lists of orders given by different writers.

It is by no means improbable that the general rule of increasing size does not hold indefinitely far back, even if only for the reason that there are very few genera that come up in size to the standard of the largest of the flowering plants. At the real top of the list, when it is finally made up by age only, there may be a shrinkage in size by reason simply of lack of material upon which to work, and such families as *Magnoliaceae* may come in near the very top.



*The first 45 families of Angiosperms, by world size*

Family	Gen.	Leader	Spp.	«Ones»	Gen.	Pl.	Position in	
							NP/1	Hutchinson
1. Comp.	1179	Senecio	2000	446	B2		B10	B67
2. Orchid.	726	Dendrobium	750	231	M1		M11	M
3. Legum.	675	Astragalus	1600	240	A11 (1)		A21 (1)	A41
4. Gramin.	548	Panicum	500	221	M7 (1)		M4 (1)	M
5. Rubi	496	Psychotria	500	232	B1		B8	B66
6. Asclep.	352	Cynanchum	200	189	B7 (1)		B5 (1)	B65 (1)
7. Crucif.	344	Draba	270	143	A2 (1)		A19	A11
8. Umbell.	334	Eryngium	220	138	A15 (1)		A30 (1)	A59 (1)
9. Acanth.	273	Justicia	325	117	B9 (1)		B6 (1)	B75 (1)
10. Lili.	269	Asparagus	300	95	M3		M9	M
11. Scroph.	259	Pedicularis	275	93	B9 (2)		B6 (2)	B75 (2)
12. Euphorb.	251	Euphorbia	750	93	Inc7 (1)		A23 (1)	A38
13. Palmac.	219	Calamus	325	73	M4		M5	M
14. Apocyn.	202	Tabernaem.	110	75	B7 (2)		B5 (2)	B65 (2)
15. Labiat.	200	Salvia	550	63	B10 (1)		B6 (3)	B76 (1)
16. Melast.	193	Miconia	600	50	A12 (1)		A29 (1)	A33 (1)
17. Sapind.	160	Serjania	175	70	A10 (1)		A24 (1)	A57 (1)
18. Rutac.	153	Fagara	200	58	A7 (1)		A23 (2)	A55
19. Rosac.	142	Potentilla	300	45	A11 (2)		A21 (2)	A40
20. Gesner.	129	Cyrtandra	250	49	B9 (3)		B6 (4)	B75 (3)
21. Eric.	122	Rhododendr.	700	48	B4		B1	B60
22. Bignon.	121	Arrabidaea	100	50	B9 (4)		B6 (5)	B75 (4)
23. Borrag.	119	Cordia	280	42	B8 (1)		B6 (6)	B73
24. Annon.	114	Uvaria	100	45	A1 (1)		A18 (1)	A2
25. Cyper.	111	Carex	900	36	M7 (2)		M4 (2)	M
26. Arac.	108	Anthurium	500	41	M5		M7	M
27. Flacourt	104	Homalium	160	47	A2 (2)		A27	A27
28. Chenop.	102	Atriplex	250	41	Inc. 1		A17 (1)	A19
29. Solan.	99	Solanum	1350	37	B8 (2)		B6 (7)	B74
30. Verben.	93	Clerodend.	175	38	B10 (2)		B6 (8)	B76 (2)
31. Myrt.	92	Eugenia	750	26	A12 (2)		A29 (2)	A33 (2)
32. Menisperm.	91	Stephania	40	45	A1 (2)		A18 (2)	A5
33. Sapot.	90	Sideroxylon	100	43	B6		B4	B61
34. Anacard.	89	Rhus	140	31	A10 (2)		A24 (2)	A57 (2)
35. Malv.	87	Hibiscus	180	30	A6 (1)		A26 (1)	A36
36. Gentian.	86	Gentiana	400	25	B7 (3)		B5 (3)	B68
37. Aral.	83	Schefflera	150	37	A15 (2)		A30 (2)	A59 (2)
38. Amaryll.	81	Agave	275	21	M2		M9 (2)	M
39. Saxifrag.	80	Saxifraga	325	47	A11 (3)		A21 (3)	A14
40. Caryoph.	79	Silene	400	30	A4		A17 (2)	A17
41. Campanul.	78	Campanula	300	25	B3		B10	B71
42. Morac.	78	Ficus	800	32	In.7 (2)		A12	A50
43. Malpigh.	73	Byrsonima	120	13	A17 (2)		A23 (3)	A37
44. Cucurb.	70	Melothria	85	24	A13		B9	A30
45. Stercul.	70	Hermannia	150	26	A6 (2)		A26 (2)	A35

A = Polypetalae or Archichlamydeae, B = Gamo- or Sym-petalae, Inc. = Incompletae, M = Monocots.

If we now sort these families into the orders wherein they are distributed, we find them well and widely scattered there. They are not, as might upon the older views have been expected, closely structurally related at all. The first three are *Compositae* (placed in *Gamopetalae-Inferae*), *Orchidaceae* (*Monocotyledones*), and *Leguminosae* (*Archichlamydeae*), as widely separated as it is possible for flowering plants to be. If we sort the first 40 into the 40 orders (cohorts) of BENTHAM and HOOKER, we find them in

	Polypetalae	Gamopetalae	Incompletae	Monocotyledones
First ten	11, 2, 15	2, 1, 7, 9	—	1, 7, 3
Second	12, 10, 7, 11	9, 7, 10, 9	7 (Euph.)	4
Third	1, 2	4, 9, 8, 8, 10	1 (Chenop.)	7, 5
Fourth	12, 1, 10, 6, 15, 11, 4	6, 7	—	2

(Numbers of orders as in my *Dict.*, pp. 1-liv at end.)

The families cover the field in very fair proportional numbers, with widest gaps, and no duplication, in the first ten. These ten families contain 5196 genera, or about 40% of all genera known (12, 571); of these 2300 are *Gamopetalae*, 1543 *Monocotyledones*, and only 1353 are *Archichlamydeae*. There are no *Incompletae* in the first ten, and only *Euphorbiaceae* and *Chenopodiaceae* in the rest. These are facts which throw some doubt upon currently received opinions as to *Archichlamydeae* and *Incompletae*, and their position in the history of the development of the flowering plants. But in any case it is clear that even if we had to deal with the whole 40 families, there would be little difficulty in placing a plant belonging to one of them in its proper family. It is only when we add the great crowd of younger and smaller families that there begins to be serious difficulty.

If we compare the various groupings into orders made by the various authors, we can see at once the great shuffling that has gone on, and that takes no notice of age, size, or area, the three great factors that have been so controlling in importance and in distribution. Like a family, an order that contains no large family or genus should probably take a lower rank, as being younger, unless it be an evidently very ancient group like the *Magnoliaceae*, that go back to the very first days of the angiosperms (*cf.* p. 338-9).

Why are there such wide gaps between families at the top unless it is that in the early days when they were being formed, the divergences, which must have been matters of indifference to selection in most cases, tended to be large? In early days, too, there was probably less material for divergence to work upon; the possible variety has probably been increasing all the time, each new one opening the way to yet more.

It would be absurd to try to show which family was actually the first; we cannot be sure that the flowering plants are even monophyletic. But everything connected with times so far back in geological history, when conditions were probably so different, is still almost entirely a matter for speculation, and one in which other sciences are involved. Much further inductive work is needed; as yet we do not even know the relative rates at which families increase and become dispersed. For example, probably neither *Compositae* nor *Dipterocarpaceae* should justly, by actual age, occupy the positions that their numbers assign to them.

It is of interest to see how soon such characters as one cotyledon, inferior ovary, tetradynamy, and a number of others, appear in these families at the top of the list, and though we cannot place them accurately in order of age, there is little doubt that on the whole these are very old families.

When one sees the regularity with which every family in turn gives the same kind of picture with its leading genera, one realises that one has come upon a general rule, or in fact a law, that is followed by a family in the course of its development. The figures are so consistent that there can be comparatively little doubt about their interpretation.

It is clear that the growth has been by divergence at every mutation. This in turn means that the evolution is working downwards towards the smaller forms, not upwards as we used to think. As GUPPY and the writer independently realised long ago, people were trying to make evolution work backwards (*cf. Evol.*, pp. 22, 32, 65-8, 88, 98, 175, especially 68, 175). The final evidence required to support our views, which really date back to GEOFFROY ST. HILAIRE, OWEN, and MIVART, seems to be provided by the many tables here given, especially that on p. 173 and the many of leaders of families, notes on genera like *Galium* on p. 182

and below, and on sub-species on pp. 182-83. This behaviour seems universal, and no other explanation of such consistent figures seems possible to the writer at the present time. All must be due to the operation of the same law, and neither adaptation nor selection, nor "upward" evolution, can even begin to explain why the taxonomic classification that we use should begin with the widest possible divergence in the oldest genera, which now possess the most numerous species and the widest dispersal. Had evolution been "upwards" and casual, it would not be possible to find this phenomenon shown as it is. The behaviour of the species, especially those of the earliest and largest genera, also goes to show that this is the more correct view to take. Like the families and the genera, especially the older ones, they too begin at once to break up into their taxonomic divisions.

Up to the genus which as the largest or oldest is the head of a family, we can still feel fairly sure that we are dealing with one family, even in the *Leguminosae*, where the top three genera are sometimes given a family each. But above this point it is clear that divergence has affected more characters at once. This tends to be more the case the larger (older) the family, so that it becomes very difficult to place a big family in its proper relationship to other big families, by structural methods of comparison. It is probable that all the top families are really closely related to one another (perhaps, if they be polyphyletic, in groups), but genetically, not taxonomically. Their divergences are more marked, affecting more of their "important" characters. These we have seen to be the oldest, upon the whole, so that they would be available for divergences at a very early period. But as time went on, they would probably become mixed with other and younger (less "important") characters, so that their chance of being affected at any individual mutation would become less.

It is clear that size simply follows from age, and that wide taxonomic divergence largely does the same thing in any one line of descent, while on the other hand the higher one goes, the closer tends to be the relationship of the genera. Neither selection nor adaptation will account for the fact that the large genera at the top tend to show such clear and well marked distinctions, nor can one call in such destruction of transitions as will account for such separation of incon-



gruous types, with such marked divergences, between which transitions can but rarely be conceived.

The principle at work seems to be first of all a division of the first parental genus of a family by a divergent mutation, followed by the same happening to each new genus in turn. The earliest divergences are the largest or the most numerous, or both, and there is a gradual diminution as time goes on, so that the rank of a genus is largely determined by its age. We cannot as yet tell what the relative rank of a single mutation of one character is, and a comparison of the early mutations in small families, as given in the table on p. 199 in *Evol.*, with those in the big families seems to show little or no difference; but there seem to be more of well marked ones in the larger families. It may therefore be worth while to look at a list of the largest genera of the flowering plants, and to note how they diverge from one another, almost all belonging at least to separate tribes, and often to separate sub-families also, whilst it is not common for them even to occupy the same family, unless that family be very large.

*The 30 largest genera of the flowering plants*

Genus	Size	Fam.	Sub-family	Tribe
1. Senecio	2000	Comp.	Tubuliflorae	Senecioneae
2. Astragalus	1600	Legum.	Papilionatae	Galegeae
3. Solanum	1350	Solan.		Solaneae
4. Carex	900	Cyper.	Caricoideae	Cariceae
5. Begonia	800	Begon.		
6. Ficus	800	Morac.	Artocarpoideae	Ficeae
7. Hieracium	800	Comp. 2	Liguliflorae	Cichorieae
8. Mesembryanth.	800	Aizo.		Mesembryanth.
9. Oxalis	800	Oxal.		
10. Dendrobium	800	Orch.	Monandreae	Epidendreae
11. Eugenia	750	Myrt.	Myrtoideae	Myrteae
12. Euphorbia	750	Euph.	Crotonoideae	Euphorbieae
13. Piper	750	Piper.		
14. Rhododendron	700	Eric.	Rhododendroideae	Rhododendreae
15. Centaurea	650	Comp. 3	Tubuliflorae (2)	Cynareae
16. Vernonia	650	Comp. 4	Tubuliflorae (3)	Vernonieae
17. Croton	600	Euph. 2	Crotonoideae (2)	Crotoneae
18. Dioscorea	600	Diosc.		Dioscoreae

Genus	Size	Fam.	Sub-family	Tribe
19. <i>Miconia</i>	600	Melast.	Melastomatoideae	Tamoneae
20. <i>Acacia</i>	550	Leg. 2	Mimosoideae	Acacieae
21. <i>Peperomia</i>	550	Piper. 2		
22. <i>Pleurothallis</i>	550	Orch. 2	Monandreae (2)	Pleurothallideae
23. <i>Salvia</i>	550	Labi.	Stachyoideae	Salvieae
24. <i>Anthurium</i>	500	Arac.	Pothoideae	Anthurieae
25. <i>Aster</i>	500	Comp. 5	Tubuliflorae (4)	Astereae
26. <i>Erica</i>	500	Eric. 2	Ericoideae	Ericaeae
27. <i>Myrcia</i>	500	Myrt. 2	Myrtoideae (2)	Myrteae
28. <i>Panicum</i>	500	Gram.		Paniceae
29. <i>Psychotria</i>	500	Rubi	Coffaeoideae	Psychotrieae
30. <i>Sedum</i>	500	Crass.		

*Myrcia* is often regarded as part of *Eugenia*, *Mesembryanthemum* often broken up into many smaller genera. *Piper*, *Peperomia*, *Begonia*, *Dioscorea*, and *Oxalis* are all much too large for their small followings, and we have given a possible explanation on pp. 288-9.

These 30 genera, which must include at any rate many of the oldest, thus belong to 20 families; five are in *Compositae*, and two each in *Eric.*, *Euph.*, *Legum.*, *Myrt.*, *Orchid.* and *Piper*. The orders to which the Dicot genera here belong are (68).

7. Piperales (2 gen.)	41. Leguminosae (2)
14. Saxifragales (1)	50. Urticales (1)
17. Caryophyllales (1)	60. Ericales (2)
20. Geraniales (1)	66. Rubiales (1)
30. Cucurbitales (1)	67. Asterales (5)
33. Myrtales (3)	74. Solanales (1)
38. Euphorbiales (2)	76. Lamiales (1).

Going upwards from species to families, the differences increase in complication and emphasis. A very little more of divergence than such as marks the difference between two sub-families, such as *Caesalpinioideae* and *Papilionatae*, would make it absolutely necessary to treat them as separate families, while now most people include both in *Leguminosae*. In reaching so nearly back to the beginning of the Angiosperms as we are doing here, we have come to a region of emphatic differences. On the other hand, in working downwards, the differences become less strongly marked, and are not so

liable to cause difficulty. We have long divided the *Papilionatae* into *Galegeae*, *Genisteae*, *Trifolieae*, and the rest of the ten tribes. The difficulty in placing a thing in its proper *structural* connection diminishes as we come downwards, though we have no longer any right to assume that there is a gradual passage of one structural form into another. We have now seen the effects of the divergences that separate species and genera at the mutations that give rise to new ones. They cannot be passed over by gradual stages, in such cases as flower x-merous/y-merous, ovule erect/pendulous, raphe dorsal/ventral, fruit loculicidal/septicidal, capsule/berry, anther opening by pores/slits, extrorse/introrse, pollen powdery/in pollinia, pollen-sac septate/not so, pollen of different patterns, as in *Acanthaceae*, corolla hypogynous/epigynous, poly-/gamo-petalous, and so on, all of them changes which must come by sudden mutation. They could not be due to gradual acquirement by selection, even if there were any reason to suppose that it could act upon such characters. It must act upon total, not individual, value, and could not bring them to the state of perfection in which we commonly find all of them, with a clean-cut differentiation like that shown in the examples just given. And while selection becomes less and less important as one goes upwards, differentiation increases (*cf. Evol.*, Testcase XXII, p. 137), and the closest relationship of all is shown by the topmost genera of a family.

Another upwards stage, offering still less opportunity to selection with the always increasing divergence, takes us to the very top of the largest families, where we always find the family ending (upwards) with a single genus that shows a wide gap in number of species between it and the next largest, it being in general almost exactly twice the size of the second. The 45 largest families in the table just given show the following result :

	Spp. in Genus 1	2	Difference	Av.	% of second to first
First 15 fams.	8650	4610	4040	269	53,3%
Second	6030	2855	3175	211	47,3%
Third	4210	2105	2105	140	50,0%
Total 45 fams.	18890	9570	9320	207	50,1%

There is great variety among these families, which in general go back to very early days indeed, when the number of characters had not yet been increased by later mutations, so that there was comparatively little to draw upon, and what we now consider the most important characters were liable in consequence to frequent and often well marked change. We have tried to make it clear in various places in this and previous books that age is one of the most important factors in the evolution and distribution of plants, because it *allows time* for the changes made by other and more active factors. Importance of a character in taxonomy depends upon age, as we have frequently pointed out, and it is their first mutations, therefore, that produce the most important characters of all.

We shall therefore, with this increasing divergence, find great difficulty in tracing structural features back into preangiospermous days. For some way back into the fossil period, say at least as far as the Eocene, we can trace a number of our present families back but we find no new ones, so far as I am aware. But there is no evidence to show that the first Angiosperm or Angiosperms did not arise directly by mutation from some Gymnosperm or Pteridophyte, remembering that we are back at a period of large mutation. In fact, probability is much in favour of this suggestion. The mutation need not be much larger than those that separated the earliest Angiosperms.

Things with some of the characters of one group, and some of another must be regarded in general not as actual transitions, but as things that have received an unusual mixture of the characters that the immediate ancestor was carrying. They may perhaps have had bad luck in meeting with some catastrophe, or may have proved in some way unsuited to the local conditions.

10. *The Incompletae* of BENTHAM and HOOKER, containing families that they were not able to place among their *Poly-* and *Gamopetalae*, have long been a very difficult problem. ENGLER made the first great change, by throwing them boldly among his *Archichlamydeae*, but they are usually so divergent from most of these that it is no easy matter to place them. In fact, it is as difficult as to place a family in its proper order, and the tendency is, as usual, to put each



one or few in a different group, temporarily shelving the difficulty. Of the 33 orders given in ENGLER-DIELS (11th ed.), a number, and especially those near the start, contain *Incompletae* only. The actual figures are

*Position of Incompletae in Engler-Diels*

Orders	Fams. contained	Fams. of Incomplt.	Gen.	Spp.	Percentage of Fams
1 to 15	21	19	286	4,516	90%
16 to 20	22	16	404	5,526	68%
21 to 25	47	8	119	2,042	15%
26 to 30	84	3	255	4,402	3.5
31 to 33	27	4	56	612	14%
33	201	50	1,120	17,098	24%

Of the last 18 orders, families of *Incompletae* are found in 12.

In the later grouping of HUTCHINSON, the Englerian view, that the *Incompletae* were earlier stages, is abandoned. This seems supported completely by the work that we have described here. *Magnoliaceae* and *Ranunculaceae* are put in their place. Upon the writer's views no living family can be accepted as a relic without detailed individual proof, nor can any fossil be taken as ancestral unless frequent and widespread.

Some of the *Incompletae*, like *Euphorbiaceae*, though as incomplete as most, are important and flourishing families, but marked by divergences that happen to cover characters usually considered as important, mainly because they have usually been found so in other families. One must not forget that importance is mainly due to age, and its occurrence in one family does not guarantee any importance whatever in another one. *Euphorbiaceae* is particularly marked by the unisexual flowers, the perianth of one whorl or none, the stamens one to many, free or variously united. It is a large family, the twelfth of all, and we have seen that variety of character is sure to occur in a large family, while this one is old enough to go far back into the earlier period when divergence tended to be greater. *Scrophulariaceae* and *Palmaceae*, on either side of it, both show wide variations, and had they not agreed rather well among themselves in vegetative habit &c, might have been split into smaller families.

As we have had no examples of any *Incompletae* in our tables, we give the first eight *Euphorbiaceae* below :

*Euphorbiaceae in order of world size*

	No. in world	Subfamily	Tribe
Euphorbia	750	Heading <i>Crotonoideae</i>	<i>Euphorbieae</i>
Croton	600	2nd <i>Crot.</i>	<i>Crotonae</i>
Phyllanthus	500	Heading <i>Phyllanthoideae</i>	<i>Phyllanthae</i>
Acalypha	400	3rd <i>Crot.</i>	<i>Acalypheae</i>
Macaranga	200	4th <i>Crot.</i>	2nd <i>Acal.</i>
Glochidion	175	2nd <i>Phyllan.</i>	2nd <i>Phyllan.</i>
Jatropha	175	5th <i>Crot.</i>	<i>Jatropheae</i>
Manihot	175	6th <i>Crot.</i>	<i>Adrianeae</i>

There are only these two sub-families in the great mass of the family, but two more with leaders of 18 and 7, separated by the simple mutational character of ovules one or two per loc., a character more "important" when older in the family.

The differences in *Incompletae* are in general such as can only be passed by sudden mutation, being usually incapable of intermediate stages. This is especially important as there is no conceivable use for intermediate stages, and still more for such upon a graduated scale of usefulness. One has only to think of the many embryo-sacs of *Casuarina*, of the scaly emergences on the leaves of *Hydrostachys*, of the distinctive characters of *Garrya*, *Myrica*, *Balanops*, *Leitneria*, and so on, to realise how widely these genera diverge from anything that one might imagine to be related, whether living or fossil.

The families of *Incompletae*, where it is even just possible to suppose them relics dying out, are usually very small, and it is only those of wide, but scattered, dispersal that are likely to come into consideration. *Magnoliaceae*, which HUTCHINSON places at the foot of the Dicots, does, on the other hand, look like a primitive family, and is not unlikely to be related to the *Ranunculaceae*, also at the foot. They probably go far back into the days of wider divergence, and the small families that are often split off are more likely to be of the nature of sub-families, while one must not forget the possibility of polyphyletic origin of some of the structural discontinuity shown. *Magnoliaceae*, too, were probably

not very capable of rapid spread in changing conditions, and might be overtaken and destroyed at times.

The suggestion in the *Gen. Pl.* is that the *Incompletae* may perhaps be, and in ENGLER that they are, primitive forms from which later families have been derived. A much sounder line appears to the writer to be that followed by HUTCHINSON, who recognises that many of them are themselves derived forms, and the work in this book goes strongly to support this supposition. While ENGLER puts 19 families of them, adding only the very small families of *Garryaceae* and *Julianiaceae* to them, in his first fifteen orders, and sixteen more follow in the next five orders, HUTCHINSON places the same families in his orders 6, 7, 16, 18, 19, 23, 44, 45, 46, 47, 48, 49, 50, of his 59 orders of *Archichlamydeae*.

Our work goes to show that in general it is probable that the very large and widespread families on the whole are at any rate very early. Divergence appears to have been one of the chief marks of evolution, diminishing in emphasis as time goes on and the material upon which to draw increases. But it is highly probable that at the very start of the flowering plants such families as *Magnoliaceae* took a large hand in the matter, being themselves slow both in evolution and in distribution.

A number of families like *Betulaceae* and *Fagaceae* have given much trouble in deciding their genetic position, which is by no means settled yet. The difficulty as usual seems to arise from the way in which more of the important characters than usual have been affected in the mutation that gave rise to the leader, so that they show a considerable taxonomic separation from any other families. Probably they are old, and date from a time when divergences were considerable, while at the same time they are woody, and slow in growth and reproduction. One great difficulty is to know how *Fagus* and *Nothofagus* came to be separated so far geographically, for they are alike in many respects, and were long considered as one genus.

11. *The sub-divisions of families* can rarely be made, if of any importance, to harmonise with the geographical distribution. The taxonomic splitting rests upon the assumption, commonly and necessarily made under Darwinism, that relationship is determined by structural characters

only, so that intermediates, destroyed by selection, were required in order to cover the vacant space, taxonomic or geographical, or both, between two things structurally closely allied. This explanation has been very hardly worked, and badly strained. We have more and more realised that structural alliance is compatible with gaps of considerable size, and any direction, and that it completely ignores such a geographical difficulty and such a barrier as is presented to the *Araceae* (pp. 268, 273) by a 6000-mile stretch of the PACIFIC OCEAN. And now that we have seen that selection to get rid of the intermediates is also a broken reed, there is really little support left upon which to base extensive destruction. It thus becomes practically impossible to explain the formation of widely separated subdivisions upon the old conceptions.

The real destruction that is almost all the time going on is a destruction of individuals which prove weaker upon the whole total of their outfit, as compared with those that are growing close to them, whether these belong to their own species or not. There is little evidence for any killing out of a whole species, unless it be one newly born and confined to a minute area sufficient to support a very few individuals. The extinct species that we find as fossils are very often quite local things, which cannot safely be considered as ancestors of things now living, when one remembers the laws of ASA. And their characters are as a rule "finished", not transitions.

The distinction between one tribe, genus, species, &c and a close relative of its own rank, is simply due to whatever divergence may have marked the mutation by which they were separated. And we have seen that in every family the same rule is followed, that the genus that begins, and heads the family, promptly breaks up into genera heading sub-families or tribes, these into the heads of sub-tribes, and so on, so that after a dozen or so of genera are formed, the future taxonomic division of the family is clearly marked out. Selection had nothing to do with it; it is a necessary corollary of the law of dichotomous divergent mutation. Each genus behaves like its immediate predecessor, but usually upon a rather smaller scale.



So long as classification tries to be genetic, so long does it lay itself open to criticism that it is practically impossible properly to meet, and so much the more will it make itself troublesome to use, by not taking full advantage of the help offered by the divergences which nature has so kindly provided, but which as often indicate close relationship as not.

12. *The small families.* Many of these have been created since the *Gen. Pl.*, for example some 58 of one genus each, 17 of two, and so on. Usually they are simply genera, often solitary or even monotypic, diverging rather markedly from the rest of a family to which they were once united, like *Adoxa* (*Caprifoliaceae*), or *Akania* (*Sapindaceae*). Some families have been much disintegrated, like the *Ternstroemiaceae* of BENTHAM and HOOKER, whose genera have been scattered among nine families, many of them new. These families in turn have been much shuffled in placing them in orders, but all this shuffling that goes on is mainly based upon different valuations of the various structural features displayed, little or no regard being paid to age, size, area occupied, or any other non-structural feature.

As is well known, it is not possible to take the "value" of a character in any one family as a standard for it elsewhere; the principal thing that gives it its value, its age in the family concerned, has been ignored. In such conditions the shuffling may go on indefinitely, leading nowhere. The logical termination of such work is that every genus, or small group of genera, shall have its own sub-tribe or other group, as we have seen in the *Araceae*, where 108 genera are put into 42 different groups, and the same in *Saxifragaceae* and other families. Families may take the place of genera, and the whole dispute about relationship may then begin afresh. It must be recognised that taxonomic work cannot, without great complication, lead to a genetic classification. Age, size, and area must in future occupy an important place in all such discussions. We need a great deal more knowledge of the incidence of character, especially now that we have seen what divergences may occur between the closest of relatives; and we must not forget the old and overriding genus from which two very similar things may spring in similar conditions at great distances apart.

Like the genera, the families are arranged in a hollow curve type of distribution by size, with an increasing increase downwards from the 45 given above. The small families are also considered below under *Behaviour of genera*.

13. *Pairs of families*. There are some curious pairs of families that should be worth more careful investigation in the light of what has been brought up about complexes, small families, and the like. The best known is *Ericaceae-Epacridaceae*, the difficulty here being the geographical separation, for while the *Ericaceae* only reach AUSTRALIA with a *Rhododendron* in the north, and a few other species, and while it would be absurd to try to bring in selection between the valueless points of difference, *Styphelia*, the leader of *Epacridaceae*, has 175 species, mostly Australian, but spreading into most surrounding countries. One cannot but connect them with the great abundance of *Erica* and others in SOUTH AFRICA, and in fact this connection seems to show in other families like *Proteaceae*.

Another pair is *Myrsinaceae-Primulaceae*, about which GUPPY has much to say, though it is not easy to trace any likely common ancestor in this case either. *Cunoniaceae* has been split off from *Saxifragaceae*, but with its leader *Weinmannia* mainly South American, with species in MADAGASCAR, NEW ZEALAND, and POLYNESIA, and most of the rest of the family confined to NEW CALEDONIA, it looks more like a polyphyletic sub-family of *Saxifragaceae*. There are other cases also. In dealing with such cases, it must be remembered that if the families are very old (headed by very large genera) they will probably go back to a time when greater variety was likely to appear.

14. *The behaviour of genera*. Nature seems to have nothing specially to correspond to our notions of species and genera; her object seems rather to be to increase the number of living things upon a plan in which increase in variety seems to keep pace with the increasing variety in conditions, and in the ways that are open for mutations, in fact, GUPPY's theory of evolution by differentiation. Each new thing, whose advent was apparently compelled by some sufficient change of conditions, must be suited to those conditions, or die out again. Except perhaps in extreme cases, it shows

no special structural adaptation. From the immediate ancestor it inherits enough of local adaptation to survive and reproduce, being, apparently, a more or less incidental product of internal changes that go on when the plant is becoming suited to new conditions. It is completely impossible to predict what may change at the next mutation, or to what it may do so.

We have already said a great deal about the behaviour of genera in *Evol.*, especially in Testcases I, p. 90 to V, p. 99, VIII, p. 101, IX, p. 110, XVI, p. 126, XVIII, p. 128, XX, p. 134, in which, incidentally, we called attention to the way in which the earliest and largest genera of a family tend to break it up at the very commencement into its future taxonomic classification, which in this book we have illustrated with so many tables, all showing the same thing, and all impossible of explanation, it seems to the writer, by adaptation or selection. The testcases continue with XXX, p. 158, XXXI, p. 161, and XXXII, p. 163, and *cf.* also pp. 184, 189-90 above.

Each genus in the dichotomous divergent series in turn tends to behave like its predecessor, which also remains living, so that, as we suggested in 1907, and have used as part of our working hypothesis ever since, there is now often no reason why the whole tree of a family should not now exist, alive, upon the earth. Evidence to the contrary is supposed to be provided by fossils, which indeed show that not every member of any family is at present alive, but do *not* show plants that are at once to be taken as ancestors of things now alive. If they were so, they ought at least to be reasonably large and widely distributed, and these are qualities that are rarely found. It is much more likely that they represent side lines of development, which were completely killed out in some catastrophe (*cf.* YULE on catastrophes in 158, p. 23), and with them, most probably, all their descendants, if any, which would occupy less areas than themselves.

There is little to suggest that many fossils may be direct ancestors of genera of the same family that are still living. Most families taper so neatly to a point in their largest genus, beyond which one cannot be sure of the ancestry *at all*, as the difficulties that occur with the orders clearly show, that it becomes a very bold assumption indeed to suppose

that some fossil may be, for example, a direct ancestor of such a thing as *Psychotria*, *Acacia*, or *Carex*. It is clear, when one looks at the facts that we have now brought up in some detail, and indeed at the great difficulty that there is in placing *any* genus with any certainty, whether living or dead, as a direct and immediate ancestor of any head of a large family, that it is going to be a very difficult matter to trace ancestry back into past ages. We have so little to go upon that it becomes very largely a matter of pure speculation, and the application of inductive methods is greatly needed. We have applied these to geographical botany for the last 50 years, and have brought out several results that have a great deal of evidence behind them, though they have met with little acceptance, as they have been contrary to many received opinions. The writer must confess to considerable curiosity as to how the early breaking up into tribes, sub-tribes, genera, species, and sub-species will be explained away, to say nothing of other things.

Fossils belong in general to existing families, and even tribes, while any fossil that was a real ancestor of any leader of a big family might probably differ from it so completely that it would not be put into the family at all. The further back we go, the greater do the divergences become, and there is, for example, no proof that the mosses did not arise in one mutation from the algae. Now that we know how large and how divergent a mutation may be, there is little use in looking for transitions, for if divergences increase upwards from species to the leader of a family, there seems no reason why above that leader they should not be larger yet.

There is quite a possibility that the ancestor behind say. *Ranunculus*, going back so far as it must do, was a genus that may be smaller (even if living), and perhaps a good deal smaller, than is *Ranunculus*, for we are going back into a time when the material available for divergences was less, and when it is not improbable that mutations were fewer. This would be especially likely if the ancestors of flowering plants were woody Gymnosperms, and it is worth consideration if they did not descend directly from the ferns.

The "downward" direction of evolution, which we have seen to be the most probable one, takes the value out of any argument derived from a fossil that belongs to a sub-family or tribe now existing whose head is the second genus on the



list or a later one, for these are younger than the head. A really ancestral fossil should belong to the first tribe, or even, much more probably, to a different family altogether.

If, as required by Darwinism, genera, tribes &c were later than species, it is rather a remarkable fact that most fossils show unmistakeable family characters, and even tribal may be seen.

It must also not be forgotten that any genus seems to tend towards giving off descendants of two kinds, species in which the generic characters go down more or less untouched for the greater part, and new genera, in which more of them have been touched, and that sometimes in a more emphatic way. The whole question of the value of fossil evidence requires careful study. There is no doubt that fossils represent facts, but the way in which on the whole divergence increases upwards till at the top, as our lists show, it is at the maximum, implies that any ancestor of any of these topmost genera should be separated by some marked divergence, and quite possibly even by several. This is a question which is very difficult to solve with the small amount of material at our disposal, and the simple fact that it cannot be treated as easily as herbarium material.

It is clear that to be ancestral to the leader of any family now existing, the fossil should probably be as widespread and as frequent, and should show such differences that were it living it would not be placed in any tribe that now exists, unless that of the parent leader, for only this is possible as an ancestor to the *whole* family. More probably it should occupy a tribe of its own, and still more probably a new family of its own. But so far as the writer is aware, new families do not often appear among the fossils, though the genera seem to differ in many cases, and some families and genera seem to go a very long way back.

Questions that require some kind of answer from inductive work, before we can properly value any fossil evidence, are whether, as the writer is inclined to suspect from such indications as Miss CHANDLER's *Stratiotes* (*Evol.*, 64), continual more or less specific change may be going on, and whether the tribal position of any of the fossils can be proved, and so on. We also need greater evidence of wide distribution, a thing which is at present very lacking. A point in favour of the idea of continual change is the way in which the *Podoste-*

*maceae* seem to go on producing new forms in extraordinarily uniform conditions (136) though it is true that one of those conditions is the perpetual action of the maximum force of plagiotropism.

We are very far yet from any understanding of what has gone on in the times that preceded the development of the bulk of the flowering plants, but what evidence we have will need to be interpreted in the light of what we have shown to be happening at the top of all our present families.

Let us now go on to take a few instances of generic behaviour, taking them from groups of families that we have so far left comparatively untouched, the Monocots and the water plants. As the matter is more simple to deal with in a small family, let us begin with the *Juncaceae*, which though small is evidently old by reason of its wide dispersal, the conditions of life that suit *Juncus* itself being also very widespread and uniform, probably putting little pressure on a species. Our list below includes the whole family :

*Juncaceae by size in the world*

1. <i>Juncus</i>	225	Cosmopolitan (montane in tropics)
2. <i>Luzula</i>	80	Temp., especially Old World
3. <i>Marsippospermum</i>	3	Southern S. Am., New Zealand
4. <i>Distichia</i>	3	Southern Andes
5. <i>Rostkovia</i>	1	Southern S. Am., New Zealand
6. <i>Oxychloe</i>	1	Southern salt deserts
7. <i>Andesia</i>	1	Southern Andes
8. <i>Prionium</i>	1	Cape Colony

The family evidently began with *Juncus*, and probably somewhere in the north, crossing the tropics at higher levels. The most widespread, almost cosmopolitan species, *J. bufonius* L., reaches 112 in BRITAIN, as do *J. effusus* L. and *J. conglomeratus* L., which though not quite so widely distributed in the world, exceed it in number of individuals.

*Luzula*, suited to rather drier and more shady northern conditions, was the first mutation from *Juncus*, and has not travelled so far. Only when *Juncus* reached the far south did it again, apparently, encounter conditions sufficiently different to give the needful stimulus for larger mutation.

Even in the tropics this does not seem to have been forthcoming; *effusus*, common in BRITAIN, is also common in the higher hills of CEYLON, and is one of the few species in common between the two countries.

The six southern genera show in S. AMERICA a structure that is largely co-ordinated with the drier and colder conditions to which they have been subjected, or, in the case of *Oxychloe*, to the conditions of salt desert. The results are seen in the well marked xerophytic characters, though we do not as yet know exactly how these were produced there. It is of special interest to notice that *Juncus* itself, the leader of the family, also shows cushion formation, one of the characters exhibited by these genera, in salt marshes and in similar places, so that it is evident that a tendency to that character is, so to speak, in the blood. It is evidently a case of like causes, like results, as one may see by comparing with the other cushion plants of the south, like *Azorella* (*Umbelliferae*), *Raoulia* (*Compositae*), *Restionaceae*, *Eriocaulaceae*, &c, or with many alpine xerophytes of the north.

In SOUTH AFRICA, on the other hand, the local genus, *Prionium*, and probably at a single mutation, developed a shrubby habit which enabled it to live more easily in the river beds, though we can see no reason why it should not have developed into something on the lines of the *Podostemaceae*; there was probably some internal reason.

The taxonomy of the large genera well illustrates the rule that we have been gradually making clearer—that the important taxonomic divergences are among the very first that appear in the history of a family, tribe, genus, or species. In NP/1 BUCHENAU makes eight sub-genera of *Juncus*. Of these 1 and 7 have each only one species, in the Mediterranean and in S. Africa; § 6 (*Junci alpini*) has a number, mostly in the Himalaya, but also in the western mountains and arctic. This and the other five subgenera all occur in BRITAIN, and are in general headed by the most widely distributed species there, as we have seen in other cases; § 2, *J. poiophylli* by *J. bufonius* L. (almost cosmopolitan, British dispersal 112), § 3, *J. genuini* by *J. effusus* L. and *J. conglomeratus* L. (dispersal 112), § 4, *J. thalassici* by *J. maritimus* (disp. 55; this coast species could not reach more than about 80, but has not yet got round the north of SCOTLAND, though, as one would expect from the less broken

coast, it has gone further north on the colder eastern side. The 5th section, *J. septati*, is headed by *J. lampocarpus* (disp. 110), the 6th by *J. triglumis* (25); § 8, *J. graminifolii*, is represented only by *J. capitatus* in JERSEY and GUERNSEY. The groups are thus headed by the most widely dispersed species in BRITAIN, as we have already seen in *Galium* (p. 179) and other genera.

The same thing shows in *Luzula*, whose three sub-genera are headed by the three most widely dispersed species in BRITAIN, which are therefore well divergent from one another—§ *Pterodes* by *L. pilosa* (111), § *Anthelaea* by *L. sylvatica* (110), and § *Gymnodes* by *L. multiflora* (111).

It is of great interest to see that all the small genera of *Juncaceae* have evidently arisen under the stimulus of altered conditions, and in the kind of broken and especially of mountainous country in which such conditions most readily occur. Those that occur on both sides of the south PACIFIC probably had other species on the now submerged land there.

By taking families from the top *downwards*, in the way in which nature evidently developed them, it thus becomes much more easy to trace that development, as we have just done in regard to *Juncaceae*. The taxonomic divisions soon become clearly marked out, though they are better shown in some families than in others (nature had not classification in view). Thus we find as leading genera:

*Amaryllidaceae by size in the world*

Agave	275	Heading	<i>Agavoideae</i>
Crinum	130	Heading	<i>Amaryllidoideae</i>
Bomarea	120	Heading	<i>Hypoxidoideae</i>

*Araceae* we have already seen on p. 267.

*Bromeliaceae by size in the world*

Tillandsia	400	Heading	<i>Tillandsieae</i>
Pitcairnia	170	Heading	<i>Pitcairnieae</i>
Aechmea	150	Heading	<i>Bromelieae</i>

and so on. The distribution of *Agavoideae*, in south U. S., MEXICO and C. AMERICA only, is much less than that of



*Crinum*, and it may be that the latter is really older than *Agave* itself. The fourth tribe in *Bromeliaceae*, *Navieae*, has only the genus *Navia*, with three species in AMAZONAS and GUIANA, marked by a supposed "important" character, few ovules against many, but one easily formed by a simple mutation (cf. *Farmeria* in *Podostemaceae*), and it cannot be regarded as on a par with the rest. If we look at *Tillandsia* itself, we find the two species with the widest dispersal, *T. usneoides* L. (CAROLINA to ARGENTINA) and *T. recurvata* L. (FLORIDA to CHILE), heading the two largest sub-genera, and so on. The law is quite general, and there are very few exceptions.

As one goes upwards, a family seems suddenly to stop at a very definite genus, the largest genus that one would put into the family without great hesitation. This, the oldest genus, was evidently that in which the "family" characters first appeared as a definite connected *combination*, which has subsequently remained comparatively unaltered. It has slightly changed at every mutation since it was made up, but has not changed the individual characters so continuously or so divergently one after the other that their presence as the family characters can no longer be recognised as a whole, sometimes A, sometimes B, changing, but enough remaining unchanged to be sure of the family concerned. Another family is

*Hydrocharitaceae by size in the world*

World size		Sub-family	Tribe	Distribution
Boottia	20	Heading <i>Stratiotoideae</i>	<i>Ottelieae</i>	Trop. As. Afr.
Ottelia	15	2nd Strat.	2nd Ott.	Warm
Blyxa	12	Heading <i>Vallisnerioideae</i>	<i>Blyxae</i>	Trop. As. Afr.
Lagarosiphon	10	2nd Vallisn.	<i>Vallisner.</i>	Afr. Mad.
Elodea	6	3rd Vallisn.	<i>Hydrilleae</i>	America
Halophila	6	Heading <i>Halophiloideae</i>	No tribes	Trop. oceans
Hydromystria	3	3rd Strat.	<i>Hydrochar.</i>	Trop. Am.
Limnobium	3	4th Strat.	2nd Hydr.	Am.
Vallisneria	3	4th Vallisn.	2nd Vallis.	Warm
Thalassia	2	Heading <i>Thalassioideae</i>	No tribes	Trop.oceans

Here we can again see the growth of the family more or less marked out. *Boottia* and *Ottelia* differ little, and may

even be sub-genera of one genus. *Blyxa* heads a new sub-family, and the last two sub-families, of oceanic dispersal and under almost completely uniform conditions, do not break into tribes as do the first two. They probably became marine at some big estuary on a nearly tideless coast, as at KALUTARA in CEYLON, where the river is fairly large. One is told by the local people that it is fairly safe to bathe at a certain belt in the estuary, where the water is about half and half, but that one is liable to be eaten by crocodiles upstream or by sharks down.

This is a small family, but being water plants they are more plastic, and have formed four subfamilies and eight tribes for about sixteen genera and about 90 species. Each genus behaves like its immediate ancestor, forming about the widest divergence possible at that particular stage, larger than in land plants perhaps on account of the plasticity. Each line of descent continues to divide when any excuse is given by the conditions, but the divisions tend to diminish, and, given time enough, would perhaps come down to a stage of sub-sub-species, or even Jordanian species.

The monotypic genera, as they make about 38% of all genera, while the ditypes make another 12%, require mention, but have been sufficiently discussed in many previous places, *e. g.* in *AA*, and in *Evol.*, and in (158).

15. *Generic sizes.* With the almost complete disappearance of adaptation and relicdom from the field of action, there seems little reason left for the great variation in sizes of genera, especially when they are all in the same family, and do not vary in concert with any other character that one can find, as all for example vary with age. Let us look at *Rubiaceae*, sub-family *Cinchonoideae*, with its eight tribes; the other sub-family, the *Coffaeoideae*, behaves in the same way.

*Variation in sizes of genera in tribes of Cinchonoideae*

Tribe	1	2	3	4	5	6	7	8	Aver.
Size of leader	20	180	100	5	40	50	60	125	72
Number of genera	12	48	24	5	43	10	48	86	34
Number of species	55	714	186	9	358	158	309	771	320
Av. size of genus	4.6	14.8	7.7	1.8	8.3	15.8	6.4	9	9.2
Number of ones	4	23	12	4	15	2	24	41	15

This is a remarkably incongruous set of figures. Let us place them in order by sizes of leaders

Tribe	2	8	3	7	6	5	1	4
Size of leader	180	125	100	60	50	40	20	5
Number of genera	48	86	24	48	10	43	12	5
Number of species	714	771	186	309	158	358	55	9
Av. size of genus	14.8	9.0	7.7	6.4	15.8	8.3	4.6	1.8
Number of ones	23	41	12	24	2	15	4	4

None of these sets of figures seems to have any correlation with the first set, or with any rule that one can think of, so that it is very hard to imagine that the grouping is genetic.

The *Coffeoideae* give a similar set of incongruous figures. Their leaders average 132 against 72, yet they have only 195 genera against 276, and 2381 species against 2560, and their average size of genus is 12.2 against 9.2.

16. *Taxonomic maxims.* We have already said a good deal about these in *AA*, pp. 217-18, and *Evol.*, p. 132, and this notice is simply a reminder that most of them are as easily explained by the new outlook as by the old. For example, two of the best known are that large and widely distributed species vary most, and that species of larger genera vary more than those of smaller. This is just what one would expect, as a simple and automatic consequence of all that we have learnt about the mechanical and automatic way in which evolution goes forward, and which we have seen illustrated by the incidence of varieties in the British flora (p. 186). Confirming this by looking at the first volume of the Indian flora, we find that 31 genera with 100 or more species *in the world* have 174 varieties, while 65 genera of less than 100 have only 168 in all, or less than half the percentage. As size and area go together, it is clear therefore that mere wide dispersal is probably sufficient to account for the variation seen. It may even be that at every birth of an individual in a definite line of descent there may be a tendency to a very small difference indeed; or again, it may be that as groups of characters are produced at each mutation, and that we make our genera by fitting together characters into the best marked groups that we can find, it is not unlikely that genera may be polyphyletic (*cf.* also BOWER's work in 16, 17). But as yet all this is mere speculation, until we

know something about the laws that govern the phenomena actually seen.

Another maxim is that "those classes and families which are the least complex in organisation are the most widely distributed, that is to say that they contain a larger proportion of widely distributed species". We have expanded this at some length in the chapter in *Evol.*, p. 65, and have there pointed out how it fits in with dichotomous divergent mutation and the hollow curve. We have dealt with the common maxims on p. 132 in the same book, showing how well they all fit in with our theories. There is also a long list of maxims in (68), vol. I, Dicots, pp. 6-7, but some of them may need a little revision to fit in so well.

17. *The discrepancy between taxonomy and geographical distribution* is often considerable, requiring explanation. The help that geography gives to taxonomy is more or less accidental, when it happens, as it sometimes does, that divergences in the two coincide. This often simply means that in that case there was no polyphyly; the marked character or combination of characters only appeared once, and was locally propagated. We have said much about this subject above, and may call attention to the most important statements. We have seen that dispersal is mainly governed by the laws of ASA, with the negative influences of barriers of all kinds. The closer relationship of the genera near the head of a family tends to be marked by wider divergence—a hopeless discrepancy. We have given many individual cases of great discrepancy, especially the *Monimiaceae* in Ch. X and *Araceae* in Ch. XI, the *Buxaceae* on p. 159, the *Dipterocarpaceae* on p. 153, and in places a reference or two to other families. We have described the cases of such genera as *Hibbertia* and *Schumacheria* on pp. 146-8, where there is no overriding genus in the family to bring similar features to two genera at great distances apart; *Tetracera* on p. 148 forms a very incongruous mixture of the two, and it is clear that it is the structural rather than the geographical side that must give way. We have also given details of *Siparuna* and *Mollinedia* on p. 246, and so on.

It is clear that one cannot neglect geographical propinquity, but if we try to add its results to those of structural likeness, we make our classification much more complicated,



without making it any more genetical, for these two seem to be utterly incompatible in broad outline; a genetic grouping cannot be made upon a structural basis only, and it is better to keep them apart. The simple but universal branching out of the head of a family and its first descendants—its nearest relatives—into the heads of the tribes, subtribes, and so on, shows that divergence tends to be greatest at the top, in the region of closest relationship.

Discrepancy seems inevitable, and so widespread and common that it may almost be regarded as a law of geographical distribution. We can see it simply shown in such a case as *Rhamnus* (p. 143), where both in CEYLON and in MADRAS the same wide has mutated off an endemic in each country, and these two endemics are both sub-generically separate from the wide, as well as widely separated from each other. In fact, had their mutual separation been older and therefore commoner and more widespread, their difference would be sub-generic also, in all likelihood. The same difference as that between the wide and the endemic in CEYLON is common all over the range of *Rhamnus* and in one district there may be only one, in another the other. Cf. also *Tetracera* (p. 148), *Psychotria*, and many other genera.

The cause of this discrepancy was considered in *Evol.*, Testcase XXVIII, p. 154; and one may see it in another way in many monographs, e. g. that of *Siparuna*, head of *Monimiacae*, in *PR* (cf. p. 246, and map on p. 224). It is broken up by the key into smaller and smaller divisions down to the single species, which approach one another structurally but not geographically; to get the latter, one must pick out species all over the list. There are some in every ten from the first to the eighth (last), in PERU, while there is also the overriding species 87, *S. guianensis*, practically covering all the rest. This type of distribution, with most of the structural subdivisions represented, is perhaps the most common of all. We have seen good examples in BRITAIN and in EUROPE generally, in CEYLON, and elsewhere, and have given a sketch of it, dealing only with species, in *Evol.*, Testcase XXVIII, p. 154. When we have realised what is shown in all the lists of genera at the heads of families shown above (condensed on p. 173) we shall of course expect this result. It is evidently a general law of evolution.

By no kind of shuffling, re-arrangement, or re-grouping,

can one be sure of harmonising the structural arrangements, and with them the taxonomic grouping, with the geography or the genetic succession. Let us take *Phytolacca* (*PR*), which happens to be upon the table, as another illustration. Each sub-genus divides into those with hermaphrodite and those with dioecious flowers (*cf.* the *Restionaceae-Eriocaulaceae* complex in *Evol.*, Testcase XXIV, p. 138), showing that one or other of these characters must be polyphyletic. It is probably more or less as a result of this very common phenomenon that the tendency of taxonomic work is to continual subdivision of the groupings, so as to give to nearly every genus or small group of leader and satellites a separate position, as we have seen in *Araceae* where 108 genera occupy 42 different divisions, and even then, have not got over the difficulty.

With the structural differences largely valueless from an adaptational point of view, destruction of intermediates, whether geographically or taxonomically, cannot be called in as was formerly done, and the larger the family, the more difficult does the position become. This fact alone goes to show that the two are more, rather than less, independent of one another. The structural changes that the mutations bring about are not necessarily accompanied by increase in distribution, though they may be in cases where, as in xerophytes, there is a steady pressure in one direction. In a small and local family, where all the genera are living in much the same conditions as the head of the family, *e. g.* the *Penaeaceae* (p. 301), structure and geography agree well enough. But in a large and cosmopolitan family like the *Compositae*, reconciliation becomes practically hopeless, and indeed is not attempted, and the subdivision goes on as in *Araceae*. A single group in the monograph in *NP/1* taken almost at random, shows the following composition :

No. 557,1 CORSICA; 558,1 NEW GUINEA; 559,1 WEST AUSTRALIA; 560,1 CENTRAL AUSTRALIA; 561,7 S. AMERICA, and 562,2 CHILE. Obviously the only possible explanation is polyphyly; they are all young, and one could not get such destruction as would be needed.

The whole process seems to be largely the continual production of new permutations and combinations of characters that are handed down from above, each new one making others possible to its descendants.

18. *The incidence of character* demands much further enquiry. Why are family, tribal, genetic, and specific characters found in successively smaller groups? Evidently the family was the oldest, and we have hitherto looked at evolution as if it were moving backwards. What determines how long the bulk of some set of characters shall remain comparatively unaltered in a line of descendants? And why should there seem to be no reason why those particular characters should go together; why one family should have extrorse anthers and an inferior ovary, another get on just as well with introrse anthers and a superior ovary. We gave *Lauraceae* as an illustration on p. 115, but any other family would do as well. Except that the characters mark all the organs, there seems no correlation among them, except in such cases as climbing plants, where a weak stem accompanies the possession of climbing organs.

Why are the family characters on the whole so constant in incidence that they can be used as such, but why are they not exactly constant, one or two changing for every tribe, but almost never all or nearly all, and rarely twice the same, or in the same way? Why, to take a simple instance, does *Cucubalus* break away from the family characters of *Caryophyllaceae* to exhibit a berry fruit, the only one in the family? But why is this breaking away so common that in all families of more than four or five genera we have to qualify almost every character by "usually" or some such expression? And why is almost every character that thus unexpectedly appears one that is common enough somewhere else, even if not found in that particular family, like the berry, which is one of the commonest of fruit patterns, and in both Mono- and Dicots? And so on.

As an instance of a distinctive character found in several places in one family, but not outside of it, we may take the familiar red and black seeds (crab's eyes) of *Abrus precatorius* (*Legum. Papil. Viciae*). This character, with the same exact straight line of demarcation, but with rather more black and less red, is found in *Adenanthera* (*Legum. Mimos. Aden.*) and in *Ormosia* (*Legum. Papil. Sophoreae*) and one or two more (*cf. Kew Bull.*, 1890, p. 1). Or again, take the case of cauliflory (flowers appearing on old wood), which is found in many tropical shrubs and trees like *Artocarpus* and *Ficus* (*Moraceae*), *Goethea* (*Malvaceae*), *Theobroma* (*Sterculia-*

*ceae*), and many more. In these two instances we have taken unusual characters, but if one take common characters, they are to be found all over the whole system of taxonomy.

Few actual generations are needed from top to bottom even in a large family, working as they appear to do by the 1-2-4-8- rule, and it is very unlikely that any divergence will strike all the family characters at once, after the first divergence from something outside the family that threw them all together, producing the genus A, which led the new family, and which had a set of characters that on the whole persisted right through it. It must be remembered that the beginning of a family, especially if large, tends to come at a period when divergence also tends to be large. The *individual* divergences in a small family (*cf. Evol.*, p. 199) are in general as large as in a big one, but the latter tends perhaps to have more of them in the early genera, so that there is less doubt as to its family rank. At an early period of time, possible mutations were probably fewer and therefore better marked.

At the second mutation the divergence will probably tend to be less marked on the whole, fewer characters, and especially fewer of the "family" characters, being affected. But they will still be so marked that the new genus B will go almost automatically into a new tribe, even though it is the immediate child of A, which will now become the head of the first tribe as well as of the family. Further mutations of B will give rise to still smaller divisions than tribes, though one must not forget that a large part of the importance of a character is due simply to its age; the older it is, the more descendants will show it.

When a divergence is very recent, and found only in one or two species of a large genus, like *Coleus elongatus* on RITIGALA summit in CEYLON (*AA*, pp. 151-2), the taxonomic tendency seems to be to retain it in that genus, even with the divergence. The RITIGALA *Coleus* no longer shows the usual calyx type of the genus, which could only be changed by a marked mutation. But if the mutation had been much older, so that there existed in CEYLON a group of species showing this calyx, there might be a tendency to give them a separate genus. We are more accustomed to find complexes in large genera than small.



On the whole, as one goes up from the monotypes at the bottom, the divergences seem to become rather more numerous, even if no better marked (*cf. Evol.*, p. 199). In a family like *Podostemaceae*, where all the divergences are rather striking, this seems to show well enough, and though both lines seem to have started from *Podostemon*, there is a great difference between the forms of AMERICA only, and those of ASIA only. As one gets near the top in a big family, one finds at last that the mutation that produced the leader A affected so many "important" characters that it is very difficult to say what was its probable parent. It is very noticeable in the list of the 45 leading families on p. 329, how many different orders they belong to, and how marked the tendency to put many of the large families each into an order, either by itself, or with a few satellites. In HUTCHINSON'S list, we find such families as *Crucif.*, *Prot.*, *Malv.*, *Euphorb.*, *Legum.*, *Myrsin.*, *Gentian.*, *Borrag.*, each in an order of its own, and such as *Annon.*, *Ranunc.*, *Papav.*, *Cappar.*, *Viol.*, *Polygal.*, *Polygon.*, &c each surrounded by satellites. These are given in the sequence in which they occur in the list, so that one can see the great shuffling that has been done; it is clear that whatever arrangement we take, the families are difficult to place, for the simple reason that in many cases the mutation that gave rise to the head of the family altered a good many of the important characters of the immediate parent of that head. The difficulty of placing thus increases with the size of the head.

Working downwards in this way, order-family-tribe-genus-species, one may perhaps suggest that what is going on is something like this. At the "order" stage, divergences are few, but well marked, inasmuch, perhaps, as they have but a comparatively small number of diverse features of the different organs upon which to work, and possibly also because the available energy for making divergences may be greater. The new forms thus produced, in very early days more particularly, will tend to differ so much that we shall now look upon them as heads of families, and especially of large ones such as we see in the list above, beginning with *Compositae*, *Orchidaceae*, and *Leguminosae*. These in turn, when they come to mutate, will have rather more material, and perhaps rather less energy, and the result of later mutations will tend to be, at first, mainly heads of smaller and younger families.

The next stage will tend to be tribal, and so on downwards. But as no two will be likely to mutate at the same rate, or to begin doing so at the same time, we shall have a great mixture of all the different stages of evolution going on at the same moment. Each new mutation will more or less closely repeat the action of its immediate ancestor, having somewhat more material to work upon by reason of foregoing mutations, and perhaps rather less energy with which to do so. Those characters of the leader A that have been left comparatively untouched in the various mutations will be the family characters, and the same for tribal, generic and other heads, and as we come downwards in the scale, the chance of any mutation giving rise to something so divergent that it cannot be easily placed will become less and less.

In the very earliest days of the flowering plants, therefore, the new forms produced will have a tendency to be the leaders of new orders, made by comprehensive mutations that will cover a good many characters; whilst those characters, being developed at so early a period, will be regarded, now, if they have persisted, as very important, for we have seen that importance goes with age. Any new form produced at that early period will tend to be a member of a new family, or even order, when judged from a taxonomic point of view. In our present state of ignorance of such matters, it will be almost impossible to say with certainty what its parent actually was, for it may diverge in several important (old) characters. Hence our difficulties in making, or grouping and arranging, the orders.

At the same time, of course, the new form will be a new order, as well as a new family, a new tribe, a new genus, a new species. But to the botanist of that date, all this latter definition would be unnecessary, and what we now call a tribe or a genus would take the place of our conception of species, and be sufficient definition, though there would doubtless be frequent opportunities for dispute as to position.

As time went on, mutation would become less and less comprehensive, and it would become easier to place new forms in taxonomic relationships as marked out at the present day. A considerable number of what we should now call new families would appear, then tribes, and so on. But all these stages would be mixed up together, according to the different ages of the things concerned, and other factors.

There is probably much to be made out by a simple study of characters and their incidence, family by family, and it may be worth while to look, for example, at some of the satellites of the *Compositae*. In *Calyceraceae* the first three of its few genera are separated by mutations of the fruit. The fruits of *Boopis* (25 spp), the leader, are all alike, but the first mutation produced *Calycera* (10) with some fruits crowned, but not all, by a hardened calyx, while in *Acicarpha* (5) the ray fruits are united, and the disc flowers sterile. The family is confined to the southern ANDES, but has spread out upon the plains also. There is at present no possibility of explaining why these particular divergent characters are shown on these three leading genera. They show no correlation with any of the conditions of life, nor can one see any reason for the casual mixture of hard and soft calices in *Calycera*, or the union of the ray fruits in *Acicarpha*. For some reason quite unknown, the mutation united these particular characters in certain cases, which by our rules of taxonomy were new genera. But, as hardly needs further insistence, the chance that just these characters, and all at the same time, shall be chosen for change at the next mutation, is in the highest degree improbable, so that the genus will continue, though in each new species there will be a great probability that one or other of the characters will change. But it is therefore unlikely that a new genus will be formed from any parents but the older ones that have now so many species that they stand fairly high in the lists. In fact it is by no means impossible that most of the genera of a family are directly descended from one or other of the first dozen or so of genera that are shown in the many lists that we have now given. Very small genera, up to perhaps ten species at least, are unlikely to have much, if any, generic progeny with more than one or two species, progeny, that is, that for the present will count for nothing in the evolution of the family. As we have shown in *Evol.*, p. 101, in 41% of the families, the first genus has more than half the total of species in the family. Even in *Compositae*, the first 30 genera have 9055 species, while the remaining 1149 genera have only 9004 among them. It is the largest or oldest genera, derived from the earliest mutations, that have been the great, probably almost the sole important, factors in determining the later history of the family, especially its division into tribes and

other groups. Except in small families with small heads, the little genera count for but little.

In other words, some of the characters that are being handed down may change at each mutation, though what the change may be, and why it should affect any particular character, is at present a mystery. Only in special cases like the *Podostemaceae* or other water plants, the plants of dry climates, parasites, saprophytes, and so on, does one seem to see any sign of cause and effect. The evidence that we now have of divergent mutation gets rid of many of the difficulties of the old school. The new theory makes no use of advantage and selection, needs no transitions, and will work equally well in either direction. But its laws need much further investigation.

If the genera of *Calyceraceae* were larger and more numerous, the descendants of *Calycera* would probably be regarded as a tribe *Calycereae*, contrasted with the tribe *Boopeae*. Age in the family, regardless of the intrinsic value of a character, is what gives it its importance. The writer has been preaching the supreme importance of age for fifty years, as enabling nature to carry out efficient and valuable change, and it was therefore a great pleasure to him to gather, from the papers and speeches at the Bicentenary of LAMARCK (79) that people seem to be realising this fact. Some of the most important characters are simply picked out by their age in their families, like the ligule of the grass leaf, the anteposed stamens of the *Primulaceae*, the tetradynamous stamens of *Cruciferae*, the ochreate stipules of *Polygonaceae*, the column of the *Orchidaceae*, the asymmetric leaf of the *Begonias*, and so on. It will of course be noticed that though this single insignificant and obviously mutational character is a mark of any of these groups, it is not *the* mark, unless found in combination with other characters. When the tetradynamous stamens are found in connection with a four-petalled flower, a superior ovary with a spurious division, and so on, we know that we are dealing with a crucifer, because that *combination* of characters is practically certain never to be found in any other group, unless possibly in *Capparidaceae*, which is very closely allied. The ordinary laws of chance forbid such a happening.

It is fairly probable that the *Calyceraceae* is an offshoot of the *Compositae*, one of which probably underwent a



divergent mutation in which it happened that the erect ovule became pendulous (*cf. Buxaceae* and *Euphorbiaceae*), the cohesion of the anthers was lost, and a little endosperm appeared. All these are simple mutation characters, and it was what as yet we must call chance that altered them all at once, and made a new family. This particular chance, however, could only operate when led up to by the mutations that gave rise to the *Compositae*, and perhaps even the mutations that in the family of the *Compositae* gave rise to whatever genus it was that became the parent of *Boopis*. A very slight difference in the starting point will make more and more difference as the mutations go on, so that the final result may be something very different from that which began with a genus closely allied to the first.

The other very small and apparently satellitic family, the *Stylidiaceae*, has one fairly large genus, *Stylidium* (100), mainly centred in AUSTRALIA, distinguished from *Compositae* by simple mutation characters. The other two chief genera are *Phyllachne*, distinguished by absence of labellum, and *Levenhookia*, with shoe-shaped labellum. It is clear that all their characters may be obtained by simple mutation, but not why it should be so. There was no definite persistent strain in one direction, and so the mutations appear to be due to chance, though in *Levenhookia*, an endemic of the drier climate of WEST AUSTRALIA, the mutation has gone in the direction of small and crowded leaves (*cf. Juncaceae*, p. 346).

Even in so small a family as this, one can see early breaking up of a genus into its taxonomic divisions going on; *Stylidium* shows four sub-genera, and *Phyllachne* three sections, several of which have been regarded as of generic rank.

There are also frequent displays of greater complication, which may be lumped together as appearances of unexpected characters at various places, often widely separated geographically or taxonomically, or both. The *Rubiaceae* have usually an inferior ovary, but *Gaertnera* in AFRICA and *Pagamea* in BRAZIL have each a superior ovary, and must have obtained it by independent mutations, but why? Why are there no African descendants of the former, showing the superior ovary? It has 30 species, enough for considerable generic parenthood. Did the offspring return to an inferior ovary?

The adoption of divergent mutation makes the old positions untenable. We are presented with two *faits accomplis*, parent and child, no longer liable to crossing, as they were in the days of gradual transition, and too different for selection to come in as a guide. We have shown on p. 27 that adaptation does not operate to separate things, and on p. 34 how *Paeonieae* regularly show two characters that may be seen singly in various *Helleboreae*. It was this repeated occurrence of the same character in more than one place that suggested the idea that a family might carry a set of characters for kaleidoscopic use, which might be shuffled into various combinations, each of which, if of stable enough equilibrium (p. 372), might be represented by a different form, sometimes of one, sometimes of another, rank. Under my conceptions, adaptational value is not *required* in single characters, provided that they are not harmful; evolution is largely a display of permutations and combinations of the individual characters, on the whole increasing in complexity as time goes on and their number increases.

These considerations show the great importance that attaches to the phenomena of teratology (pp. 100-105), for they show clearly what large and unexpected mutations are easily possible. We have no proof that their usual non-viability may not at times be due to the fact that that particular combination of characters was not in stable equilibrium, or was not one which simply proved unsuited to its environment, and died out.

Such phenomena as we have been describing occur mainly in larger families, because, upon our conceptions, there have been more mutations, giving the chance of getting more of the less usual characters. One need no longer feel surprised that it is the large families that depart most from their prescribed family characters in one place or another, nor need one feel that one must spend so much time in trying to explain complexes and such phenomena, which are perfectly normal under the conceptions that we have brought up. A family simply happens to show in common a group of characters, often, so far as we can see, unconnected with one another in any definite way, but covering all or most of the parts of the plant.

The natural supposition seems to be that the combinations of characters that mark families and other groups are almost

pure chance. At any rate, a large element of chance, as we must at present call it, is introduced into our taxonomy. A family (or tribe, genus, species) is defined by the general presence of such characters as *happen* to fulfil the necessities of divergence from others (result of divergent mutation), and constant or nearly constant occurrence throughout the family (tribe, genus, species), which is the result of early acquisition, due to comparative age. Only rarely does one find traces of actual structural adaptation about the characters, and then it is in such cases as for example the *Podostemaceae*, where the constant pressure of external conditions is largely in one definite direction only, and species that indicate suitability to that pressure are mainly favoured. But there must of course be some law or laws that determine what happens, for the happening is evidently compulsory.

In *Connaraceae* (p. 141), our first list of leaders of a family, the first three generic mutations divided the family into its four great groups, the tribes. The original set of characters, descending from *Connarus*, was thus being altered, but *differently* each time, by divergent mutation. We have now seen, in many lists of leaders, and in the tables on p. 173 and in *Evol.*, p. 199, that this is a law of evolution, closely adhered to by all families. Had *Connarus* remained the only genus of the family, its characters would have been the standard throughout, though of course necessarily altered a little in every species. But after the family has become early divided into four tribes we have to add the qualification "usually", or some such word, to nearly all the characters that mark *Connarus*. All families, unless a few of the very small ones of 2-5 genera, show the same kind of thing. In *Ranunculaceae*, for example, *Clematis* shows a more or less woody habit with opposite leaves, and being now a large (old) genus, has passed most of its characters, but not all, on to various groups or single species, according to their relative age. *Clematis* itself is the overriding genus (151), covering all the localities of the others, and many people are still doubtful about the acceptance as independent genera of these "satellites"—*Viorna* (18 N. AM.), *Clematopsis* (10 MADAGASCAR, trop. AFR.), *Naravelia* (7 INDOMALAYA), and *Viticella* (1 EUR.). In many floras these genera are marked as "*Clematis*" p. p. and as they are evidently descended from it, it seems a matter of little moment how they are named.





of guesswork. The third genus is most likely a direct descendant of the leader, and it seems probable that for a long period most genera will be so. We have seen in Testcase VIII (*Evol.* p. 101), which should be read in this connection, that for a long time the first genus makes up more than half the family with its species. The chance is perhaps greater that the earlier subsequent genera that belong to the same tribe as the leader may be its direct descendants, while those below the leader in any tribe are more likely to descend from the leader of the tribe, but as yet we have no information to go upon. It is only as the family grows in size that the genera following the first become large enough to be in their turn important as parents. This one may see clearly in the table on p. 102 (*Evol.*), where with one small exception the figures rise steadily with age.

As a general rule the incidence of characters seems to be governed by what at present we can only call chance, and examples of this are abundant. A frequent teratological phenomenon in *Cruciferae* is the production of bracts, which in this family are usually recessive; but in *Schizopetalon* (5 CHILE) we get them regularly formed (p. 104), with no possible adaptational explanation, but apparently owing to the operation of some unknown law in the mutation that formed the genus. It is another illustration of the fact that almost any character may at some time or other appear anywhere in a family. Cf. pp. 133, 135-6, 142-43, 148-9, &c, &c. There seems no reason why such characters as in

<i>Gramineae</i>	Leaf net-veined in	<i>Olyra</i> and <i>Leptaspis</i>
<i>Orchidaceae</i>	Leaf net-veined in	<i>Corysanthes</i>
<i>Liliaceae</i>	Leaf net-veined in	<i>Smilacoideae</i>
<i>Gramineae</i>	Stamens 10-40 in	<i>Pariana</i>
	Stamens 6-120 in	<i>Ochlandra</i>
<i>Orchidaceae</i>	Pollinia $\infty$	<i>Calopogon</i>

to take just a few from the Monocots, should appear at all.

Pappus in *Compositae*, often regarded as an adaptation, is not a very efficient one, except in a few cases like *Taraxacum*. In many it is almost immediately deciduous, a feature explained by selectionists of the writer's youth as a design to drop the seeds not too far away from places where the

parent had succeeded, though how such an altruistic arrangement came about was left to the imagination. Many show scales and bristles symmetrically mixed, and even the most enthusiastic selectionist hardly dared to suggest that if the one failed, there was the other to fall back upon. Others, like *Adenostemma*, have sticky glands as well as the pappus proper. In *Eriosphaera* the tips of the pappus hairs have a number of inflated cells, like a bunch of stalkless grapes. We have shown in (155) how the characters of pappus and other things vary from genus to genus in the usual apparently purposeless manner.

A convenient list of things that *may* happen, inasmuch as they *have* happened, is PENZIG's *Pflanzenzenteratologie*, 2nd. ed., where great numbers of mutations are described, some of which were instanced on pp. 100-05. It is not clear why these changes are impermanent except in one or two instances, and one wonders whether they might be mutations that were in some way unsuited to local conditions. One cannot see any evident reason why they should be so temporary, as a rule.

If characters come together by what at present we can only call chance, such a case as the tribe *Brownlowieae* in *Tiliaceae* becomes more intelligible (pp. 156-7). Here we have a group which shows a number of characters in common, but is geographically scattered, while at the same time a number of characters, usually considered more important than those that mark the tribe, are found in various members of it. A few of the tribe fit together well geographically, and in the usual curve, and are probably a genetic assortment, while the rest have acquired certain characters by chance that have brought them into the same tribe.

Into the tribe *Shoreae* of *Dipterocarpaceae* we put things that show a certain group of characters, that may often be found singly in other parts of the family, as the imbricate calyx is found in *Vaterieae* or *Dryobalanopseae*. As we have said on p. 155, almost any character may turn up anywhere, for anything that we know to the contrary, though it is not common. Every genus tends to show some character that was not visible in its parent, where it must have been recessive, so that the probability is that all characters, or their potentialities, descend from the leader of the family.

19. *The lack of transitions between characters.* It used to be supposed that any character found was derived from some ancestral one with which it could be connected by a series of easy stages, so that there must have been enormous numbers of these transitions. But their destruction could hardly be so absolute as the facts would indicate; many would survive in odd corners of less competition, yet it is the rarest of occurrences to find anything that can be said to show an intermediate single character. What is usually found, especially in extinct groups (cf. pp. 168-9) is things that show a different *combination* of characters, some from one more or less related thing, some from another, usually together with some that show in neither. We have seen that the action of selection is little or nothing, and that dispersal is controlled, positively by the laws of ASA, negatively by barriers. We can therefore no longer expect to find transitions, except in very rare cases. This view agrees with the actual facts much better than the former one.

There are often great gaps in the geographical display of "finished" characters, like for example an anther opening by pores, formerly explained by the same hard-worked explanation of destruction of transitions; and the same criticism is applicable. One cannot believe in such enormous destruction, with no trace left, over such great distances, such large areas, in so many directions, and at such different times, and this unbelief is much strengthened when one realises that selection cannot be invoked, so that there is no apparent urge to force changes. A great many differences again are so divergent that transition is impossible, and we now know that divergence is the rule, and as the divergence does away with the risk of loss by crossing, it is still more probable that this is the right view to take of the matter, and that the old conceptions must be abandoned. As yet we cannot predict in the least what will happen at any divergence, but it is evidently governed by laws which we must try to make out.

The logical conclusion to all this is almost necessarily that all the characters of a family, or the possibility of producing them after one or two necessary previous mutations have, so to speak, prepared the way for their appearance, should be present in the original first ancestor or parent of that family, like *Senecio* or *Ranunculus*. The same line of thought may be carried right back to the beginnings of life,

each new divergence opening the way for yet others, but with no guarantee whatever as to what the ultimate result should be. A very slight difference in an early mutation might ultimately lead to quite different results, as the people of Mars or the moon differ from man in the works of the imaginative writers.

We have been so much under the influence of the theory of gradual acquirement by selection, that we have assumed, for example, that the follicle must be an older type of fruit than the achene, for it is hard to conceive of the latter turning gradually into the former. We have therefore to make the *Anemoneae*, with their greater numbers and wider dispersal, a younger and more successful group than the more restricted *Helleboreae*, though they show no sign of relicdom, and their dispersal follows the laws of ASA and the hollow curve. The change either way seems equally easy to mutation (cf. Testcases XIV, XV, *Evol.*, pp. 122-6).

As having some bearing on the case, let us look at the fruit characters of *Ericaceae*, such characters being usually supposed of great value. The usual list is now headed by *Rhododendron*, which has proved larger than *Erica*. As it centres in the north, and the latter in the south, the question of polyphyly is at once raised (and remember the *Epacridaceae* on p. 342), but cannot be discussed here. There are four sub-families, and ten tribes.

*Ericaceae in order of size in the world*

Spp.		Sub-family	Tribe
Rhododendron	700	Heading <i>Rhododendroideae</i>	<i>Rhododendr.</i>
Erica	500	Heading <i>Ericoideae</i>	<i>Ericaceae</i>
Vaccinium	150	Heading <i>Vaccinioideae</i>	<i>Vaccinieae</i>
Gaultheria	120	Heading <i>Arbutoideae</i>	<i>Gaultherieae</i>
Thibaudia	50	2nd Vaccinioid.	<i>Thibaudieae</i>
Gaylussacia	45	3rd Vaccinioid.	2nd Vaccin.
Agapetes	45	4th Vaccinioid.	2nd Thibaud.
Simocheilus	40	2nd Ericoid.	<i>Salaxideae</i>
Leucothoe	35	2nd Arbutoid.	<i>Andromedeae</i>
Psammisia	35	5th Vaccinioid.	3rd Thibaud.
Arctostaphylos	30	3rd Arbutoid.	<i>Arbuteae</i>

Two tribes only have no heads in this list, *Ledeae* (Rhod. 1), headed by *Befaria* (20 warm AM.), and *Phyllodoceae* (Rhod. 3), by *Phyllodoce* (10 N. circumpolar and boreal).



In *Ericaceae* we have an instance of divergence in the fruit. The first three mutations produce the types of fruit seen in the first four tribes, a dehiscent septicidal capsule in the *Rhododendreae*, a loculicidal capsule in the *Ericaeae*, a berry or drupe from an inferior ovary in the *Vaccinieae*, and a fleshy calyx enclosing a capsule, usually loculicidal, in the *Gaultherieae*. This incidence makes the "naturalness" of the first three sub-families of *Acanthaceae* (p. 216) look somewhat doubtful, and goes to show how the value of a character really depends upon its age in the family concerned, and not upon the particular features that it displays. Berry-capsule is evidently a simple mutational divergence that is liable to happen anywhere, and without having properly understood this simple fact, we have given to the difference an importance to which it has no right except when old and inherited by many descendants.

20. *Complexes*. We have given an account of this phenomenon on pp. 211-14 to which little need be added. As all the characters of a family or genus are being handed downwards, there is little or no reason, so far as we can see, why any character in that family, or in its related families to a lesser and lesser degree as the relationship becomes more distant, should not appear anywhere, so that a complex is a normal occurrence. Nature is passing on potentialities that differentiate as the conditions differentiate, though it is but rarely that we can see any actual structural adaptation in any divergent change.

21. *Polyphyletic descent*. This comes into greater importance with the turning from back to front of our conceptions of the local direction of evolution. If the parent of a family hand down characters to all the rest in different combinations, it seems probable that the same individual character should appear in different places, perhaps even frequently. Ancient characters, visibly present in the early days of a family, tend to be inherited by many descendants, and especially those characters of flower and fruit which are less liable to be affected by outside conditions, and so become "important in the family". But this rule must not be narrowed down to individual characters, as is well known, for any single character may at any birth be the subject of a divergent

mutation. The production of new species &c repeats to a considerable degree the phenomena of human birth and descent, but with great intervals of time between births. What is inherited by any individual is the large part of a certain number of characters, of which all or most occurred either visibly or recessively (potentially) in the original parent of the family. In spite of the change that is liable to happen to a few at any mutation—and those usually different, in whole or in part, at every mutation—enough of the original characters survive to mark all the members of that family as one related group. If a considerable number were to change at any single mutation, an event which the ordinary laws of probability show to be extremely unlikely, the offspring would automatically go into another group.

BOWER's work on the ferns (16) was perhaps the first to bring the question of possible polyphyletic origin into prominence, and it will be well to quote some of his remarks. He says that "early writers, taking one very conspicuous character for the genus *Acrostichum*, freely exposed sporangia springing from a considerable area of leaf-surface, mixed up a lot of things that were at first placed in sub-genera, and were gradually found not to be necessarily closely related because their divergences were too great". We have pointed out above, however, that great divergence may go with the closest possible relationship. BOWER goes on to say "It is becoming evident that the *Acrostichoid* condition is not in itself a sign of affinity at all, but a state or condition, which may have been attained by ferns of quite distinct evolutionary history. If this be accepted, then *Acrostichum* is not really a genus of common descent, nor even a natural group. But it expresses merely that condition or state of soral development in which freely exposed sporangia spring from a considerable area of leaf-surface."

"The case is parallel with that of *Polypodium*... Such single characters as those defining *Acrostichum* or *Polypodium* in the old sense are in fact too wide to be of service in a system which aims at a true phyletic grouping". To this we would add that divergences are frequently so great that one needs to be very careful not to mix up a phyletic grouping with a supposed natural classification. One can hardly make up phyletic groupings for more than a few genera together, and will not get easy characters by which to classify.

If it be admitted as very probable that characters are all handed down from ancestors, and not casually picked up, then there is nothing to be surprised at if any character suddenly appears in a new form when there was no visible sign of that character in the parent. The surprise in fact would come if there were no such happenings. The evidence of the sudden appearance of new characters in the formation of local endemics, whether species or genera, in that of the very many small genera everywhere to be found, and in that of the evolution of the genera at the head of every family, is so complete that it is clear that divergent dichotomous mutation is a law of evolution, and the onus of proof that polyphyly does not frequently occur is thrown upon the other side.

As a simple illustration we may take the case of the very well marked character of the reflexed calyx that turns up in so many *Ranunculi*. There is no single wide-ranging species that carries this character, as it is carried by *R. sceleratus* in the north, yet it is found in a considerable number of species in most of the range of the genus, *e. g.* in S. AFRICA. It would be absurd to attribute it to selection, and its source must therefore be the genus itself. Whether it were visible or not in the first *Ranunculus*, the potentiality must have been there, to appear at various independent places. This kind of thing is very frequent, as one may see in the red and black seeds of various *Leguminosae*, or in the frequent appearance of cauliflory in unrelated things (p. 355). It probably occurs more often than has been supposed, and is indeed one that should be expected to occur with some frequency.

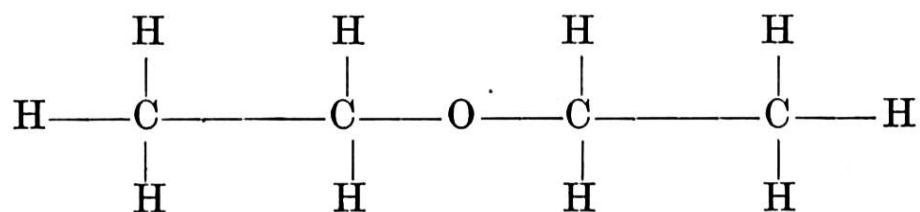
The facts of teratology must come into notice here, for though they are not usually viable, they prove that a great number of unexpected characters can be passed on by the parent individual, which carried them in a "recessive" condition, and become visible, or "dominant", in the sport. A study of the work of PENZIG (102) will show what a wonderful variety there is in such characters.

In Testcase XXIV, *Evol.*, p. 138 we have described a case which involves polyphyletic origin of the groups with monotheous and ditheous anthers, and similar cases are not infrequent, for example in the *Cochlospermaceae*, where two genera both show a division of this kind, or in the *Marantaceae*,

where the first division is into 3-locular and 1-locular ovary, and each lot divides into those with one and those with two staminodes, and so on. Different sub-families of palms show division into those with fan and with feather leaves, and so on.

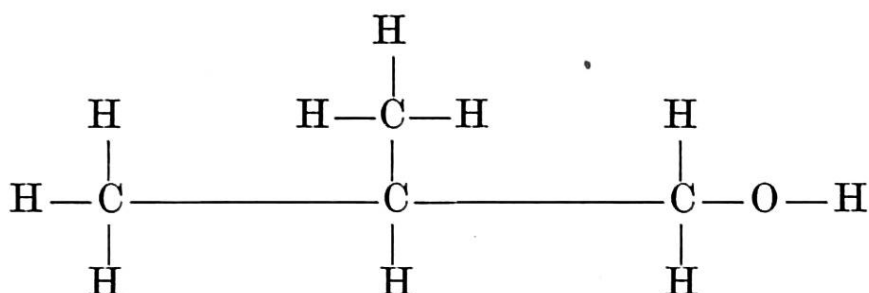
22. *The chemical analogies.* One cannot but be struck by the chemical resemblances that show themselves in these changes from one species to another. In the writer's youth, two bodies like ether and isobutyl alcohol were known to have the same crude formula  $C_4 H_{10} O$ , but were widely different in character and in properties, boiling for example at about  $35^\circ$  and  $108^\circ$  respectively. Beyond this, one could not then go, but now one knows that their molecules represent two different combinations of the same kind and the same number of atoms, both stable, but differently arranged and with different properties. This at once suggests that two allied species represent some kind of difference in the arrangement of the genes, or parts of genes, or even in the intimate physico-chemical arrangement of their molecules. The variety seen is probably due to their assumption of certain stable positions of equilibrium, as suggested in the working hypothesis that we have used since 1907. Some strain is supposed to be acting upon the nucleus, which presently relieves itself by undergoing some change in this way, a change which automatically brings about a change of structure. The change is not necessarily adaptive; adaptation is mainly internal and functional, the new species probably only changing that of the parent, born somewhere else, in such a way as to centre it upon the new conditions.

The ether molecule is represented by an assembly of two groups of two carbon atoms each, united by an oxygen atom in the centre, and with the remaining valencies satisfied by ten hydrogen atoms, each of which has a valency of one, while oxygen has two, and carbon four, represented by the lines that radiate from each. The whole molecule is thus made up, in a diagrammatic way





It thus forms a symmetrical and stable molecule, differentiated from isobutyl alcohol by the arrangement of the atoms, which in the latter make a pattern as follows



One can hardly talk of recessive characters in reactions like these, but the dominant (displayed) characters of ether are "recessive" in the alcohol. The combination  $\text{CH}_3$  which has remaining valency of one occurs in two places in the ether-isobutyl alcohol pair, and perhaps may almost be looked upon as corresponding to a character in a group of plants.

A mere rearrangement of the atoms has thus made as wellmarked and complete a difference in the structure and properties of the resulting compounds as is the difference between one family or genus and another in living things. We can now make these chemical differences by the comparatively crude methods of the laboratory, and this is evidently the first step towards making them by nature's more refined and delicate methods, which do no harm to the living being. Already in the laboratory we have progressed a long way from the famous experiment of BERTHELOT in 1866, where he found that under the action of heat three molecules of acetylene became transformed into one molecule of benzene. A later discovery in this direction was that in the presence of zinc oxide, which acted as a catalyst without being itself altered in the reaction, carbon monoxide and hydrogen are transformed synthetically into methyl alcohol, at a temperature of  $400^\circ \text{C}$ . and a pressure of 160-200 atmospheres. Catalysts are not unknown in nature, and it would look as if there might be here an opening for work in what we may perhaps call phytochemistry. A good many substances hitherto only known in organic beings, animals or plants, are now being synthesised in the laboratory. The next step is evidently to find out how this is done by nature's

methods. A conspicuous example is the synthesis of urea, formerly only known in animals, but now carried out on the large scale under the patents of the Badische Anilin und Soda Fabrik, producing one of the most useful substances of the celluloid kind. If a rearrangement of atoms can make at a stroke such complete changes in the structure, composition, and properties of lifeless substances, it is clear that similar mutational changes should make very important and evident changes in the structure of living things.

Chemistry was at first necessarily inorganic, carbon being simply one element among many, and not marked out for special importance until the appearance of life, which gave it great prominence on account of its combinations with hydrogen, oxygen, nitrogen, &c, which formed the basis of most organic substances, that have increased in number with the increasing variety of living things. The number of such compounds, most of them perhaps unknown in nature, that have been made in the laboratory is now, I am told, over 600,000, and no finality is in sight—if anything, it is the other way. The reactions produced in plants by colchicine, and other substances, are perhaps an indication of future possibilities.

This seems to the writer to be a fairly close parallel to the formation of species, vast numbers of which are known, especially in insects. We may perhaps call attention here to what has been said about the chemistry of plants and the possibilities of economic botany in *Evol.*, pp. 8, 89, 177. The great masses of facts accumulated, in such a book as WIESNER for example, at present remind one of the chemistry books of one's youth, before the study of the atom and the molecule had thrown so much light upon the subject.

I am deeply indebted to my cousin JEAN-PIERRE DE CHANAZ, who by his knowledge of chemistry has given me the information and help necessary in writing the above.

23. *Permutations and combinations.* The divergent mutation that is going on seems simply to be repeating upon a larger scale the kind of thing that goes on in human descent. Sets of permutations and combinations are being formed of the characters that are available, which in animals, more especially, are continually being mixed up by the agency of sex. One need not suppose that an individual in the

genetic chain carries all of them, or that any individual character is sure to appear in the offspring; the individual is carrying some set of potentialities, which may vary very slightly even between individuals. For all that we know, any character may at any time appear anywhere, but the greatest probability is, that if for example the plant is a crucifer, the potentialities will have a marked leaning towards cruciferism. By the ordinary laws of chance, it is very unlikely that more change will come at one mutation than will carry the offspring say into another genus, and not into monocotism or labiatism. Divergences like these belong to the older period of greater differentiation. Marked divergence is needed in several characters at once. The mere production of one cotyledon would not take a thing into the Monocots; one at least of the other common characters of that group, like the trimerous flowers, or the parallel-veined leaves is needed; that one cannot safely accept genetic relation on one character only has long been a maxim in taxonomy, and one can now clearly see the reason for it. The Monocots are in fact a group in which a particular combination of characters happened to appear at an early date, and the combination ran with only small changes through their descendants. Why this was so, we do not in the least understand, but whether, as is very probable, polyphyletic, or not, the group has had plenty of time to break up into families, tribes, &c.

A simple mutational change from some early Ranunculaceous plant, for example, might have made a monocot water plant which largely retained the less easily altered floral characters, and became leader of the *Alismaceae*, whose resemblance to the *Ranunculaceae* is well known.

The grand total of characters (*cf. Evol.*, p. 194) is less than that of species, so that the latter must depend for their number upon the possibilities opened by combinations of them differently made up. And it is upon the whole combination, not upon individual characters, that a species depends for its success or failure in the struggle for existence. And as this struggle varies from place to place with the variations in most of the factors, it is extremely unlikely that the whole, or even a large part of any single species should be killed out, unless at the very beginning of its life, when it represents but a feeble folk.

At mutation a new position of equilibrium has been taken up, and the new form, of whatever rank, is genetically as closely related as is possible to its also surviving parent. The new characters produced at any mutation seem to have nothing about them which should make them more likely to be preserved in heredity than their immediate ancestors. It is in the highest degree unlikely that the same *set* of characters should be altered at the next mutation, though one or a few may be affected. Thus on the whole the descendants of any particular grouping of characters will tend to inherit sufficient of them to be recognisable as probably related. Hence our familiar rule that genetic affinities can only be shown by agreement in two, or still better more, characters.

There is obviously a great element of what at present we can only call chance in the evolution that is going on around us. But nothing in nature occurs contradictory to her laws of operation, though there are evidently a good many of these at work. But they will gradually be discovered, as Mendel's law was discovered, by induction and deduction, and we shall slowly obtain a mastery of the processes of evolution, which will enable us to bring about desirable results influencing the future of mankind.

Nature is slowly constructing a great edifice by adding one atom to another, one molecule to another, and probably by increasing the complication of the genes, to say nothing of the cytoplasm. "Darwinism" laid too great a stress upon the "nature red in tooth and claw" side of life, making it the principal urge towards improvement, while its main function is to keep up the standard of work by taking the best individual for any particular job that has to be done under certain conditions that are local to that particular place. But as yet we have very little idea as to the aim of nature, if indeed she have one at all.

24. *Kaleidoscopic mutation.* An essential contradiction exists between the theory of evolution hitherto current, which implies that any character is descended from some other that was at least like it, and our system of taxonomy, as displayed in keys implying that there is somewhere a divergence between any character and some other. The possibility of making keys depends upon this. The difficulty of reconciling these two has long existed.



Somewhere or other in the familiar genus *Ranunculus*, which has been seen to be due to the branching out of parent species into younger and younger ones, these divergent pairs of characters must unite. They are so divergent, so unamenable to selection, and so valueless from an adaptational point of view, that it is clear that the union cannot be gradual, even were it possible, which is frequently not the case. It must rather be a case of one side of the divergence being sometimes dominant, sometimes recessive, and at any mutation, for all that we can tell, the positions may be reversed. Taking the characters of the buttercups from BENTHAM's flora, we find in BRITAIN alone the following divergences:

Plant aquatic	terrestrial
perennial	annual
Runners	none
Stem erect	decumbent
Leaves undivided	divided
glabrous	hairy
Flowers yellow	white
Receptacle glabrous	hairy
Calyx spreading	reflexed
Petals five or less	eight or more
longer than calyx	minute
Head of carpels ovate or oblong	globular
Carpels smooth	tubercular or wrinkled
with stout beak	with short point
Many more divergences might be cited from other floras.	

Looking at such a list, one can see no reason why the characters should go together at all, nor for the divergences they show, other than what we usually term chance. There can be little or no question of any special adaptation, nor of any selection among them. We can conceive no reason why *R. Flammula* should have a carpel ending in a short point, even if sometimes more or less hooked, while that of *R. Lingua* has a broad flat beak. The same difficulties are met with in any plants of an average mesophytic climate, like BRITAIN. Only when conditions show a definite bias in one direction, do the plants sometimes show a corresponding structural bias, as in xerophytes.

Nor can we see any reason to account for the changes that take place when one species or genus gives rise to another. One cannot attribute it to adaptation, except perhaps in cases like that just mentioned, nor can we see any sign of law about the matter. It occurs in so many places geographically unconnected that its presence cannot be traced back to a common ancestor that showed it, unless that ancestor was the original ancestor, which even then might have been carrying the character recessively.

We have seen that the number of species is greater than that of single characters, so that the variety of species must be due to different combinations of characters. It will evidently be long before the laws that govern all this complicated inheritance will be clearly brought out, and in the meantime we need some kind of illustration to help any working hypothesis that may be formed. This must not do too much violence to the probable course of things in nature, and must afford changes not too unlike the natural ones, so that it may lead to suggestions. It is much too early yet to press the chemical analogy, and we shall fall back on the one that we have used for 40 years, the kaleidoscope, a familiar drawing-room toy of the writer's youth. One may imagine in a general way that a group of allied genera or species is represented by the series of slightly different patterns that one obtains by gently turning the tube. Each piece of glass may represent a character, and those that *happen* to be nearest to the top are those that will be most likely to change their relative positions. Thus the change of aestivation imbricate/convolute may happen to be near the bottom, as in *Acanthaceae*, and does not change again for a very long time, and thus is very important "in that family", while in *Primulaceae* it is part way up the side, gets sooner changed, and is less important, marking only the difference between two tribes out of five. Or it may be at the top, become changed almost at once, and mark, as in *Rubiaceae*, only part of the tribe *Gardenieae* or *Rondeletieae*, or even only part of the very small group of small genera, the *Henriquezieae*, where its importance is trifling.

The total amount of light, and the individual amount of each colour, remains the same whatever pattern be displayed. But among the species of a genus, as we have seen, one character or another is liable to become recessive at any

mutation, and to make the analogy more complete, it would perhaps be better to screen off one half of the circle, so that any piece of glass going behind the screen might represent a character becoming recessive, though sure to appear again (become dominant, or displayed, once more) as one continued to turn the tube, but in a different place perhaps, and in different relations to the surrounding characters.

Another thing that one must remember, that cannot be easily matched in the kaleidoscope, is that the characters of reproductive organs are, as compared with those of the vegetative organs, always more like the pieces of glass at the bottom of the circle, and it is not easy to design any way of showing this.

Sometimes two characters may be in contact by one pair of sides, sometimes by another. The permutations and combinations open to a dozen characters are almost endless, but it is all but impossible to pick out, except by chance, any one as definitely superior to another. A pattern is never twice exactly repeated. The way in which each individual bit of glass behaves is ordered by the laws of gravity, friction, and so on, but the total movement to the new positions is due to so complex an interaction of all these laws that one can hardly hope to disentangle them, for the present at any rate. We may therefore regard the formation of a new species, as we regard the formation of a new pattern in the machine, as being due to chance. A certain unpredictable combination of the available characters happens to be made under a certain stress, mainly of outside conditions, just as does that of the bits of glass. The result of a new combination of the latter is hardly ever seriously different from what went before, and the same is the case with species; there is little to choose among them, and practically no opening whatever for selection of one as against another. The differences that matter in the struggle for existence are more probably the *fluctuating* differences between individuals. This fluctuation, for example of height of plant, or of area of leaf, is not possible of representation in the machine.

In the operations of the kaleidoscope, one may get, apparently by simple chance :

- 1) The same two characters appearing in two allied species, but not in exactly the same mutual relationship—two bits of glass meeting by different edges in each.

2) The total value of the characters in any one of the innumerable possible combinations is the same—the light passing, and its colours.

3) The putting together of a new species out of characters carried, in a dominant or recessive condition, by the old. This might be easily shown by blackening out say an eighth of the circle; any piece of glass that went behind the screen might be regarded as having become recessive, the corresponding piece that had emerged as having become dominant.

4) The appearance of the same character in two different places—the same piece of glass in contact with A, B, C, D in one place, with W, X, Y and Z at another.

5) The re-appearance of a character that had apparently disappeared—a reappearance from behind the screen.

6) The appearance of an unexpected character—a piece that had long remained behind the screen, for some unexpected reason.

In (155) we have discussed the use of the Kaleidoscope at greater length.

## 25. *Concluding remarks.*

What it comes to then is in broad outline that the main stream of evolution runs on with little regard for other factors, which only deflect its line temporarily to one side or the other, the dominant direction being resumed as soon as the temporary interference is removed. The apparently needful stimulus for mutation seems to be provided by a change of external conditions, ultimately making so great a strain that mutation occurs. What exactly happens we do not know, but one result is evident, that there is such a re-arrangement of parts of the sexual cells that when the product appears it has quite a different structural constitution, especially in the fact that one or more of its characters have undergone a definite divergence, as we saw in the CEYLON endemic species quoted on p. 111-13 where the local *Ranunculus* showed a change from a divided to an undivided leaf, the local *Rhamnus* from 5-mery to 4-mery, and so on.

The characters found at times in tables are not the only points of difference, but are the most evident, those that are seized upon for keys. But in practically all the 51 Ceylon cases they are incompatible characters due to direct mutation and not allowing of transition. At some point in



the ancestry of two such characters in two species of the same genus, we shall come upon the mutation at which they diverged. The original species of the genus could only show visibly one side of the divergence, but must have been carrying the other in some kind of potential or recessive, invisible, condition.

The divergences that appear in the very earliest days of a family seem largely to result in the production of sub-families or tribes, for about three quarters of the first few genera diverge markedly from one another in a few characters that remain more or less constant in the heredity, thus marking out a group in the family to which we give the name of sub-family or tribe. The two are not distinguished except by valuation, which says that in one case the divergences are of more "value" than in the other.

We must also realise that each head of a tribe thus formed is also at the same time a genus and a species in the family that descends from the original parental genus. For example in the *Connaraceae* (p. 141) the first four genera by world size each head a tribe, while only three of the first four *Dipterocarpaceae* (p. 153) do so. The characters that distinguish the tribes are much the same as those that distinguish genera elsewhere, but they are *combinations of characters* that appeared at a very early stage in the family history. By the ordinary laws of probability it is unlikely that this combination will again appear *except in direct descendants of the one that first showed it*. Simple age in the family is the secret of the importance of a character, for there has been time for it to be inherited by many descendants. Floral characters on the whole are better inherited, and less liable to frequent alteration, so that as a general rule they are more important. But in *Ericaceae* (p. 368) we have seen great variation in them at the very start of the family.

The individual characters that mark out the tribe are much like those that mark the distinction between the two genera in a bigeneric family (*Evol.*, p. 199), which there mark out its future classification when it has grown large. There is no doubt that the earliest mutations in a family give rise to its earliest divisions, these being followed by the smaller, but to work out in proper detail whether the earlier divisions show larger and more numerous divergences would need more time than is available to the writer at 80. On the whole,

however, as one goes back through the past history of plants, it would seem that the smallest divergences, and perhaps the least numerous, mark the most recent divisions into species and subspecies, down to Jordanian.

On the other hand, as one goes upward, the divergences seem to become more clearly marked, and to involve more of the *available* characters, which will on the whole be less numerous in the early days of the flowering plants. Thus it comes about that above the leading genus of a family, which as the largest is growing the most rapidly (AA, p. 34), so that it occupies the tip of an acuminate apex, we are likely to find difficulty in tracing the ancestry further.

At the period when the leading genera of the family were formed, there were only the characters of the ancestors to draw upon for divergences, and these would be but few compared to the great variety subsequently developed as continually, and with ever greater rapidity, the family increased in size. Half a dozen divergences would affect, comparatively, a larger proportion of these ancient characters, and we have now seen that it is age which confers importance. Above the heads of such families as the *Compositae*, *Orchidaceae*, or *Leguminosae*, therefore, as there were but few characters to draw upon, there would likely be a great disturbance of characters at every birth, characters which would of necessity be old and "important". The result of these mutations would thus be something which we now regard as widely different from the ancestor, though it would not strike the botanist of that date as anything out of the normal.

This consideration explains the great difficulty that exists in placing any family of the flowering plants into its proper "order", as well as the tendency that there is towards giving a separate order<sup>1</sup> to each important family, which is often accompanied by what are obviously satellites. To place the orders into still larger groups becomes, for the same reasons as we have just considered, a very difficult undertaking indeed, and on the whole, the further back we go, the greater the difficulty of tracing even immediate ancestry, while if we go the other way, the immediate ancestor,

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<sup>1</sup> A better word than order, which has a different meaning in ordinary use, might be found, such as cohort, for example.

for example, of a lot of sub-species, is fairly evident. Divergence is more and more strongly marked as we go back in time, and affects more and more of the ancient and therefore important characters at a single operation.

All the time, or more probably, in the latter part of it at any rate, besides the production of new genera in a family, which at first largely head new tribes, there is a continual production of new species, and as the species grows, of new sub-species. This is probably owing to the continual production of more and more potential differences of character which enable more divergences to appear. It would seem more probable, if this be so, that most of the genera in the lists that we have given of the first ten or so of a family, are the immediate descendants of the head, so that it was quite probably the direct parent of most of the important tribes; and so on downwards. The larger or older the family is, too, the more sub-families or tribes shall we expect it to possess, for it goes further back into the period when fewer characters were available. With very old genera, too, it is more possible that some, or even many, of the descendants would diverge at once to new genera, and so on all the way down.

In going back through the past history of evolution we are necessarily somewhat handicapped by our now almost intuitive conceptions of variety, species, and genus, divisions that were probably not recognisable as such in early days, and to which there would certainly not be given the importance that we now attach to them. We shall see on p. 384 that it is not impossible that the list of the very earliest mutations known was something upon the lines of the list of the earliest mutations that followed the appearance of the head of a great family, like the *Compositae* on p. 176. In those early days the frequency of mutations was small, owing to the probable comparative uniformity of conditions, and to the small possibilities of divergence that were present with only a few simple characters. Mutations might even be millions of years apart, but when they did appear they would be such as we should *now* class as very important, because they have *now* lasted as marks for an enormous period of time, and so have become very important, by being handed down to a great number of descendants. The characters of reproductive organs, as less liable to serious interference

from outside circumstances, have become, or rather have always been, of greater importance than those of vegetative organs.

In very early days, the differences between an alga and a fungus would be of no greater importance than that between say *Convolvulus* and *Cuscuta* now; it is age that has given such high importance to the former. It is by no means impossible that the very first mutations might have been upon something of the following lines

- |    |         |            |           |
|----|---------|------------|-----------|
| A. | Heading | Algae      |           |
| B. | Heading | Liverworts |           |
| C. | Heading | Fungi      |           |
| D. | 2nd     | Algae      |           |
| E. | Heading | Mosses     |           |
| F. | 3rd     | Algae      |           |
| G. | 2nd     | Fungi      | and so on |

It is probable that later descendants of A would mainly keep to the group in which their leader is now found, as we may see in the *Senecioneae* on p. 177, where the great gap at the top was probably filled by genera that have mutated into other tribes.

As time goes on, the number of characters available at any mutation will probably be increased as the result of previous mutations, so that there will be greater choice, with less likelihood of a fresh and important mutation of some character lately changed, so that, judged by the botanical standards of later times, these later and younger mutations will be less important, and will less often give rise to new groups, which themselves will tend to be less important. This procedure of diminishing importance of the characters, mainly by reason of greater youth, will continue, and we shall arrive, in any given line, at the stage of orders, then of families, tribes, genera, and so on, while the simple divisions of early times will become of greater and greater importance as giving their characters to increasing masses of descendants. Age gives time for the results of changes to accumulate, and is thus one of the most important factors that are at work.