Endemic Genera of Plants in their Relation to Others.

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With six Diagrams in the Text.

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REVIEW OF THE HYPOTHESIS OF AGE AND AREA.

INQUIRY is frequently made as to where a brief summary can be found of the ideas meant to be conveyed by what I have termed the hypothesis of Age and Area, and it will be well perhaps to commence this paper, which is the first of a new series in which somewhat larger issues will be treated, with such a summary. The new facts to which attention will be called below were discovered by aid of the hypothesis.

Examining on many occasions, from 1896 onwards, the volumes of the Flora of Ceylon (7, 8), so carefully worked up by Thwaites and Trimen, I gradually found, somewhat to my surprise, that the strictly local species confined to that island, or *endemic* species, as we usually call them, which are very numerous in Ceylon, showed on the average the smallest areas of distribution there, whether in the grand total or in individual families (cf. 10, p. 12). On the older view of the meaning of endemic species, which I then held, this seemed a very remarkable thing—that species which were generally looked upon as having been specially evolved to suit the local conditions should be so rare in those very conditions. If these species were specially adapted to Ceylon, therefore, it could not be to the general conditions of the island, but must be to strictly local conditions within its area. There was clearly no difference between island endemics and those of the mainland. Accordingly, still more remarkable did it seem when I came to study in detail the local distribution of these endemic species in Ceylon, and found that, as a rule, they were *not* confined each to one spot or small region characterized by some special local peculiarity in conditions, to suit

which they might have been supposed to have evolved. Not only so, but such spots were frequently to be found with no local species upon them. Only about a quarter of the whole number were confined to single spots, and more than half of those were restricted to the tops of single mountains (12). The remaining three-quarters occupied areas of larger and larger size, and in diminishing numbers as one went up the scale. The three diagrams here reproduced give the ranges of the species in half of vol. i of Trimen's 'Flora', belonging to the three lowest of the six classes according to range into which he divided them. The VR (very rare) species are as a rule well localized, but the R (rare) and RR (rather rare), it will at once be observed, cover areas that *overlap* one another like the rings

DIAGRAM 1. Distribution in Ceylon of the earlier VR, R, and RR species from Trimen's 'Flora'.

in a shirt of chain-mail. Now a little consideration will soon show that from the point of view of evolution to suit local conditions this is a very remarkable state of affairs.¹ If A and B grow in overlapping areas, both must be growing in the coincident portion, and what keeps A from growing into the rest of B's territory, B into A's? In reality the case is more complex, for if all the species were entered, there would be at least a dozen overlapping at any one point. It is all but inconceivable that local adaptation should be so minute as this, with soil essentially the same throughout, and the rainfall, &c., varying much from year to year. The species would have to be adapted to wide range in rainfall, and to very slight in a *combination* of other factors. It was clear that the old ideas of particular adaptation were quite untenable.

¹ It is of course obvious that if a species newly evolved does *not* suit local conditions it will not survive, but this is a different point of view from supposing it evolved *to* suit them.

Nor would the other popular theory, which equally survives to-day, satisfy the knowledge that I now had about local distribution. How could species be dying out in this remarkable chain-mail pattern, and why were there so many with small areas? Had one perhaps arrived in Ceylon just in time to see the dying out of a considerable flora? And why did so many choose mountain-tops as a last resort? If they had climbed from below, they must have plenty of adaptative capacity, and should be able to compete with the new-comers. Still more, why did each one or two choose a different mountain? One had not credited plants with the animal desire to die in solitude, and it was difficult to believe that the plains were once inhabited by different species at every few miles, whilst many mountains with endemics did not even rise direct from the plains, but from a high plateau.

Counting up all the species of the Ceylon flora, and dividing them into three groups—those endemic to Ceylon, those found only in Ceylon and South India, and those with a wider distribution abroad than this (which I termed *wides* for short)—I found (14, 15) the endemics to be graduated downwards from few of large distribution area to many of small (e.g. Common 90, Rare 192), and the *wides* in the other direction (e.g. Common 462, Rare 159), with the Ceylon-South India species intermediate. In other words, the average area occupied by an endemic was small, that by a Ceylon-South India species larger, and that by a wide the largest of all. A cursory examination of other floras showed me that their endemic species also behaved in the same way, occupying overlapping areas, and I was at last furnished with what seemed to me to be a much more feasible explanation of the distribution of species in general, and endemics in particular.

Having disposed, to my own satisfaction, of the notion that endemics were moribund species, I adopted the view that in Ceylon the *wides* were the first species (*on the whole*¹) to arrive, and had therefore on the whole occupied the largest areas. The Ceylon-South India species, on my view, must have arisen from them at points in general south of the middle of the peninsula, and would on the whole be younger in Ceylon than the *wides*, and therefore occupy lesser areas on the average. The Ceylon endemics would arise from the *wides* (or Ceylon-South Indians) in Ceylon, and would be the youngest, and on the average occupy the least areas. All the figures of course must be worked in averages, for an endemic of one group might be occupying a large area when the first wide of another arrived.

Such in brief was the gradual evolution in my mind, during twenty years, of the hypothesis which I have christened 'Age and Area', and which has been a good deal discussed of recent years. Before proceeding farther, I will quote the most recent expression of it, published in 1919 (22, p. 290):

¹ i. e. in any genus the wide would usually be the first to arrive.

'The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next or other ecological boundaries, and the like, also by the action of man, and by other causes.'

The Ceylon figures were strong evidence in favour of Age and Area, but as soon as possible I obtained confirmatory evidence by work upon the flora of New Zealand (16, also 17-24), where I was able to give actual longitudinal measurements of the areas where the species occurred, and where the results came out with much greater clearness. Still further work (19) on the Orchids of Jamaica, on *Callitris* (a Conifer) in Australia, and on the flora of the Sandwich Islands (both flowering plants and ferns, separately treated), also confirmed my conclusions. It will be well to quote here the distribution figures for New Zealand, as illustrating what I have said about the graduation of endemics one way and wides the other:

<i>Range in N.Z.</i>	<i>Wides.</i>	<i>Endemics.</i>
881-1080 miles	201	112
641-880 „	77	120
401-640 „	53	184
161-400 „	38	190
1-160 „	30 ¹	296

Many people who have tried to apply Age and Area to their own work have become dissatisfied with it because they have ignored the reservations which are given in the statement of the rule above, and we must now devote a few moments to their consideration. To begin with, it must never be applied to single species, but only to groups of at least ten allied forms, in order to cancel out the effects of differences among them in degree of local adaptation, of luck in transportation in the earlier rarer stages, and other more or less chance effects. In the second place, allied species must be taken, as in general they will belong to the same ecological type, and will react to their surroundings in more or less the same manner. It cannot be too often repeated that Age and Area does not as yet offer any means of distinguishing the *comparative* ages of differing ecological types, though I hope to show in a later paper that this is beginning to be possible to a slight extent. A group of Compositae may occupy the same area in the same country as a group of Dipterocarpaceae, but no one would suggest that they were of the same age within the country, though both groups obey the Age and Area rule. An area which might take the latter one thousand years to cover might be covered by the Compositae in one or two. Again, the conditions must remain reasonably constant. Any serious change might kill out some species. In essence, a change of conditions means

¹ Largely undoubted introductions of recent years.

a shifting of the ecological barriers, or the erection of such. Lastly, a fourth great reservation is expressed in what is said about barriers. The very great majority of species, for example, will be absolutely cut off from spreading by meeting a sea of any serious width, and the comparatively few species that may at times be able to cross may be easily appreciated by a study of Guppy's monumental labours on the subject. A broad river may act as a barrier to many, and probably will usually tend to delay spread, at any rate. The same is true of a high range of mountains, especially if they reach the snows, but here the barrier also as a rule becomes partly ecological, inasmuch as the climates on the two sides usually differ, to say nothing of the different climate at high levels. Other ecological boundaries than climatic changes are usually, in my opinion, too narrow to stop completely

DIAGRAM 2.

the passage of species, though they may deflect, distort, or delay it; but the wording of the rule is framed so as to cover all possibilities. And finally, in modern times, as every one knows, man has done more than any of nature's agencies in the distribution of species about the globe, partly by intentional or accidental transport, partly by the great clearances, involving change of conditions, that he has made.

In studying the local distribution of species in New Zealand, where it was more exactly worked out than in Ceylon, I worked with the aid of a prediction that I made from a consideration of the bearings of Age and Area upon the subject (16, p. 442), that the number of endemic species in any genus would rise gradually to a maximum at or near the point or region where the genus entered New Zealand in the first place. The diagram here reproduced shows the way in which this occurs. A single wide (W) is supposed to enter New Zealand at the centre, and to follow

Age and Area with exactness in its distribution, as indicated by the right-angled triangle showing it gradually extending its area till at the same moment it reaches both north and south ends of New Zealand. Casually, it or some of its derivatives give rise to ten endemics (E, 1 to 10), which

DIAGRAM 3. Wides dotted; extension N. includes Kermadecs, E. Chathams.

spread in the same way. If a vertical line be drawn at each tenth of the total distance from north to south, and the number of endemics in each zone counted, they will give a curve rising to a maximum at or near the middle (sometimes two maxima). Here for example the figures run 0, 3, 5, 8, 9, 8, 7, 3, 2, 2. On examination, I found this maximum exhibited by every

genus in the flora that had more than one species, and a planning of the areas occupied by the different species resulted in giving for all the larger genera such maps as that for *Ranunculus* here reproduced, which shows clearly the massing of the species near the middle of the South Island. Examination of all the genera showed that these maxima occurred, not casually all over New Zealand, but in masses, especially at the far north, at the centre, and at the point where they show in *Ranunculus*, rather to the south of the middle of the South Island. Upon these results I have based my contention that the flora of New Zealand has been the result (24, p. 475) of four separate invasions—one from Indo-Malaya direct (northern invasion, reaching New Zealand at the far north, and when added together giving the

DIAGRAM 4. Northern invasion: vertical figures are numbers of species, horizontal the distances in miles from North Cape of New Zealand.

curves in Diagram 4, which shows the numbers of wides and endemics at each successive zone of one hundred miles, working south), one from Polynesia by way of the Kermadec Islands, one from Australia (western or central invasion), and one from the south (southern invasion, curves given in Diagram 5, with maxima¹ at 800–900 miles south of the North Cape, i. e. rather south of the middle of the South Island.

Results were now flowing in so easily and naturally that I became a firm believer in the truth of my hypothesis, and applied it to predictions of what would or would not be found in certain places or under certain conditions. Some of these predictions were simple tests, as when I predicted (21, p. 27) nearly half the species that would be found upon Stewart Island from a knowledge of the flora of New Zealand, or all but fourteen of those

¹ The double curve given for wides is explained thus: a few species of some of the genera are evidently northern, and die out as one goes south. The upper curve includes these, the lower and more correct curve excludes them. The narrowing distance between the curves shows the way in which they die out to the south.

upon the Chathams (22, p. 288); but most have been devoted to the discovery of new facts, or still more to the regrouping and marshalling of old and incompletely known or understood facts. Over ninety predictions

DIAGRAM 5. Southern invasion: figures as in northern invasion.

have now been made, and verified by a subsequent study of the facts, but it would lead too far to go into further details. As I am sometimes accused of making the prediction subsequently to the knowledge of the facts, I may perhaps be allowed to state that this is not the case, but that I have con-

sidered each case carefully, and thought out what should be found if Age and Area were true, and then have subsequently verified it by an examination of the facts, in all cases finding that my prediction was correct. In the case about to be described, for example, I first thought out the predictions, and then sat down to count and classify genera for six weeks, in perfect confidence that the result would come out in accordance with my anticipations—as in fact it did. The present era in the history of the world and its peopling with plants seems to be an era governed mainly by Age and Area, which has determined in broad outline the distribution of plants about the world, leaving to ecology the settlement of the details.

ENDEMIC GENERA.

In this paper I propose to attempt to extend the applicability of Age and Area, which hitherto has been confined to the plants of one country, and to species only, with occasional incidental references to genera. It will of course be understood that the larger the area and the number of plants dealt with, the less clearly does its operation show in detail, but I venture to hope that it will be admitted, after consideration of what is set forth below, that it does hold in a wide and general manner for all flowering plants and for the whole world.

I shall deal principally with what are called endemic genera, confined to one island, one mountain chain, or other restricted locality. In one of my first papers (15, p. 5) I pointed out an obvious deduction to be drawn from an acceptance of Age and Area, viz. that as a rule endemic species confined to small areas are in reality species in the earlier stages of spreading about the globe, and given time enough and absence of barriers they might ultimately be found covering large areas. The corollary to this, that endemic genera are similarly young genera, I have left to be inferred, but it will be elaborated below.

The expression of this view has met with considerable opposition, for it involves a break with the opinion that has for so long held the field, that endemic forms, whether species or genera, represent some kind of losers in the struggle for existence, and that the regions characterized by their presence are therefore to be regarded as a kind of refuges for the destitute, where, on account of the smaller number of species, there was less keen competition, and these forms had been able to survive it. It is thus expressed in a recent paper (3, p. 215), 'Very many endemics owe their limited distribution to the circumstance that they are remnants of comparatively unsuccessful types which have been exterminated elsewhere, and

which even in these isolated floras are waging a losing fight against more vigorous and adaptable new-comers.'

This explanation has always been unsatisfactory to me since I began to study *in situ* the numerous endemic forms of Ceylon, and a great argument against it, which has always been passed over and left unanswered by its supporters, is the fact that endemic species usually occupy continuous areas. In other words, from the point of view of the current explanation, the endemics have not retired in confusion, but have kept their formation. Other arguments which also turned up in the course of my work confirmed me in this disbelief of the usual explanation. For example, I found it very difficult to reconcile with the idea that endemics were in general moribund the fact that in a single country there was a regular graduation of endemics upwards from many of small area of distribution to few of large, and of species of wider distribution than endemic in the opposite direction (cf. tables in 14, p. 310; 15, p. 3; 16, p. 449; 19, pp. 336, 338, 344). Again, practically all the endemics of a country, if they possess more than one or two species, show graduated maps like that given for *Ranunculus* in New Zealand, and the same is the case whether they have or have not widely distributed species of the same genus beside them. Another awkward point for the supporter of generally moribund endemics (i. e. other than a comparatively few, too small in number to affect the figures) is the fact that in the far outlying islands round New Zealand (Chathams, &c.) the more widely distributed species there are, the more endemics (18, p. 332, Table III), and the wides are more numerous in proportion (figures in 20, bottom of p. 352). Further, the endemics of New Zealand and Ceylon are most numerous where there are most wides, least where there are fewest, which is not at all what one would expect if the endemics are moribund species. The comparatively few endemics found near the outer ends of New Zealand range over a much greater area than do those in the middle (cf. the map of *Ranunculus* above, and table in 16, p. 448). Yet another great difficulty, from the old point of view, is the fact that species endemic to New Zealand and its immediately outlying islands (Kermadecs, Chathams, Aucklands) are on the average more widespread in New Zealand than the species common to New Zealand and the outside world, but *not* found on these little islands, while the species found in the outside world, and occurring also in New Zealand *and* these islands, are the most widespread in New Zealand of all. Fern endemics, which must on the whole be older than angiosperm endemics, occupy more area than the latter. Lastly, and perhaps most important of all, the endemic species belong principally to the *large*, or what on the old view are considered the successful genera, and much less, even in proportion, to the small.

All these, and many other arguments which might be brought forward (cf. 20, p. 352), rendered it impossible for me any longer to adhere to the

view that endemics were moribunds—at least in any serious proportion—but it is only during the last seven years that I have been able to bring proofs for what seems to me a more satisfactory explanation, viz. that they represent different early stages on the way *upwards*, not downwards. One cannot imagine species dying out in the regularly graduated way shown in the map of *Ranunculus* above, but if one imagine that these are new species formed in successive order, and just in the early stages of dispersal, one arrives at a perfectly simple explanation, which completely fits the facts so far as we know them.

In view of the incisive figures which have been set forth in recent papers, a number of botanists are now beginning to admit that endemic species of small area of distribution are really young species, or at least have been formed *in situ*, but few are as yet prepared to admit this for endemic genera, and most people continue to regard them as survivals.

If my view be the correct one to take, then it is clear that there is no difference between endemic genera and species, and others that occupy larger areas, except that in general they are younger; so that while one may call *Coleus elongatus* endemic to the summit of Ritigala in Ceylon, or the genus *Carpodetus* endemic to New Zealand (it has one species, reaching to both ends of New Zealand), one may with equal justice talk about *Hottonia palustris* as endemic to temperate Europe and Asia, or the genus *Senecio* as endemic to the world. My aim in the present paper is to show that this is the more correct view to take, and that there is no appreciable difference but age.

So firmly has the old view, that endemics are relics of old floras, held sway, that it never seems to have occurred to any botanist to try the simple test whose results I am about to set forth, and yet this test might have been made at any time in the last thirty years. Although it was suggested by a consideration of Age and Area, the results here set forth are simple facts which may be considered purely on their merits, without reference to any hypothesis whatsoever.

One may test this question, whether endemic genera are or are not in general relics, in a very simple way, by making a prediction which shall at the same time be a crucial test, inasmuch as the result must be different on the two hypotheses, and then verifying it by comparison with the actual fact. The prediction, however, being as to what, in a broad general way, will be found upon the islands of the world, involves various complications.

In the first place, if the islands have received their floras by casual oversea transport, it is clearly all but impossible to predict what will be found upon them. If a successful prediction is made, therefore, the fact speaks very strongly in favour of their having (in the mass) received their floras by land, not necessarily continuous, but with no very large gaps. If

any really large islands received by water, the prediction would probably break down.

If endemic genera are survivals, one cannot predict to what families they will belong, except that it would seem highly improbable that they should belong *mainly* to the large and what are usually called the 'successful' families, like Compositae or Rubiaceae. It would seem more probable that they would show a tendency, at any rate, to belong to families that are small, or of broken distribution, such as we have been accustomed to consider as unsuccessful and more or less moribund. In any case, one would expect some marked differences in composition of the list from that of the mainland.

If then, examining the endemic genera of islands, we find them to be a miscellaneous assortment, we may imagine either that the islands received their floras mainly by casual oversea transport, or that the endemics represent survivals, and if we also find that they show a distinct tendency to belong to the small and broken families, we may then with a fair degree of probability accept the second of these suppositions.

If, on the other hand, endemic genera be young genera in the earlier stages of spreading, as is the case if we accept the hypothesis of Age and Area, we shall expect them (provided of course that the connexion was mainly by land) to appear in families in proportions not dissimilar to the proportions of genera appearing in those families at the present time. There should be among them many Compositae and Rubiaceae, few Magnoliaceae or Myristicaceae, more Melastomaceae than Ranunculaceae, and so on.

But we may go farther than this. As I have already pointed out (21, p. 34), if Age and Area holds, then on the whole a large family will be older than a small one of the same circle of affinity. And as the islands were mostly cut off from the mainland at a remote period, the families that reach them will on the whole be the older, that is to say, rather the larger than the smaller. And as the larger would be more likely to get to them first (as being on the whole older than the smaller), they will tend to have rather more genera in proportion upon the islands. One will therefore expect the proportion of endemic genera upon the islands to be if anything rather greater in the large than in the small families.

Other factors will also come in to influence the result. Some families, like Compositae or Orchidaceae, may be well able to travel across wide stretches of water, and may thus be better represented than their age would indicate. If herbs are younger, as there is good reason to suppose (5), we shall expect many herbaceous families, even though they may be large, to be badly represented, and so on.

This second prediction, then, if it prove successful, will on the whole show that the bulk of the connexion to the islands at the time they

received their floras was by land and not by casual oversea transport, and it will also show that the distribution accorded in general with the rule of Age and Area, and that the endemic genera in general are young genera in their early stages, and not survivals.

In order to arrive at a result which cannot be the subject of cavil on account of incompleteness, I have included in the present paper all the endemic genera of all the islands in the world, amounting to 1,582, or 12.6 per cent. of the 12,517 in the world. I have taken them from my Dictionary (4th ed., 1919), thus including many that would generally be merged in others, but at least getting a complete list of all that are at all frequently considered as separate genera.

The three great groups of islands in the world are all in the tropics, and one must bear this in mind in considering the composition of their lists of genera. A counting of the genera in each of these three groups—(1) the Indo-Malayan Islands, including Ceylon, the Malay Archipelago, Polynesia, New Caledonia, &c.; (2) the African Islands, including Madagascar, the Mascarenes, Socotra, &c.; (3) the American Islands, including the West Indies and Galapagos—soon shows that in all much the same families stand at the top of the list of genera. The following table shows the first ten families in each case, with the number of endemic genera belonging to them :

1. <i>Indomal. Islands.</i>		2. <i>African Islands.</i>		3. <i>American Islands.</i>	
1. *†Orchidaceae	79	*†Rubiaceae	29	*†Rubiaceae	25
2. *†Rubiaceae	67	* Palmaceae	27	†Compositae	20
3. * Palmaceae	41	†Asclepiadaceae	25	*†Euphorbiaceae	13
4. *†Euphorbiaceae	38	†Acanthaceae	24	*†Leguminosae	13
5. Araliaceae	26	†Compositae	22	* Palmaceae	13
6. Melastomaceae	23	*†Orchidaceae	19	*†Orchidaceae	12
7. Anonaceae	19	*†Leguminosae	15	†Acanthaceae	8
8. *†Leguminosae	19	Sapindaceae	14	†Asclepiadaceae	7
9. Sapindaceae	19	*†Euphorbiaceae	13	Apocynaceae	6
10. Apocynaceae	17	Bignoniaceae	10	†Gramineae	6

* In all three lists.

† In the first ten largest families of the world.

This table, incomplete though it be, does not offer any suggestion that the endemics of the islands are survivals. There are only seven families in all that do not come into the first ten in the world: of these Palmaceae, Melastomaceae, Sapindaceae, and Apocynaceae are found in the second ten, and of the rest Bignoniaceae are twenty-second in the world with 119 genera, Anonaceae twenty-sixth with 108, and Araliaceae thirty-ninth with 81.

The enormous majority of the endemic genera of islands belong to the three island groups just mentioned, and when one adds up the grand total for all islands in the world one arrives at the following table :

		<i>Gen. on Islands.</i>	<i>Gen. in the World.</i>		<i>Gen. on Islands.</i>	<i>Gen. in the World.</i>
1. Rubiaceae	(5)	124	506	21. Icacinaceae	18	63
2. Orchidaceae	(2)	120	666	22. Flacourtiaceae	17	104
3. Palmaceae		86	216	23. Menispermaceae	17	96
4. Compositae	(1)	81	1,143	24. Zingiberaceae	17	60
5. Euphorbiaceae	(7)	65	326	25. Bignoniaceae	16	119
6. Leguminosae	(3)	56	645	26. Liliaceae	16	254
7. Asclepiadaceae	(6)	47	347	27. Myrtaceae	15	90
8. Acanthaceae	(10)	45	266	28. Verbenaceae	15	89
9. Gramineae	(4)	43	506	29. Monimiaceae	14	34
10. Melastomaceae		36	186	30. Umbelliferae	(8) 14	325
		703	4,807		159	1,234
11. Sapindaceae		34	156	31. Urticaceae	14	50
12. Araliaceae		33	81	32. Labiatae	13	197
13. Apocynaceae		29	198	33. Meliaceae	13	68
14. Rutaceae		22	144	34. Ericaceae	12	119
15. Saxifragaceae		22	96	35. Guttiferae	12	54
16. Araceae		21	131	36. Myrsinaceae	12	41
17. Sapotaceae		21	81	37. Boraginaceae	11	114
18. Anonaceae		20	108	38. Campanulaceae	11	73
19. Scrophulariaceae		20	241	39. Cruciferae	(9) 11	289
20. Gesneriaceae		19	120	40. Cunoniaceae	11	30
		241	1,356		120	1,035

The first ten in the world in order of size are marked in brackets after the name.

These first 40 families, in order of number of endemic genera upon islands, include 31 of the first 40 families in the world in order of size. The 9 others included are Campanulaceae (forty-third in the world), Meliaceae (forty-seventh), Icacinaceae (fiftieth), Zingiberaceae (fifty-second), Guttiferae (fifty-ninth), Urticaceae (sixty-second), Myrsinaceae (sixty-eighth), Monimiaceae (seventy-eighth), and Cunoniaceae (eighty-fifth). The corresponding nine in the world list that are missing are (in order of size) Rosaceae (eighteenth), Cucurbitaceae (twenty-fifth), Cyperaceae (twenty-seventh), Solanaceae (thirty-first), Amaryllidaceae (thirty-second), Caryophyllaceae (thirty-third), Chenopodiaceae (thirty-sixth), Anacardiaceae (thirty-seventh), and Gentianaceae (thirty-eighth), practically all herbaceous or shrubby families.

These first 40 families include 1,223 out of 1,582 endemic genera of islands, or 77 per cent. of the total, the remaining 23 per cent. being comprised in the other 110 (of the 252 remaining) families in the world which possess endemic genera upon islands. These families are:

With 11 genera endemic upon islands, Tiliaceae; with 10, Celastraceae, Malvaceae, Moraceae; with 9, Anacardiaceae, Lauraceae, Thymelaeaceae; with 8, Chlaenaceae, Coniferae, Loranthaceae, Proteaceae, Rhizophoraceae, Rosaceae, Solanaceae, Sterculiaceae; with 7, Cucurbitaceae, Loganiaceae, Rhamnaceae, Simarubaceae; with 6, Caryophyllaceae, Dipterocarpaceae, Gentianaceae, Hamamelidaceae, Olacaceae, Theaceae; with 5, Bombacaceae, Burseraceae, Burmanniaceae, Convolvulaceae, Cornaceae, Elaeocarpaceae,

Malpighiaceae, Violaceae ; with 4, Amarantaceae, Ochnaceae, Piperaceae ; with 3, Caprifoliaceae, Cyperaceae, Dilleniaceae, Lecythidaceae, Lythraceae, Marantaceae, Nyctaginaceae, Passifloraceae ; with 2, Amaryllidaceae, Aquifoliaceae, Balanophoraceae, Balanopsidaceae, Begoniaceae, Bromeliaceae, Dioscoreaceae, Epacridaceae, Geraniaceae, Globulariaceae, Linaceae, Magnoliaceae, Orobanchaceae, Papaveraceae, Polygonaceae, Portulacaceae, Rafflesiaceae, Ranunculaceae, Staphyleaceae, Turneraceae, Winteranaceae ; with 1, Aizoaceae, Berberidaceae, Cactaceae, Cercidiphyllaceae, Chloranthaceae, Cneoraceae, Cochlospermaceae, Combretaceae, Commelinaceae, Connaraceae, Corynocarpaceae, Crassulaceae, Cycadaceae, Datisceae, Diapensiaceae, Ebenaceae, Flagellariaceae, Frankeniaceae, Gonystilaceae, Goodeniaceae, Hippocrateaceae, Hydrophyllaceae, Lactoridaceae, Loasaceae, Myoporaceae, Myristicaceae, Opiliaceae, Oxalidaceae, Pandanaceae, Pedaliaceae, Philydraceae, Phytolaccaceae, Podostemaceae, Polygalaceae, Primulaceae, Sabiaceae, Santalaceae, Sonneratiaceae, Stylidiaceae, Styracaceae, Theophrastaceae, Triuridaceae, Trochodendraceae, Ulmaceae, Vitaceae. Grand total 150 fams., 1,582 gen.

It is clear from a cursory inspection of this table, that the endemic genera of islands belong to the families in rough proportion to the actual totals of genera contained in them, though, as we shall see in detail in a later paper, a number of herbaceous families like Compositae, Cruciferae, Caryophyllaceae, Liliaceae, Umbelliferae, Chenopodiaceae, &c., are distinctly low in the scale of island genera, a fact indicating that they are probably on the whole younger (cf. 5).

The families that are missing in the list of island genera also bear out the same conclusion. They are 142 in all, out of a total of 292, or nearly half, are mostly families with small totals of genera in the world, and are chiefly herbaceous, or undershrubs. They form the following list :

Chenopodiaceae	with 86 genera in the world
Iridaceae	„ 68 „ „ „
Onagraceae	„ 51 „ „ „
Capparidaceae	„ 49 „ „ „
Zygophyllaceae	„ 31 „ „ „
Oleaceae	„ 27 „ „ „
Restionaceae	„ 25 „ „ „
Polemoniaceae	„ 23 „ „ „
Haemodoraceae	„ 21 „ „ „
Hydrocharidaceae	„ 21 „ „ „

With 7 families with 11 to 18 genera
„ 24 „ „ 6 to 10 „
„ 49 „ „ 2 to 5 „
„ 52 „ „ 1 genus

One may compare this list with the list of 150 families that contain the endemic genera of islands, and get the following table :

<i>Fams. with endemic genera on islands.</i>			<i>Fams. without</i>
With	1 genus	3	52
„	2-5 genera	19	49
„	6-10 „	12	24
„	11-30 „	36	12
„	31-50 „	21	2
„	51-80 „	19	2
„	81-150 „	23	1
„	over 150 „	17	—

which shows that the families with no island endemic genera are crowded towards the bottom of the list. Or yet again, one may take the total of genera in the families of the two lists, when one finds that the 150 families in the first list, that contain endemic genera on islands, contain in all 11,627 genera, an average of 77 per family, while the 142 in the second list contain in all 890, or an average of 6 per family.

It is quite clear that the facts do not bear out any prophecy based on the idea that endemics are moribund. The small families, and families of disconnected distribution, show no unusual prominence, but are on the contrary very badly represented.

But the final proof against the moribund nature of endemic genera as a whole, both for islands and for other places in which they abound, such as South Africa or West Australia, is given by adding up all the genera found *only* in

1. The islands of the World.
2. West Australia, South Africa, and Brazil, all areas rich in endemic forms, and among them showing much variety in conditions, with forest, campo, and desert.
3. Australia, Africa, and South America.
4. The World.

Just as in the case of the groups of islands, the individual families vary in their arrangement amongst themselves in the various lists; indeed, were it not so, the fact would be perfectly astonishing. But it is generally found that any one family (unless herbaceous) is not *very* far apart in its situations in the different lists, and if we add the families together in groups of ten, local variation will be quite sufficiently covered. Taking as a standard the groups of ten into which the world list divides, and adding together in each of the other lists the genera found in the *same* ten families, we arrive at the table on p. 509.

The figures in this table are very striking, and bear out in a very complete manner the prediction based upon the supposition that endemic genera cannot be survivals, except in rare cases. The percentage numbers are so close together in the different columns that the largest difference of all is that in the second line, between 18.0 for islands and 14.6 for Australia, Africa, and South America combined. It is clear in the first place that the islands, with few exceptions, and those almost certainly not the large

islands like Madagascar, New Zealand, or Borneo, must have been connected with the mainland at the time when they received the bulk of their flora, though the connexion need not have been absolutely continuous, but might have been interrupted by narrow straits. And it is also, I think, clear in the second place that endemic genera, with few exceptions, are really young genera in the earlier stages of dispersal. Just as it was all but inconceivable that endemic species, which showed as 'wheels within wheels', as in the map of *Ranunculus* in New Zealand given above, should be dying out in so regular a manner, so here it is extraordinarily hard to imagine that the genera can be survivals, and yet appear in a regular proportion to the totals of genera in their various groups.

<i>Tens of Fams.</i>	<i>World.</i>		<i>Austr. &c.</i>		<i>W. Austr. &c.</i>		<i>Islands.</i>	
	%		%		%		%	
1.	5,019	40.1	1,579	39.1	459	40.5	606	38.3
2.	1,868	14.9	592	14.6	176	15.5	285	18.0
3.	1,094	8.7	360	8.9	86	7.6	144	9.1
4.	874	6.9	325	8.0	78	6.8	115	7.2
5.	695	5.5	271	6.7	75	6.6	83	5.2
6.	561	4.4	216	5.3	57	5.0	82	5.1
7.	456	3.6	83	2.0	19	1.6	55	3.4
8.	355	2.8	111	2.7	30	2.6	48	3.0
9.	296	2.3	99	2.4	24	2.1	29	1.8
10.	233	1.8	79	1.9	29	2.5	37	2.3
Total	11,451	91.4	3,715	92.1	1,033	91.1	1,484	93.7
11 to 20	919	7.3	278	6.8	90	7.9	86	5.4
21 to 29.2	147	1.1	38	0.94	10	0.88	12	0.75
Grand Total	12,517		4,031		1,133		1,582	

The percentages may be plotted as curves (Diagram 6, p. 510), when their agreement is seen in a still more striking manner.

These curves are very remarkable in their close coincidence, and after sight of them it is difficult any longer to maintain the position that endemic genera in general are survivals of old floras. Survivals are not likely to be nicely graduated in proportion to the size of the groups of families to which they belong.

The first and principal part of the prediction is thus fully borne out, and comparison shows with equal clearness that the proportional representation of the different families among the endemic genera of islands decreases as one goes down the scale. There are 292 families of Spermaphyta in the world, and the first 100 of these have island endemic genera in 92, the genera being 12.9 per cent. of the total genera in the families. The intermediate 92 families are represented in the islands by 45 only, with 9.28 per cent. of their genera, while the final 100 are represented only by 13 (4 families endemic) with 8.72 per cent. of their genera. This bears out the second part of the prediction, whose complete success may be taken to mean that in general, with few and comparatively insignificant exceptions, the islands were united to the mainland at the time they received their floras,

and that they received these floras in accordance with the principles of Age and Area, the endemic genera in them being in general simply the younger genera that have not yet spread very far.

A little more must be said to make clear the position with regard to relic endemics, and possibility of genuinely oceanic islands. Nothing that has been said above is to be read as denying that either of these may exist, but it is clear from the figures that they are unimportant as compared with the endemics which are not relics, and the islands which are not truly oceanic, but have been peopled with plants by land connexions. There is

DIAGRAM 6.

an appreciable sprinkling of plants, such as *Ginkgo* for example, which are now confined to small areas, and which we know from geological evidence to have been formerly widespread; but these are but few and far between in the grand total of endemics. In the mass, it is no longer possible to look upon endemic genera as being survivals; evidence must be definitely brought up in each individual case in which it is desired to prove that an endemic is a survival. And the same general statement is true with regard to the oceanic nature of islands. It is not possible to regard islands, in the bulk, as having received their floras across the present existing wide stretches of water; they must in general have received their floras by way of land con-

nexions, but that statement does not exclude the possibility that some few may have been oceanic, such for instance as the Sandwich Islands, or St. Helena. These far outlying islands have so few endemic genera that they do not appreciably affect the totals.

Confirmatory evidence may be obtained in various ways. One may, for example, point out that since many families have been long enough upon islands to have given rise there to endemic genera, these families must be very old. But now, to have reached both the Old and the New Worlds in the course of its dispersal, a family must also be very old. One will therefore expect that a very great proportion of those families that are represented upon islands by endemic genera will also reach both worlds. Examining the facts, one finds that 5 families with endemic genera upon islands are themselves endemic there. Of the remaining 145, no fewer than 131 (90 per cent.) reach both Old and New Worlds, while of the other 142 families that have no endemic genera upon islands, only 75 (52 per cent.) occur in both land masses.

Or again, on the whole the islands that are farthest out from the mainland should have almost solely the very oldest families (of the nearest mainland) in their various affinity circles, and we have seen that these are usually also the largest families. Thus, on the whole, the endemic genera of the far out islands should belong to larger families, averaging larger than the islands as a whole, though these should average larger than those of the mainland. We may test this on the flora of Madagascar. This island has endemic genera in 80 families, while the islands of the world have them in 150. Of the 70 families thus missing, no fewer than 57 belong to the 75 smaller, and only 13 to the 75 larger families. In New Zealand the proportion of families with endemic genera is 16 in the first 75 larger to 4 in the 75 smaller families, while in the Sandwich Islands the proportion is 13 to 1. The prediction is thus fully borne out, and it is confirmed by the fact that the bulk of the small families occur only on the nearer islands. Or reference may be made to the comparison between the floras of New Zealand and the outlying Chatham Islands (22, p. 287).

If the island endemic genera were really survivals, they should, in virtue of their total number of 1,582, or 12.6 per cent. of the genera of the world, contain at least that percentage of the monotypic families, but in fact, of the 55 such families, they contain only 3. Of the other 52, 12 are found in both hemispheres, 6 are palaeotropical, 6 neotropical, 6 in Africa, and smaller numbers elsewhere.

The oldest families of all will in general have reached most islands. One will therefore expect the bulk of the endemic genera to belong to families that reach many islands. This is easily found to be the case, so there is no need to go into detail, but give simply one instance. The West Indies have 195 endemic genera in 43 families that also occur in the islands

of Indo-Malaya, and only 19 in the 16 families that do not; they have 187 in 39 families that occur on the African islands, and 27 in 20 families that do not.

Postscript. Since writing the above, I have been working at the endemic genera of N. temperate America, and I find, as I shall show in a later paper, that the misunderstanding between Prof. Sinnott and myself is due to the fact that there *are* many relics there, while there are not in the tropics, to which most of the islands belong, nor in Europe. Each of us has reasoned from the territory that he has most closely examined.

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And cf. List of Literature in 20.

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