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## CHAPTER IX

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

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

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

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

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

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

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

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

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

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

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

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

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

As they stand, group B is definitely larger than A, therefore possibly the older. Disregarding the taxonomic classification altogether, except for the primary division into A



and B, let us divide up these groups geographically only, when we get a rather striking result, partly shown in the table below. Scores of such tables can be, and have been, made up for the larger families and sub-families, so that one realises that geography is of great importance, not only for distribution, but in taxonomic work, and in the study of evolution. To set out all the *Acanthaceae* in detail would make an inconveniently large table, so we have given detail only for ASIA, which has the smallest numbers. The tables for AFRICA and AMERICA match this in proportions, but are much larger.

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

*The Distribution of Acanthaceae, geographically  
and numerically treated*

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

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

### Asiatic Genera

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

By placing all the continents in parallel tables with that of ASIA, which is much the smallest, one obtains a very impressive table of the distribution of all the *Acanthaceae*, but it occupies too much space, and we shall continue simply

with the actual numbers, for the three great continents, of the genera that are confined to them. The pan- and palaeo-tropical genera are given above, and the neo-tropical are the same as the American.

### B (*Imbricatae*)

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

### A (*Contortae*)

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

Total of <i>Imbricatae</i>	152 genera with 745 spp.	Average 4.9
<i>Contortae</i>	75	322 4.3

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

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

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

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

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

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

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

As new species and genera are necessarily very local, one will expect them, if formed in accordance with my working hypothesis, to be frequently, but far from exclusively, formed

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

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

The earliest genera to reach AFRICA, or to be born there, in the northern parts at any rate, would usually be in time also to reach ASIA. The separation of these two continents was less complete and thorough than that with AMERICA,



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

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

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

Reaching the W. I., in B	325 100 100.80 80 60 45 30 20 10 6 4 3 3 1/1
Not reaching	25 12 10 8 8 7 6 5 5 4 4 4 4 3 3 3 3 2 2 2 2 2 2 2 32/1
Reaching the W. I., in A	225 80 50 40 10 4 2 2 2 and <i>Bar-</i> <i>leria</i> (150) very doubtful
Not reaching	180 ( <i>Strobilanthes</i> ) 12 10 2 14/1



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

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

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

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

in MADAGASCAR and the MASCARENES, it is confined to the INDOMALAYAN region. HOOKER's *Flora* shows 146 species of *Strobilanthes* in INDOMALAYA, where the only pan-tropical member of the *Strobilantheae*, *Dyschoriste* (*Calophanes*), has only 4 species, and evidently could not be its parent.

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

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

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

*The taxonomic classification of the Acanthaceae.* The usually accepted system is that of LINDAU in *NP/1*, IV, 3, p. 287. It is largely based upon the very marked sculptural

characters of the pollen grains, which lend themselves admirably to mutation, and to that alone, and which were adopted as fulfilling the often expressed desires of taxonomists by not being in any way useful, or possible subjects for natural selection. The classification, given in full in *NP-1*, *l. c.*, forms an instructive comparison with our geographical list. Let us begin with our usual list of the leading genera by size in the world :

*The leading genera of Acanthaceae, in order of size*

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

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

There are many duplicates at all numbers below 25.

It will be seen as usual that the leading members of the family by simple age are, as one would expect, leaders of

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

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



with taxonomy has some resemblance to trying to make ropes out of sand, and it would seem better to regard the two as separate aims, both of which have to be reached.

*Distribution of pollen patterns among the leading Acanthaceae*

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

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

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

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

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

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

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

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

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

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

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

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

no longer be accepted as an unquestionable proof of descent from *Ruellia*.

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

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

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



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

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

The divergence, whose appearance seems to be one of the regular features of evolution, and which caused us in *Evol.* to give the book the full title of *Evolution by Divergent Mutation*, seems, upon the whole, to be more marked (?affecting more characters at once) as one goes back in time, thus suggesting a more reasonable explanation of the great divergences that mark the first early divisions into Algae, Ferns, Conifers, &c, than the attempt to explain them by selection,

involving the destruction of innumerable transitional forms. The whole of the large step from one of these groups to another (including in the total any groups of reasonable size now only found as fossils) was probably taken at one operation.

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

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

In their descent, the characters behave in such a complex or intermingled way, that the genera that are thus formed are liable, *when they grow large*, to make what we may term a complex by showing, in some of their species, characters that we are accustomed to regard as belonging to some other

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

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

What happens in the formation of a complex is perhaps something like this. *When young*, the genera that now compose it were probably quite separate in their characters. Genus A might begin with characters 1, 2, 3, 4, 5 taken from the parent, genus B with 6-10, but in some of the later mutations (for of course all would start as single species, so that there would be little difficulty in defining their characters; it is only as new species begin to bring in more characters that the difficulty of defining the genus increases) a character or two belonging to another genus of the group might

put in an appearance in some of the species. At first local, these species would grow and produce new ones, and if the character proved persistent, would soon complicate matters as to the generic rank of the genus or species concerned. To explain the matter reasonably, some system by which all characters are directly handed down from above seems the most simple.

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

Looking through the genera of any family that are arranged in order of size, one usually notes genera at frequent intervals that are p. p. of the head of the family, *e. g.* of *Justicia*. Their placing depends upon the general judgment of taxonomists, for they possess some, but not all, of the characters of *Justicia*, sometimes more, sometimes fewer, and we are trying to indicate that the phenomenon depends upon the laws that regulate the incidence of characters, all being the descendants, direct or indirect, of *Justicia*, from which they



inherited characters. Genera are artificial divisions, made at what seem to be the more marked points of separation, and often depend upon judgments arrived at only after much dispute, and often not universally adhered to.

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

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

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

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

35.8, 34.5, 30, 22.6, 21.6, 21.1, 19.2, 15.8, 12.9, 10.1, 6.5, 6, 5.9, 5.6, 4.8, 3.75, 2.6, 2.2.

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

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

To look at the numbers just given, and the same thing may be seen almost anywhere, one would never suspect that they were definitely connected upon an arithmetical plan—the law of compound interest. The divergences that take place rob a purely structural arrangement of its naturalness, and the same character may turn up almost anywhere, with the necessary combination of circumstances. If the characters of a family are all in the keeping of its original parent, this is



what we should at times expect, though one must not forget what we suggested as to increase in number of possible characters from older genera downwards. There is probably some mathematical rule controlling it, but the writer has not been fortunate enough to stumble upon it.

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

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

However natural these groups might be, they are very small, and cannot be regarded as in the same rank as even *Contortae*. They are based purely upon structural features, and it is clear at a glance that their geographical relationships are rather impossible. The differences in character are principally those between a capsule and a drupe, and between few and  $\infty$  ovules, both of them common mutational differences between groups of genera or species, large or small. As regards the drupe and capsule, cf. *Evol.* pp. 122-126. One cannot fit these groups into any system of evolution by dichotomy, at least without enormous destruction, which is put out of court by the very small size of most of the genera, and their lack of geographical relation. They are convenient divisions for the identification of plants, but probably

nothing more; it would seem much more probable that the peculiar divergent characters had been handed down from the ancestry, and that at some point a double divergence gave rise for example to *Nelsonia*, and at another the same thing gave *Ixtlania*.

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

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

system becomes a very difficult thing to construct. It is like trying to classify the population of a town by physical or mental characters, and expecting to get their relationships by the same process.

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

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

*The Growth of the Acanthaceae.* *Justicia* and *Ruellia*, being the largest genera in the family, were presumably its oldest, and the first important event to occur in its history was the splitting off of the latter from the former by an early, divergent, but simple, mutation, the results of which show in the fact that practically all members of the family have their aestivation either imbricate or convolute. Thus the very first mutation split the family into its two chief subdivisions, and we have already seen in Chapter VIII, and App. III of *Evol.*, p. 199, that this is the rule throughout the whole taxonomy. Thus, in the *Acanthaceae*, but not necessarily anywhere else, the divergence between imbrication and convolution has become a sub-family or super-tribe character. It owes this position simply to the fact that it was a very early divergence to occur in the family, and once formed, was largely so persistent in the heredity that practically all the family show one or the other type of aestivation. The same identical change may be found in many other families, as for example in *Gentianaceae* it distinguishes some of the *Gentianoideae* from others of the same sub-family, while in

yet other families it may occupy an even lower position, simply because there it is of more recent acquisition or occurrence. Whilst on the whole characters of the essential organs of the flower are the most likely to be of early or of more permanent acquisition, and therefore of great importance, *any* character may at times be found in this position. As yet, we have no knowledge of the rules of character-incidence. Any character that by its divergent forms will divide a family into two main portions is gladly seized upon for that purpose. It is the age of the character *in its family* that matters, when reflected, as it is in many cases, by inheritance in many smaller genera.

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

As each genus, when it is formed and has reached some little size and importance, tends to give rise to another, the lines of descent will continually increase in number, and that more and more rapidly the older the family grows. Thus in the early days, and of course always among the now large genera then produced, there are very few lines of descent, so that the production of genera of the same age and size is unlikely. But as we come further down the list, the probabilities of such things will continually increase, and duplicates, of the same general size and age, will begin to appear, as one



may see in the lists of the *Compositae* in Chap. VIII. Below this point they will rapidly increase, till at the very foot there is a large display of "ones", which probably remain longer in that stage, when they are just beginners, than in the stage of two, or of higher numbers. The hollow curve, forming the logarithmic straight/line, is thus automatically and inevitably produced.

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

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

The process of growth of a family is thus at bottom a fairly simple one, but it is of course almost at once liable

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

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