# CHAPTER VIII

## Divergent mutation in some of its manifestations

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

It is not only in endemics that divergence shows itself in the ways that we have described in the last chapters. It is just as evident in any small genera, whether considered endemic or not, especially if the country be outlying. I have worked over the characters of many such genera, finding in the keys to their species ample evidence of what we may call incompatible divergences, transitions between which are impossible. If one go back into ancestry, all divergences

must go back ultimately to a common ancestor. In the enormous majority of taxonomic differences, there is nothing upon which natural selection could get a grip to make a transformation even possible, so that there is nothing for it but to consider that in these cases the ancestor was carrying *both* characters, or the factors for them, with one of them in a kind of recessive condition, while the then dominant one was displayed. Such, for example, would be the case with leaves alt./opp., flowers 5-merous/4-merous, stamens 5/10, ovary apo/syn-carpous, endosperm/none, &c. There are such numbers of cases, too, where the same markedly divergent character appears in different places, and evidently independently, that one cannot put them down to selection. The explanation we have just proposed appears much more reasonable.

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

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

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

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

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

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

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

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

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

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

parts of BRITAIN, though the conditions differ so greatly in its 112 vice-counties. They had the necessary time available to become suited to all of them.

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

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

We have seen in the testcases in *Evol.* that the evidence is almost overwhelming that shows that evolution went in the direction family-genus-species, not, as Darwinism would have it, in the reverse way. On the whole, with the passage of time, the mutations that mark it have decreased in what we may call emphasis. The further back that one goes, the " larger " do the mutations appear to be, but it would seem more likely that this means that they affect more characters, than that they make larger differences in single characters. But if this rule runs right back through evolution, we have

at last a clue to the meaning of the great differences that we see between such classes as the algae and the mosses, or the ferns and the conifers, and we shall no longer search for *transitions* between them, or for missing links, though there *may* have been organisms between that had mixtures of characters, some from one side, some from the other.

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

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

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

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

All our work goes to show that there is no serious difference in rate of spread, in large space and in long time, between genera that are allied to one another like the members of a smallish group of any one family—all will have much the

same reaction to outside influences. The survival of the parent as well as the offspring results in the formation of the familiar hollow curve for any family of reasonable size, though the taxonomic (structural) divisions of the family rarely show anything of the kind, unless very large. The new form produced anywhere will of necessity be suited to its environment enough to survive and reproduce, or it will at once be killed out. But whether it anywhere goes in front of its parent in the distribution will depend upon local circumstances, and it rarely happens over any large front.

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

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

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

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

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

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

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

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

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

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

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

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

in them. We have used the tribe here, as the best marked of the divisions; when tribe and sub-family are the same, we have used the termination -*oideae*.

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

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

[1] Different sub-tribes here.

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

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

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[1] Different sub-tribes here.

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

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

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

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

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

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

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

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

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

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[1] Nominal.

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

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

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

and 2/12, 10, 4/8, 7, 6, 2/5, 2/4, 6/3, 8/2, 26/1, one of these British

| | | | | | | |
|---|---|---|---|---|---|---|
| Tussilago | 1 | | Senecioninae | Br. 1 | 112 | |

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

### Tribe Astereae in order of size in the world

| | World size | Subtribe | Br. | Spp. | Max. | Disp. Ceyl. |
|---|---|---|---|---|---|---|
| 1. Aster | 500 | Heading *Asterinae* | Br. | 2 | 70 | |
| 2. Baccharis | 380 | Heading *Baccharidin.* | | | | |
| 3. Erigeron | 180 | 2nd *Asterinae* | Br. | 2 | 70 | C. |
| 4. Aplopappus | 125 | Heading *Solidaginin.* | | | | |
| 5. Olearia | 100 | 3rd *Asterinae* | | | | |
| 6. Solidago | 100 | 2nd *Solidagin.* | Br. | 1 | 111 | |
| 7. Brachycome | 60 | Heading *Bellidin.* | | | | |
| 8. Conyza | 60 | Heading *Conyzin.* | | | | C. |
| 9. Felicia | 60 | 4th *Asterinae* | | | | |
| 10. Pteronia | 60 | 3rd *Solidaginin.* | | | | |

and 3/50, 45, 40, 2/35, 2/30, 7/20, 5/15, including

| Bellis | 15 | *Bellidin.* | Br. | 1 | 112 | |

and 3/12, 9/10, 3/8, 4/7, 10/6, 9/5, and so on

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

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

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

### Tribe Inuleae in order of size in the world

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

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

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

Finally there comes the tribe *Anthemideae* :

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

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

There are only the two subtribes here.

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

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

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

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

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

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

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

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

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

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

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

If one were to take the trouble to measure the areas of dispersal of all the many *Hieracia* and *Rubi*, one would probably find that most of the species mentioned above as leaders in BRITAIN had also the largest areas of any in their particular groups. The point of special interest is that these

species are divided from their " equals " by the largest diver-
gences *available at that stage*. It is another proof that the
great characteristic of evolution is divergence.

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

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

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

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

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

It is evidently to some extent a mere question of time, or age, before a genus gives rise to a new genus, or to more species, a species to sub-species, and so on. Probably, however, some stimulus of change of conditions in some way (*cf.* my working hypothesis, p. 96) is also required, for we see so many more new (endemic) species in broken and mountainous country than under the comparatively uniform conditions of

open plains. But if this be the case, we shall expect to find more varieties in the older species that have larger areas. If we take, from HAYWARD (58), the varieties recorded in the British (Dicot) flora, we find that

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

a marked agreement with the prediction.

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

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

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

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

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

There are only the two subtribes in this group.

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

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

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

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

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

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

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

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

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

What really seems to happen is that genera &c are

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

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

The first genus of a new family necessarily begins as a
single species of very local dispersal, in fact endemic to its
birthplace. It must at birth have been reasonably adapted
to growth there, or it would not have survived. As yet we
have no idea whatever as to the number of non-survivors,
whether through any lack in their adaptation, or through
sheer bad luck. But in general one may surely expect enough
adaptation to survive to reproduction, and it will always
improve. But here is at once the first factor that may
interfere with the regularity of the figures in the curves, which
are largely concerned with size in the world. This character
of size in the world (number of species), and its connected
character of area occupied and its continuity, both of them
figuring in the laws of ASA (p. 23), though hitherto neglected
almost entirely, are of very great importance. This was
brought home to the writer when in 1889 he began to prepare
facts of generic sizes for his *Dictionary*, and soon began to
realise that there were laws underlying their distribution.
Using the Hookerian conception of species, he made allowance
for synonyms by a careful estimation of the relative space
that they occupied in the *Index Kewensis*, which in those

days gave synonymy. He counted the actual species in small genera, usually lumping after five at 8, 10, 12, 15, 18, &c, but in the larger he measured the actual space occupied, and allowed for the synonyms, increasing the proportion when the authors were notoriously " splitters ". Thus all these figures were prepared upon one plan, and that they have been regarded as very useful and reliable is shown by the way in which they are used in so many places. For the new edition of the *Dictionary* which it is hoped to publish when this present book is out, the figures are being very carefully prepared by Mr W. T. STEARN, one of the joint editors. The old ones, however, remain almost as useful as ever for comparisons, for which they are used in this book, and have the great advantage of being all prepared upon the same system throughout.

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

Another question that at once arises is whether a character, once acquired, is handed down to all descendants of the form that shows it. Considering the ease with which mutation can change a character, and the fact that the

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

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

Another question of importance is to what extent the first genus of a family continues to lead, after others have begun to form and to arrive in the country concerned. In our present state of ignorance of the influences of many factors, all we can do is to make a statistical comparison of the families found for example in BRITAIN. Of the 99,44 have only one genus each, and in 28 of these, or 63.6%, that genus is the actual first genus in the family in world size. The same is the case in 68.2% of families with two or three genera, 85.7% of those with 4-10, and 92.3% of those with more genera than ten. Thus there is no certainty that the first genus will always arrive, though it might arrive if time enough were allowed. Another comparison will perhaps give a

better result. All the families with one genus only show the first in 63.6%; all with one or two genera show it in 66.6%; all with one to ten in 69.7% and all the families, of whatever size, in 71.0%. Thus in about nine families, the first genus was later than first in arrival, and in the other 27 it did not arrive at all.

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

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

Various minor laws, based upon the laws of ASA and upon the growth by compound interest, seem gradually to be making themselves felt, and to be bringing some semblance of order into the hitherto confused mass of facts that has made up the subject of geographical distribution. It is fairly evident that the inductive method can be applied here as elsewhere. Everything seems to point to the probability

that the whole process was directed from above downwards by the production of descendants by a more or less regular dichotomy. At the same time the characters of those descendants were not primarily produced by a method of trial and error, as used to be supposed, but were handed down in some way by their ancestors, which carried the potentialities of producing them under certain circumstances that as yet we do not in the least understand.

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

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