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CHAPTER V

The characters of endemics I

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

and so on

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

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

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

In *Rubiaceae* we find

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

In connected families we find for example

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

The general composition of the flora of Ceylon

I. Genera with no species endemic

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

II. Endemic Genera

Dicots	20		
Monocots	5	Total of II	25

III. Genera containing endemic species

A. Dicots.

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

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

206

B. Monocots.

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

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

80

Total of III (with endemics) 286
Grand total 1001

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

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

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

Ceylon genera of two species, one wide and one endemic

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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