PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Endemic Flora of Ceylon, with Reference to Geographical Distribution and Evolution in General

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VII. *The Endemic Flora of Ceylon, with Reference to Geographical Distribution and Evolution in General.*

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The completion of my revised catalogue of the Ceylon flora* has enabled me to put together statistical notes on some of its more interesting features, and in the present paper I shall deal with the endemic flora. Though only separated from India by a narrow strait, which at Adam's Bridge is barely 28 miles across, sprinkled with islets and sandbanks, and from 6 to 12 feet in depth at low water, Ceylon contains an immense endemic flora, which enables it to rank with many oceanic islands: even the Sandwich Islands have not so many. The flora of Ceylon consists of 2809 species of flowering plants,† and of these no fewer than 809 are endemic, or a proportion of 28·8 per cent. And these are not mere varieties, or doubtful species, but good Linnean species, accepted by such authorities as Trimen and Sir Joseph Hooker. On the other hand, the number of endemic genera is only 23 out of 1027, so that the island does not rise to the rank of a widely separated province in geographical botany.

Incidentally, the facts about to be brought forward are an apparently insuperable objection to the theory of natural selection and adaptation. In previous papers

* 'A Revised Catalogue of the Indigenous Flowering Plants and Ferns of Ceylon,' Colombo and London (Dulau), 1911.

† The 2808 of the Catalogue includes two Cycads, but three new species have since been discovered (see 'Ann. Perad.,' vol. 5, pp. 167, 217, 387).

dealing with the endemic flora of Ceylon I have endeavoured to prove that the endemic species have not been evolved in any kind of advantageous response to local conditions, and I have called attention* to the fact that they are much rarer than the species of wider distribution that occur alongside of them. But only in the present year have I completed the laborious task of extracting from the great Flora of Ceylon by TRIMEN and HOOKER the statistics that are required. This Flora is beyond doubt the most complete yet published for any tropical country, and thanks to 70 years' work on this comparatively small island (25,000 square miles) by such men as GARDNER, HOOKER, THWAITES, TRIMEN, and many more, the local flora is thoroughly well known, and it is unlikely that further work will do anything more than add half-a-dozen species or so to the list, without changing in any but a very few cases the very useful indications given as to relative abundance.

The Ceylon flora contains 149 families, with 1027 genera and 2809 species, of Angiosperms (*sensu* HOOKER), 58 with 105 genera and 196 species contain no endemic forms, but these are mostly small families. The average number of species in a family in Ceylon is 19, and the only family with more than 19 that contains no endemics is the Capparidaceæ with 20. It may be noticed here, as a fact that has possibly some bearing on the mechanism of evolution, that this family contains nine species endemic to Ceylon and South India, a very large proportion. The only other families of any important size without endemics are the Menispermaceæ and Solanaceæ with 13 species each, the Ficoideæ with 11, the Lentibulariaceæ and Polygonaceæ with 10 each, while there is 1 family with 8, 1 with 7, 1 with 6, 2 with 5, 1 with 4, 10 with 3, and 18 each with 2 and 1 species.

The families with the most endemic species, arranged in order, are :—

TABLE I.

Orchidaceæ	78	or	9·6	per cent. of all the endemics,
Rubiaceæ	71	,,	8·7	,, ,,
Dipterocarpaceæ	47	,,	5·8	,, ,,
Euphorbiaceæ	45	,,	5·5	,, ,,
Acanthaceæ	39	,,	4·8	,, ,,
Melastomaceæ	36	,,	4·4	,, ,,
Gramineæ	31	,,	3·8	,, ,,
Myrtaceæ	30	,,	3·7	,, ,,
Lauraceæ	23	,,	2·8	,, ,,
Anonaceæ	21	,,	2·6	,, ,,
Compositæ	19	,,	2·3	,, ,,
Geraniaceæ	18	,,	2·2	,, ,,
Scitamineæ	17	,,	2·1	,, ,,
Styraceæ	17	,,	2·1	,, ,,

* "Some Evidence against . . . . Natural Selection . . . .," 'Ann. Perad.,' vol. 4, p. 12 (1907).

TABLE I—*continued.*

Anacardiaceæ	15	or	1·8	per cent. of all the endemics,
Araceæ	14	,,	1·7	,, ,,
Dilleniaceæ	12	,,	1·4	,, ,,
Leguminosæ	12	,,	1·4	,, ,,
Cyperaceæ	12	,,	1·4	,, ,,
Ebenaceæ	11	,,	1·3	,, ,,
Guttiferæ	11	,,	1·3	,, ,,
Sapotaceæ	11	,,	1·3	,, ,,
Palmaceæ	11	,,	1·3	,, ,,
Labiatæ	10	,,	1·2	,, ,,
Loranthaceæ	10	,,	1·2	,, ,,

besides 3 families with 8, 4 with 7, 2 with 6, 4 with 5, 2 with 4, 13 with 3, 19 with 2, and 19 with 1 species.

Of the families with endemics 6, the Monimiaceæ with 2 and the Ancistrocladaceæ, Dipsaceæ, Nepenthaceæ, Proteaceæ, and Valerianaceæ with 1 species each, have all their species endemic. The Dipterocarpaceæ (47 out of 48), Styraceæ (17/20), Dilleniaceæ (12/15), and Anacardiaceæ (15/19) have over 75 per cent. endemic. The Lauraceæ (23/33), Melastomaceæ (36/52), Triuridaceæ (2/3), Gesneraceæ (8/12), Sapotaceæ (11/17), Bixaceæ (7/11), Geraniaceæ (18/29), Myrtaceæ (30/49), Pandanaceæ (3/5), Guttiferæ (11/19), Ternstroemiaceæ (4/7), Anonaceæ (21/39), Palmaceæ (11/21), and Rubiaceæ (71/138) have over 50 per cent. The Balanophoraceæ, Burmanniaceæ, Connaraceæ, Cornaceæ, Myristicaceæ, Pittosporaceæ, and Thymelæaceæ have each exactly 50 per cent. of their members endemic.

Local Commonness of Endemic and other Species.

We may now go on to consider the distribution of these endemic forms within the island. TRIMEN divides all species into six classes—Very Common, Common, Rather Common, Rather Rare, Rare, and Very Rare.* Now as Very Rare is applied to any species which has only been found in one place, or in two close together (or more rarely at some distance apart), and as there are 455 of these, it is evident that if these classifications were used with absolute uniformity they should show approximately equal numbers in each heading—one-sixth of the total, or 468 in each. But in actual fact they show, for the whole flora—

* TRIMEN died leaving no material for Gramineæ, and I have myself calculated the rarities of the species, adhering as closely as possible to the system he appears to have employed.

TABLE II.

	Number.	Marks.	Percentage.
1. Very common	285	285	10·1
2. Common	670	1340	23·8
3. Rather common	555	1665	19·7
4. Rather rare	429	1716	15·2
5. Rare	415	2075	14·7
6. Very rare	455	2730	16·1

If we mark these from 1 to 6 and calculate the average rarity, we find 2809 species with 9811 marks, or an average rarity of 3·49, when theoretically it should be 3·5.

There can be little doubt that at some former period Ceylon and Southern or Peninsular India formed part of one land mass, even if they were not at the end of a long continental projection from Africa. This being so, we have divided the plants of Ceylon into three groups to make the comparisons that follow. In the first place we have taken those that are endemic to Ceylon only, of which, as we have already said, there are 809. In the second we have taken those that are only found in Ceylon and Peninsular India; of these there are 492, and it may reasonably be taken for granted that they are on the whole older than the first. The third group, which comprises 1508 plants, is composed of those that have a wider distribution than this—not necessarily very much wider, but still going beyond the limits we have marked out for the second group, *e.g.*, into Assam.

Now, if we take the distribution of these three groups in point of commonness, as given in TRIMEN'S Flora, we arrive at a somewhat unexpected and remarkable result. I had long known, and in fact published, that the endemics were rarer than the others, but was agreeably surprised when the final totals came out with such arithmetical precision as they actually show.

TABLE III.

	Endemic to Ceylon.	Ceylon and P. India.	Wider distribution.
VC . . .	19	45	221
C	90	118	462
RC . . .	139	103	313
RR . . .	136	84	209
R	192	64	159
VR . . .	233	78	144
	809 Marks 3518	492 Marks 1714	1508 Marks 4579
Rarity* . .	4·3	3·5	3·0

* *I.e.* in figures from 1 to 6. To reduce this rarity even to 4·2 would require that 80 species should each be placed a class higher in the scale.

The endemic species increase in number from VC to VR, while the species of wide distribution follow the reverse direction. This result shows much more clearly* if one multiplies the figures by the necessary factors to bring them to the same number under each of the headings of VC, C, &c., *i.e.* to a total of 468 (one-sixth of the total number of species) under each. These factors are 1·64, 0·70, 0·84, 1·09, 1·12 and 1·03, respectively. We thus get the following Table :—

TABLE IV.

	Endemic to Ceylon.	Ceylon and P. India.	Wider distribution.
VC . . .	31	74	362
C	63	83	323
RC . . .	117	87	263
RR . . .	148	92	228
R	215	72	178
VR . . .	240	80	148
Rarity . .	4·4	3·5	2·9

The result which was distinctly enough indicated in the first table now comes clearly out, and it is evident that the Ceylon endemics are on the whole much below the average in their degree of commonness, while the species of wide distribution are much above it, both of them at the same time showing figures that progress regularly from one end of the scale to the other. The species common only to Ceylon and Peninsular India, on the other hand, are fairly normally distributed over the scale, as many under one head as under another, and with the average rarity of the whole flora.

Thus in general the rarest plants in Ceylon are the local endemics, and the commonest those of wide distribution. This is not at all the result that one would expect had the endemics, as is usually supposed, been developed by the aid of natural selection to suit the local conditions. One would at least have expected that they would have been as common as the species of wide distribution, or at any rate as those developed to suit Ceylon and South India, but they are much rarer than both, and of these two groups the latter is rarer than the former. Only 2·3 per cent. of the Ceylon endemics have reached the stage indicated by Very Common, and no less than 14·6 per cent. of the species of wide distribution have reached it.

Another interesting comparison may be made by taking the second table above and placing alongside the numbers the theoretical figures, supposing all species to have reached their final distribution of one-sixth under each head. We thus get :

* It of course shows exactly the same result if calculated as percentages.

TABLE V.

	Ceylon.			Ceylon and P. India.			Wide.		
	Actual.	Theoretical.	Difference.	Actual.	Theoretical.	Difference.	Actual.	Theoretical.	Difference.
VC .	31	135	−104	74	82	− 8	362	251	+111
C . .	63	135	− 72	83	82	+ 1	323	251	+ 72
RC .	117	135	− 18	87	82	+ 5	263	251	+ 12
RR .	148	135	+ 13	92	82	+10	228	251	− 23
R . .	215	135	+ 80	72	82	−10	178	251	− 73
VR .	240	135	+105	80	82	− 2	148	251	−103

It is evident on comparing the numbers that a simple perfectly indifferent regrouping, by which some of the endemics would gradually become more common, and some of the "wides" more rare, would reduce all to much the same level of commonness, with approximately equal numbers under every heading.

It must of course be made clear that we are here dealing only with averages, but the numbers under each head are large enough to give averages that may be fairly well relied upon. We may safely say that on the average the local endemic species are the rarest, those of Ceylon and Peninsular India next most rare, and those of wide distribution commonest.

Having thus traced, on the grand totals of species of each type of distribution, the result of the summing up of the endemic flora, as compared with the other two sections of which the Ceylon flora is composed, we may go on to show that this result is not one which simply comes out on the total, but also holds in detail, and is not due to any such fact as that some one or two families are very rare, and might be regarded as being driven to the wall. The detailed figures show the results given in Table VI.

Looking this over, we see that the whole range of the rarity of the Ceylon endemics is only from 3·9 to 4·9*, working with not less than 14 species in a group; and in fact a great proportion even of the families with only a few endemics, which are put together in the list, also come within these figures. The species common to Ceylon and South India similarly vary only from 2·0 to 4·0, and if a minimum of 20 species be taken, vary only from 3·0 to 4·0. The species of wide distribution vary from 1·0 to 4·6, and again if groups of not less than 20 be taken, the variation is only from 2·2 to 3·8.† The means of these extremes correspond very nearly with the actual means of the whole summing up.

The variation in rarity between the different families or groups of families of Ceylon endemics is small, and goes to show that no one family has any particular advantage over another, and that there is no case that can be pointed to as showing that any of

* *I.e.* they are never so common as the mean rarity (3·5) of the whole flora.

† *I.e.* never so rare as the commonest endemics.

TABLE VI.

Family	Endemic species.	Marks.	Rarity.	Ceylon and P. India species.	Marks.	Rarity.	Wides.	Marks.	Rarity.
Orchidaceæ	78	343	4·4	39	153	3·9	45	175	3·8
Rubiaceæ	71	306	4·3	25	75	3·0	42	122	2·9
Dipterocarpaceæ	47	233	4·9	1	3	3·0	—	—	—
Euphorbiaceæ	45	201	4·4	26	83	3·1	59	184	3·1
Acanthaceæ	39	170	4·3	30	111	3·7	24	54	2·2
Melastomaceæ	36	165	4·5	11	35	3·1	5	17	3·4
Gramineæ	31	146	4·7	20	80	4·0	189	557	2·9
Myrtaceæ	30	133	4·4	6	17	2·8	13	34	2·6
Lauraceæ	23	94	4·0	4	10	2·5	6	16	2·6
Anonaceæ	21	89	4·2	12	32	2·6	6	28	4·6
Compositæ	19	78	4·1	22	71	3·2	37	92	2·4
Geraniaceæ	18	71	3·9	5	14	2·8	6	12	2·0
Scitamineæ	17	77	4·5	4	16	4·0	16	47	2·9
Styraceæ	17	78	4·5	2	4	2·0	1	1	1·0
Anacardiaceæ	15	62	4·1	2	6	3·0	2	4	2·0
Araceæ	14	63	4·5	4	9	2·2	15	41	2·7
3 families with 12*	36	163	4·4	43	170	3·9	304	958	3·1
4 ,, 11†	44	189	4·2	16	51	3·1	21	60	2·8
2 ,, 10‡	20	78	3·9	21	77	3·6	26	79	3·0
7 ,, 8 or 7§	52	226	4·3	34	126	3·7	111	333	3·0
6 ,, 6 or 5‖	32	128	4·0	23	84	3·6	50	139	2·7
15 ,, 4 or 3¶	47	190	4·0	43	158	3·6	152	449	2·9
38 ,, 2 or 1**	57	235	4·1	63	204	3·2	218	710	3·2
91 families	809	3518	4·3	456	1589	3·4	1348	4112	3·0

* Dilleniaceæ, Leguminosæ, Cyperaceæ.

† Guttiferæ, Ebenaceæ, Sapotaceæ, Palmaceæ.

‡ Labiatæ, Loranthaceæ.

§ Apocynaceæ, Gesneraceæ, Urticaceæ, with 8; Bixaceæ, Tiliaceæ, Asclepiadaceæ, Eriocaulonaceæ with 7.

‖ Loganiaceæ, Celastraceæ, with 6; Ampelidaceæ, Sapindaceæ, Gentianaceæ, Piperaceæ, with 5.

¶ Ternstroemiaceæ, Meliaceæ, with 4; Violaceæ, Polygalaceæ, Linaceæ, Rosaceæ, Cucurbitaceæ, Myrsinaceæ, Convolvulaceæ, Orobanchaceæ, Verbenaceæ, Amarantaceæ, Liliaceæ, Commelinaceæ, Pandanaceæ, with 3.

** Malvaceæ, Rutaceæ, Burseraceæ, Olacineæ, Rhamnaceæ, Connaraceæ, Rhizophoraceæ, Samydaceæ, Begoniaceæ, Umbelliferæ, Cornaceæ, Boraginaceæ, Scrophulariaceæ, Podostemaceæ, Myristicaceæ, Monimiaceæ, Thymelæaceæ, Burmanniaceæ, Triuridaceæ, with 2; Ranunculaceæ, Pittosporaceæ, Caryophyllaceæ, Ancistrocladaceæ, Sterculiaceæ, Ochnaceæ, Haloragiaceæ, Combretaceæ, Lythraceæ, Araliaceæ, Valerianaceæ, Dipsaceæ, Oleaceæ, Nepenthaceæ, Proteaceæ, Balanophoraceæ, Hydrocharidaceæ, Dioscoreaceæ, Naiadaceæ, with 1.

the larger families is being driven to the wall in the struggle for existence. Within the limits marked out by the degrees of rarity indicated by 3·9 and 4·9 practically all families are alike; some are probably a little better suited to the local conditions than others, and are commoner, but even here we have not the least idea how much of the greater commonness is due to age or other factors.

This fact, that there is little difference between the different orders, also comes out if we take the rarities of the orders as a whole, in those cases where they have more than 19 species, the average number in a family in Ceylon. This shows Anonaceæ 3·8, Capparidaceæ 3·9, Dipterocarpaceæ 4·9, Malvaceæ 2·9, Tiliaceæ 3·6, Geraniaceæ 3·3, Rutaceæ 3·3, Ampelidaceæ 2·9, Leguminosæ 3·4, Myrtaceæ 3·7, Melastomaceæ 4·1, Cucurbitaceæ 3·1, Rubiaceæ 3·6, Compositæ 3·0, Ebenaceæ 4·1, Styraceæ 4·1, Apocynaceæ 3·1, Asclepiadaceæ 3·9, Convolvulaceæ 3·5, Scrophulariaceæ 3·0, Acanthaceæ 3·6, Verbenaceæ 3·1, Labiatæ 3·1, Amarantaceæ 2·9, Lauraceæ 3·6, Loranthaceæ 4·0, Euphorbiaceæ 3·6, Urticaceæ 3·0, Orchidaceæ 4·1, Scitamineæ 3·7, Commelinaceæ 3·6, Palmaceæ 3·1, Araceæ 3·4, Cyperaceæ 3·2, and Gramineæ 3·2.

Examination of this list shows that the whole range of rarity is only from 2·9 to 4·9, and if the Dipterocarpaceæ (47 out of 48 endemic) be omitted only from 2·9 to 4·1, or equal distances on either side of the averages. And of this range a large part is due to the greater or less percentage of endemics in the orders.

TABLE VII.

	Ceylon.	Ceylon—P. India.	Wider.	Total.	Ceylon endemics.
Those families with rarity above 3·5 show—					
	462 2075	209 733	298 951	969 3759	Per cent. 47·6
Rarity . .	4·27	3·50	·3·19	3·87	
Those with rarity 3·5 (one family) or under show—					
	166 699	168 608	806 2386	1140 3693	14·5
Rarity . .	4·21	3·61	2·96	3·23	

It is thus evident that the greater rarity of some families is largely due to the endemics that they contain, for the difference in the third column is only 0·23, and in the fourth 0·64. If allowance be made for this, the range of variation is considerably reduced.

We may even follow the comparison into the genera. Taking the first 22 that come, with reasonable numbers of endemic and non-endemic species, we find

TABLE VIII.

55 endemic species with 224 marks.	56 non-endemic species with 154 marks.
Rarity 4·0.	Rarity 2·7.

There are more individual exceptions among the genera than among the families, but on the average the rule comes out in an unmistakable manner.

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Another very striking comparison may be obtained by taking those genera in which there occur species of all the different types of distribution—endemic, Ceylon and India, and wider. In this way we obtain the following :—

TABLE IX.

Genus.	Species and Marks.					
	Ceylon.	Rarity.	Ceylon and P. India.	Rarity.	Wider.	Rarity.
Uvaria	2/8	4·0	2/4	2·0	2/10	5·0
Polyalthia	3/11	3·6	3/5	1·6	1/4	4·0
Alphonsea	1/6	6·0	1/2	2·0	1/6	6·0
Garcinia	2/7	3·5	2/4	2·0	1/2	2·0
Calophyllum	7/30	4·2	1/2	2·0	3/13	4·3
Biophytum	3/8	2·6	1/5	5·0	1/1	1·0
Impatiens	15/63	4·2	4/9	2·2	2/3	1·5
Ochna	1/6	6·0	1/3	3·0	1/4	4·0
Vitis	5/21	4·2	7/21	3·0	7/16	2·2
Sapindus	2/10	5·0	1/4	4·0	2/5	2·5
Crotalaria	1/3	3·0	7/35	5·0	15/50	3·3
Desmodium	2/11	5·5	2/7	3·5	17/42	2·4
Derris	2/11	5·5	1/5	5·0	3/7	2·3
Pithecolobium	1/2	2·0	1/2	2·0	2/7	3·5
Eugenia	29/128	4·4	6/17	2·8	8/20	2·5
Osbeckia	5/20	4·0	3/4	1·3	1/4	4·0
Sonerila	8/41	5·1	3/15	5·0	1/6	6·0
Memecylon	21/97	4·6	3/13	4·3	3/7	2·3
Hedyotis	16/76	4·7	4/9	2·2	1/2	2·0
Ophiorrhiza	3/14	4·6	1/1	1·0	2/4	2·0
Randia	1/4	4·0	2/6	3·0	2/5	2·5
Knoxia	2/2	1·0	1/5	5·0	1/3	3·0
Canthium	4/20	5·0	2/5	2·5	1/2	2·0
Pavetta	3/10	3·3	1/4	4·0	1/2	2·0
Vernonia	9/30	3·3	1/4	4·0	3/6	2·0
Blumea	2/11	5·5	3/11	3·6	5/15	3·0
Anaphalis	4/20	5·0	3/5	1·6	1/2	2·0
Senecio	1/6	6·0	3/9	3·0	2/5	2·5
Ardisia	3/15	5·0	2/6	3·0	3/7	2·3
Diospyros	8/38	4·7	8/36	4·5	4/9	2·2
Symplocos	17/78	4·5	2/4	2·0	1/1	1·0
Linociera	1/1	1·0	1/5	5·0	1/3	3·0
Tylophora	3/13	4·3	2/8	4·0	3/12	4·0
Strychnos	3/13	4·3	2/8	4·0	2/6	3·0
Argyreia	1/1	1·0	2/11	5·5	2/7	3·5
Lettsomia	1/6	6·0	1/2	2·0	1/1	1·0
Ipomœa	1/6	6·0	2/10	5·0	8/27	3·3
Barleria	2/10	5·0	3/11	3·6	3/11	3·6
Justicia	3/11	3·6	2/7	3·5	4/9	2·2
Premna	2/11	5·5	1/4	4·0	4/12	3·0
Coleus	2/8	4·0	1/2	2·0	1/3	3·0
Anisochilus	1/4	4·0	1/6	6·0	1/5	5·0
Piper	3/9	3·0	1/2	2·0	5/11	2·2
Peperomia	2/7	3·5	2/9	4·5	1/2	2·0
Myristica	2/7	3·5	1/2	2·0	1/3	3·0
Litsea	9/35	3·8	1/2	2·0	2/2	1·0
Loranthus	8/40	5·0	5/17	3·4	4/11	2·7

TABLE IX—*continued.*

Genus.	Species and marks.					
	Ceylon.	Rarity.	Ceylon and P. India.	Rarity.	Wider.	Rarity.
Phyllanthus	9/46	5·1	2/6	3·0	9/25	2·7
Glochidion	8/31	3·8	1/6	6·0	1/2	2·0
Croton	2/10	5·0	3/9	3·0	2/10	5·0
Agrostistachys	1/6	6·0	1/4	4·0	1/2	2·0
Mallotus	3/9	3·0	2/8	4·0	3/8	2·6
Macaranga	1/5	5·0	1/1	1·0	1/2	2·0
Ficus	3/12	4·0	4/14	3·5	14/40	2·8
Pouzolzia	1/3	3·0	2/6	3·0	2/5	2·5
Microstylis	3/15	5·0	2/10	5·0	1/3	3·0
Liparis	5/27	5·4	3/12	4·0	4/12	3·0
Dendrobium	3/12	4·0	3/10	3·3	3/9	3·0
Vanda	1/6	6·0	1/3	3·0	2/6	3·0
Saccolabium	5/17	3·4	2/8	4·0	2/9	4·5
Habenaria	8/37	4·6	7/26	3·7	2/6	3·0
Dioscorea	1/3	3·0	1/2	2·0	4/5	1·2
Asparagus	1/2	2·0	1/2	2·0	2/4	2·0
Commelina	1/6	6·0	1/4	4·0	8/31	3·8
Cyanotis	2/9	4·5	4/12	3·0	2/4	2·0
Eriocaulon	7/38	5·4	3/14	4·6	8/17	2·1
Fimbristylis	3/16	5·3	2/7	3·5	24/63	2·6
Carex	5/20	4·0	3/8	2·6	13/47	3·5
Isachne	2/9	4·5	2/6	3·0	3/8	2·6
Panicum	1/6	6·0	1/4	4·0	40/109	2·7
Arundinella	3/13	4·3	1/4	4·0	2/7	3·5
Pollinia	1/5	5·0	1/4	4·0	2/7	3·5
Cymbopogon	1/6	6·0	1/4	4·0	7/27	3·8
Eragrostis	2/9	4·5	1/5	5·0	10/26	2·6
Total	321/1367	—	166/569	—	315/895	—
Rarity	4·2		3·4		2·8	

Of the 74 genera enumerated in this list 29 only are exceptions to the rule that the order of rarity is Ceylon, Ceylon and India, Wider distribution, but of these 29 only one (Saccolabium) goes in the exact reverse direction all through. Most of them show Ceylon commoner than Ceylon-Peninsular India, or the latter than Wide. If we add the whole 29 together we get—

TABLE X.

	Ceylon.		Ceylon–P. India.		Wider.	
	Number.	Marks.	Number.	Marks.	Number.	Marks.
	91	349	52	178	80	260
Rarity	3·8		3·4		3·2	

So that even the exceptions give a result in the right direction when added together. If we add these genera together into their families, we find 33 represented. Of these

TABLE XI.

Genus.	Species and marks.					
	Ceylon.	Rarity.	Ceylon and P. India.	Rarity.	Wider.	Rarity.
Anonaceæ	6/25	4·1	6/11	1·8	4/10	2·5
Guttiferæ	9/37	4·1	3/6	2·0	4/15	3·7
Oleaceæ	1/1	1·0	1/5	5·0	1/3	3·0
Convolvulaceæ	3/13	4·3	5/23	4·6	11/35	3·1
Piperaceæ	5/16	3·2	3/11	3·6	6/13	2·1
Myristicaceæ	2/7	3·5	1/2	2·0	1/3	3·0
Commelinaceæ	3/15	5·0	5/16	3·2	10/35	3·5
	29/114	—	24/74	—	37/114	
Rarity	3·9		3·0		3·0	

TABLE XII.

Genus.	Endemic species.	Non-endemic species.		Genus.	Endemic species.	Non-endemic species.	
Ranunculus	C	C	Equal.	Cyathula	VR	VC	
Dillenia	RC	C		Psilotrichum	R	R	Equal.
Miliusa	C	RC	*	Cryptocarya	R	RC	
Pittosporum	RC	RC	Equal.	Balanophora	R	C	
Salomonia	RR	RC		Putranjiva	VR	R	
Mesua	RC	C		Trigonostemon	VR	R	
Ternstrœmia	RR	C		Claoxylon	RR	C	
Hugonia	R	RC		Artocarpus	C	RR	*
Glycosmis	VR	VC		Debregeasia	RR	C	
Aglaia	RC	C		Calanthe	RC	RR	*
Walsura	RR	VC		Hetæria	R	R	Equal.
Microtropis	RC	RC	Equal.	Cheirostylis	R	R	Equal.
Gymnosporia	VR	RR		Vanilla	RR	C	
Rhamnus	RR	C		Phrynium	R	C	
Nephelium	VR	C		Areca	RR	VC	
Connarus	RR	VC		Phœnix	VC	VC	Equal.
Pygeum	RC	C		Amorphophallus	R	C	
Carallia	C	RC	*	Aponogeton	C	C	Equal.
Alangium	RR	RC		Mapania	VR	RR	
Mastixia	RR	RR	Equal.	Leptaspis	RR	RC	
Emilia	C	VC		Zenkeria	RR	RC	
Caralluma	VR	R		Cœlachne	RR	RC	
Tournefortia	R	R	Equal.	Lophatherum	R	C	
Klugia	C	C	Equal.				

24 show the expected order of rarity, two have Ceylon-India and Wide equal, though less than Ceylon, and there are seven exceptions which, however, when added together give the result indicated in Table XI.

Another interesting comparison is between the species in those genera which contain one endemic and one non-endemic species each. In this way we obtain the result shown in Table XII.

Here we find that the endemic species is rarer in 32 cases, the non-endemic rarer in four cases, which are marked with an *, whilst the records are equal in 11 cases. In 15 cases the non-endemic species is confined to India and Ceylon, and in these cases the endemic species shows an average rarity of 3·5, while in the 32 cases where the non-endemic species is of wider range the endemic shows a rarity of 4·2.

Adding up all these species we get the following result :—

TABLE XIII.

Class.	Endemic species.	Marks.	Non-endemic species.	Marks.
VC	1	1	7	7
C	7	14	17	34
RC	7	21	11	33
RR	14	56	5	20
R	10	50	7	35
VR	8	48	0	0
	47	190	47	129
Rarity	4·0		2·7	

Even yet the possibilities of comparison are not exhausted. If we take the seven genera in which there are three species, one of each type of distribution, we get the following Table :—

TABLE XIV.

Genus.	Ceylon species.	Ceylon and P. India.	Wider.
1. Alphonsea	VR	C	VR
2. Ochna	VR	RC	RR
3. Linociera	VC	R	RC
4. Lettsomia	VR	C	VC
5. Anisochilus	RR	VR	R
6. Agrostistachys	VR	RR	C
7. Macaranga	R	VC	C
Marks	34	23	23
Rarity	4·8	3·2	3·2

The last two figures are equal, but we are dealing here only with seven species, five of which are exceptions to the rule.

It is thus clearly evident that the rule that we enunciated above, that the order of rarity is Ceylon, Ceylon and Peninsular India, Wider dispersal, holds throughout the comparison with the most extraordinary regularity. Though there are a number of individual exceptions in the genera, as would be expected, for all species cannot be at the same exact degree of adaptation, nor have had the same favourable or unfavourable chances, the rule in any group of more than about 15 species comes out with the regularity of Mendel's law, especially when we consider that we are dealing with estimates, and not directly with actual facts of observation.

Incidentally, a comparison may be applied to the numbers of species of each type of distribution found in the different climatic zones of the island, whether the wet zone, with the well distributed rain, or the dry, with its long dry season. In this way we obtain the following figures :—

TABLE XV.

	Ceylon endemics.			Ceylon and P. India.			Wider.		
	Dry.	Dry and wet.	Wet.	Dry.	Dry and wet.	Wet.	Dry.	Dry and wet.	Wet.
VC. . . .	1	1	17	9	12	24	25	145	51
C. . . .	6	8	76	22	27	69	53	231	178
RC. . . .	5	3	131	17	19	67	69	102	142
RR. . . .	8	0	128	21	6	57	55	46	108
R. . . .	16	4	172	18	6	40	49	25	85
VR. . . .	12	2	219	33	1	44	53	7	84
Total . .	48	18	743	120	71	301	304	556	648
Marks . .	212	58	3248	476	183	1055	1121	1264	2194
Rarity . .	4·4	3·2	4·3	3·9	2·5	3·5	3·6	2·2	3·3

Adding up all the species of the dry zone, we find 472 confined to it with 1809 marks, or a rarity of 3·8 ; those of the wet zone only are 1692 with 6497 marks, or also a rarity of 3·8. But the species that occur in both zones, 645 with 1505 marks, are much commoner in both, and show a rarity of 2·3, *i.e.* are fairly near to the level of "Common." How this result is to be interpreted it is difficult to say; whether it is that these species are really specially adapted to both zones, and have become common in both, or whether it is that they are on the whole the first arrivals in the country, and that most species can really live in both zones, or what, we do not at present know; but the facts are very striking. It is also very noteworthy that in the dry zone there are only 48 endemic species against

743 in the wet, though the species of wide distribution are only in the proportions of 304 to 648, and the dry zone has twice the area of the wet.

Invalidity of the Theory of Natural Selection.

Now, when one comes to look into all this, it is seen to be a somewhat important result. One may, so it seems to me, draw from it two or more conclusions, the first of which is that the local endemic species have not been—as I have already shown in other ways in other papers—developed in any kind of advantageous response to local conditions, as must have occurred did natural selection obtain.

Had this been the case, one might reasonably have expected them to be on the whole, at least, as common as the species of wide distribution. But by no conceivable argument can this be maintained. TRIMEN doubtless made errors in his estimates, but there is no reason to suppose that he always gave the widely distributed species the preference to the others in the direction of commonness.* The mere fact that the figures come out in such remarkable arithmetical progression is sufficient to show this, and the fact that the local endemics increase in number down to Very Rare, instead of up to Very Common (as do the species of wide distribution), is enough to show that the endemics were not developed in advantageous response to local conditions.

A second great argument in favour of this contention is that the species common to Ceylon and Southern India, *i.e.*, species which must, on the whole, have been developed before the separation of those two countries, and which must therefore, on the whole, be older than those endemic to Ceylon only, are more common than the latter. If we imagine that they were all developed in Ceylon, and spread subsequently to South India—a purely gratuitous assumption—we might then say that they had been developed to suit the Ceylon conditions, and, being older, had had more time to spread, and thus become commoner. But, unfortunately for this hypothesis, these very species are still much less common than the species of wide distribution, and this fact is very difficult to explain on any theory of adaptation. If they have been able to spread over Ceylon and Peninsular India, they have had ample time to become common in Ceylon (*i.e.*, as common as the species of wide distribution) if they were specially suited to the local conditions.

This leads on to another argument. If these Ceylon endemics had been specially adapted by natural selection to the local conditions, there has unquestionably been ample time for them to become very common. TRIMEN accepts as Very Common a species which is very common in the district which is suitable to it, whether wet or dry, warm or cold. For instance, he labels *Impatiens leptopoda* (endemic) as Very Common, though it does not occur in the warm or dry zones, but is only to be found in the wet, cool zone of the higher mountains, where it may be seen in nearly every

* To equalise the endemics and the "wides" there would have to be made 1040 corrections in *one* direction; *i.e.* an inconceivable amount of error must have taken place in the estimates.

damp corner. Out of the whole number of 809 endemics only 19 have spread to the stage indicated by Very Common. And yet several introduced species have spread to this stage in a comparatively few years, though they belong to Ceylon families or even, as in the case of the famous Lantana, to Ceylon genera. *Tithonia diversifolia* (Compositæ), which was introduced in 1851, began to spread about fifteen years later, and in 1900 was all over the island in damp enough spots, though its seeds have no pappus, and it spread almost entirely by vegetative reproduction. *Mikania scandens*, which only began to spread about ten years ago, is already common over a large area near Peradeniya, reaches about 30 miles along the railway to Colombo, and has reached Trincomali down the river, and established itself near that place. There has been ample time for any of the endemic species, had they been really well adapted to the local conditions, to have spread to the stage of Very Common, and the fact that they have not done so goes to show that they are no better adapted, on the average, than their forerunners.

Natural selection, again, to be effective, requires that many forms shall modify in the same direction, as DARWIN himself admitted after the criticisms of FLEEMING JENKIN. Now, this is exactly what cannot be allowed in the case of the numerous endemic species of Ceylon, which very commonly are confined to one spot, where they cannot ever have been very numerous, and where yet, as I have already pointed out, they must have been evolved. *Coleus elongatus* must have evolved on the summit of Ritigala, where it exists as about a dozen individuals, and cannot ever have been much more numerous. The most numerous group of the Ceylon endemics are these Very Rares, and the numbers decrease steadily up to Very Common. They must obviously have begun at one or other end of the scale. They could not begin at Very Rare (on the theory of natural selection), because the numbers are insufficient. But if they began at Very Common, and were developed to suit the local conditions, it is a very remarkable thing that they increase steadily in number down to Very Rare, and are therefore, so far as one can see, in process of dying out.

Yet another argument against natural selection, though it is not a very strong one, may be derived from the fact that the families with many endemics, *i.e.*, the families which on the theory of natural selection one would suppose very well suited to local conditions, have their endemics rarer than they are in families that possess only few. If we arrange the families in the order of the number of endemics contained in them, as in Table VI above, and add them up in approximately equal groups, we get the result indicated in Table XVI.

There is thus quite a perceptible difference in the degree of rarity between families that have many, and families that have few, endemic species, and the figures progress arithmetically, without a break.

These conclusions can be further confirmed by looking at the endemic genera. If local species had been evolved to suit local conditions, one would, at any rate, expect

TABLE XVI.

	Endemic species.	Marks.	Rarity.
3 families . .	196	882	4·50
6 " . .	204	909	4·39
14 " . .	201	870	4·31
68 " . .	208	857	4·11

the genera to be common, but this is by no means the case. The degrees of commonness of the 52 species of the 23 endemic genera are shown in the following Table :—

TABLE XVII.

Schumacheria .	C, RC, R.
Trichadenia . .	RR.
Doona	C, VR, RR, R, RC, R, RR, R, VR, VR, R.
Stemonoporus .	RR, R, R, VR, R, VR, RR, VR, VR, VR, R, VR, VR, VR, VR.
Monoporandra .	R, VR.
Julostylis . . .	RC.
Pityranthe . .	C.
Pseudocarapa .	RR.
Gleniea . . .	C.
Pericopsis . . .	C.
Leucocodon . .	R.
Schizostigma . .	RC.
Nargedia . . .	VR.
Scyphostachys .	VR, R.
Championia . .	R.
Ptyssiglottis . .	R.
Hortonia . . .	RC, R.
Podadenia. . .	VR.
Adrorhizon . .	RC.
Alvisia	RR.
Octarrhena . .	RC.
Cyphostigma . .	RC.
Loxococcus . .	RC.

Classifying these into their headings, we find :—

TABLE XVIII.

			Marks.
VC	0	with	0
C	5		10
RC	9		27
RR	7		28
R	15		75
VR	16		96

52 with 236 marks, or a rarity of 4·5.

Or, in other words, the species of these endemic genera are even rarer than the endemic species as a whole, and are grouped in the table in a similar way, with numbers increasing down to Very Rare.

But we may go further yet, and take the two genera, Doona and Stemonoporus, which have 11 and 15 species respectively, and on the theory of natural selection would therefore be supposed to be especially suitable to the local conditions. These show—

TABLE XIX.

	Doona.	Stemonoporus.
VC	0	0
C	1	0
RC	1	0
RR	2	2
R	4	4
VR	3	9
	11 Marks 51	15 Marks 82
Rarity	4·6	5·4

Or, in other words, both these genera are rarer than the average of all the endemic genera, and Stemonoporus, which has more species than Doona, is the rarer of the two. One gathers the impression that these two genera have perhaps been formed by what one may almost term explosive methods, a number of new species being formed comparatively rapidly, and in Stemonoporus later than in Doona.

It will bring out these points more clearly if we give them in tabular form, thus :—

TABLE XX.

	Number.	Marks.	Rarity.
Species of wide distribution	1508	4579	3·0
Species confined to Ceylon and Peninsular India	492	1714	3·48
Mean rarity of all	—	—	3·49
Species endemic to Ceylon	809	3518	4·3
Species of all 23 endemic genera	52	236	4·5
Species of Doona	11	51	4·6
Species of Stemonoporus	15	82	5·4

Such figures as these no ingenuity can torture into any kind of support for a theory of the development of endemics to suit the local conditions. There is not even a break in the continuity of the figures, which go in the exact reverse direction to what they should follow if the theory of natural selection could be relied upon.

Taking these arguments, together with those which I have already given elsewhere,* to show that endemic species have not in any way been developed to suit local conditions, there can, I think, be no hesitation in rejecting the latter hypothesis. I may perhaps quote, as bearing upon the present paper, two short paragraphs from the paper referred to: "How can the existence of numerous endemic species, all closely allied to one common species, and all separated by some distance from one another, be explained on any but the parent and child theory? Take the Indian flora as an example. To begin again at the beginning, in the genus Clematis § Cheiropsis, we have *C. montana* common all along the Himalaya, while *C. napaulensis*, *C. barbellata*, and *C. acutangula* are confined to particular sections. We have *Anemone rivularis* common throughout the Himalaya, and various local allied species"; and "It is possible, if not probable, that a group of allied species represents so many more or less stable positions of equilibrium in cell division, and it is at least entirely doubtful if any given species is specially adapted for the circumstances in which it is found."

If all the species that now exist in Ceylon had been introduced at the same time by mixing their seeds in equal (and excessive) quantity, and sowing them broadcast over the island, their relative degree of abundance, and their particular geographical distribution, would undoubtedly, as these figures clearly show, have been entirely different from what they now are, and they would to some extent have afforded a test of the relative degree of adaptation of the different species to the local conditions. At present, when we have no idea of the relative age of different species, to talk of them as if one were well adapted, and another not, is purely an effort of the imagination.

We have been in the habit of looking upon endemic species with very small range

* "Some Evidence against . . . . Natural Selection . . . . ," 'Ann. Perad.,' vol. 4, p. 1 (1907). And *cf.* other papers in same journal, 1906–11.

as if they were suited to very special local conditions, and yet some of these, when planted elsewhere, grow with remarkable success. A very notable example is that of *Cupressus macrocarpa*, confined in nature to a small area in California, and yet proving to be one of the most successful Conifers in all the sub-tropical regions of the world. If a species happen to get into a locality where its local adaptation is good, as, for instance, any of the weeds which have at different times become common in different parts of the world, it may spread rapidly to the stage of Very Common. But this will only rarely happen. Out of the many hundreds of species introduced into Ceylon at different times, not more than about 60 at most have become common.

Commonness chiefly Dependent on Age.

The second conclusion that we may, I think, justly draw from the remarkable Tables which have been set out is that, on the average, the commonness of a species depends upon the time that has elapsed from the period when it was first evolved in, or arrived in, the country. No other explanation appears to me to fit the striking facts that the species of wide distribution are commoner than the species confined to Ceylon and India (even within one family), and these commoner than the species confined to Ceylon, while at the same time the first show numbers increasing towards VC and the latter to VR. The widely distributed species must, on the whole, be the oldest, the Ceylon-Indian the next, and the Ceylon endemics the youngest. There is no evidence that any are dying out.

In other words, species are, on the whole, developed quite indifferently to local conditions, but, having evolved, they spread, if their degree of local adaptation is sufficient, and as they must have descended from others already growing in the neighbourhood, this should, in general, be the case. They will in some cases, doubtless, from having bad local adaptation or meeting with unfavourable chance, die out, but most will spread to one of the stages VR, R, RR, RC, C, or VC, according to the time allowed, their degree of local adaptation, and the incidence upon them of favourable or unfavourable chance. The same species may perhaps be ultimately VC in one country, say, Ceylon, and VR in another similar one, say, South India, owing to the action of one of these factors. But on the average the commonness will mainly depend upon the age. And to judge from the figures set forth, for example, in Table VI, no very large number of species need be taken to get an average ; apparently from 15 to 20 is enough.

All the figures given in this paper go to show that in all reasonable probability there is little to choose between species in their degree of adaptation to local conditions. This comes out especially clearly in Table VI, where the whole of the endemics, taken in groups of not less than 14, show rarity greater than the average of the whole flora, and yet agree wonderfully closely among themselves in the degree of rarity, which only ranges from 3·9 to 4·9. When one remembers that the figures are not taken directly from facts, but from estimates, of observation, this regularity is wonderful, and the regular order and progression of the figures goes to show that it cannot be accidental.

From these and other facts one may reasonably, it seems to me, conclude that in the peopling of Ceylon with flowering plants the first species to appear, whether coming from elsewhere or developed for the first time within the island—then probably still attached to Southern India, if not also to Africa—were those which are now of wider distribution than Ceylon or Ceylon and South India. They would find the island presumably more or less covered with cryptogamic vegetation—just as Krakatoa was at a certain period after the eruption—but they would begin to spread, and probably, as their demands for food would, on the whole, be slightly different, they would gradually cover large areas, and in time a great number of them would reach the stage of commonness now represented by the expression VC, while those of them, which from lack of adaptation, late arrival, or ill chance, only reached the stage then represented by VR, would perhaps be at the stage of commonness now represented by R or RR. Later on, and probably long before all the widely distributed species had arrived, there would begin to arrive, or to evolve locally, the species now confined to Ceylon and Peninsular India, which in turn would begin to force their way up in the scale. These, having to compete with other flowering plants of the same genera, would probably be slower in ascending, but gradually they have done so, and in so doing have forced some of the "wides" to climb down a bit. Still later, on the whole, would appear the species endemic to Ceylon, and begin forcing their way up. As yet they have by no means succeeded in arriving at anything like an average dispersal, and a corresponding number of "wides" are similarly in their wrong positions. But if time enough could be given, one might expect ultimately to find all three classes distributed fairly evenly over the scale.

We may I think reasonably draw the deduction that on the average of say 15 to 20 a species develops indifferently. But each species in itself starts with the capacity of ultimately reaching (under given circumstances) one of the stages VC, C, RC, RR, R, VR, or extinction, according to how well it is adapted to the local conditions. We are using the word adaptation here to include all the relationships of the species to its environment, *e.g.*, its liability to any diseases that may exist there. This last is a very important point. Some experiments which I have been carrying on upon the struggle for existence among closely crowded plants go to show that it is disease which kills the bulk of the losers, and that these are not necessarily the weakest but often well-grown plants.

The species then, will tend, on the whole, to spread to the local degree of commonness to which it is entitled by its degree of adaptation to local conditions. But it must not be forgotten that this may be completely changed as time goes on, by the introduction of some new factor in the situation, such for instance as the arrival in the district of some new disease to which it falls an easy prey. There is no doubt that on the whole, natural selection, given enough time, will finally ensure that each species takes up the local distribution and degree of commonness to which it is entitled, but there must be an enormous element of chance. The process must be extraordinarily slow; we have no evidence that it is complete in any given case, and good indication in the figures that we have given above that it may be far from complete. Ultimately, one would expect, the figures under the different degrees of commonness or rarity would equalise themselves for the various Ceylon species, and in so doing would force many of the species of wide dispersal to climb to some extent down the ladder, so as also to equalise them among the different headings. On the average, or in some cases, possibly, the species endemic to Ceylon which have already reached the stages indicated by VC or C are species which are really better adapted to the local conditions than the average of all or of the endemic species, but we do not know that they are not simply the oldest endemic species, which were very early developed from species of wide distribution which arrived very early. There are 19 of these species, belonging to the families Geraniaceæ (Balsaminaceæ), Myrtaceæ, Rubiaceæ, Compositæ, Oleaceæ, Apocynaceæ, Gentianaceæ, Convolvulaceæ, Labiatæ, Palmaceæ, Pandanaceæ, Araceæ, and Gramineæ, all of which are widely distributed orders, and often orders which we have other reasons to suppose are old. The rarity of these orders taken together is 3·36, against 3·5, so that on the whole they are probably old.* The rarity of the Ceylon and Indian species of those genera which contain the endemics is 3·2, or less than the rarity of these species as a whole (3·5), and the rarity of the widely dispersed species (20 in number) contained in these genera is 2·3, or less than the rarity of the widely dispersed species as a whole, which is 3. All these facts go together to show that perhaps the commonness of these 19 endemic forms is really only a question of age. As we have already said, it perhaps becomes harder for every new species that comes along to reach the Very Common stage, as the ground will be more closely taken up by a greater variety of species.

The wonderful regularity and uniformity with which these figures come out goes to show the great accuracy of the estimates made by TRIMEN in his Flora, and at the same time shows that there must be an important general law underlying them, which, as I have endeavoured to show, must be that on the average the commonness of species depends on their age, and is independent of their local adaptation. The latter will in each individual case have a determining effect in the degree of commonness ultimately reached, but we have no ground whatever for making statements to the effect that a given species is common and is therefore well adapted. Probably mere chance has also a great deal to do with the commonness of a given species in any particular place.

Relative Age of the Monocotyledons in Ceylon.

But now, if we accept these estimates of TRIMEN as reliable, as we are obviously bound to do, and if we accept the deduction that I have made, that commonness on

* They contain 29·8 per cent. of endemics against an average of 28·8 per cent., so that their rarity should be a fraction above the average.

the whole depends on age, we may test many other points. Some of these will be dealt with in subsequent papers, but we may give two instances here. For example, if there be any truth in the current theory that the Monocotyledons are younger than the Dicotyledons, then, unless the former group was developed in or near Ceylon, so as to start there as soon as the latter, it should be the rarer group. By comparing the plants of these two groups, the rarity of the Dicotyledons as compared with the Monocotyledons proves to be

TABLE XXI.

	Dicots.		Monocots.
In the Ceylon endemics as	4·31	to	4·46
Ceylon and P. India species	3·44		3·65
Widely distributed species	3·01		3·08

The Monocotyledons are the rarer, and therefore perhaps the younger, in each case. But when we add up the totals of each kind, such is the greater proportion of endemic Dicotyledons that the Dicotyledons as a whole have a rarity of 3·49 to 3·47. On the other hand, this greater proportion of endemic Dicotyledons may be used as an argument that they are the older group, and have therefore had more time to give rise to endemics. We find in fact:

TABLE XXII.

	Species of wide distribution.	Ceylon and P. India.	Ceylon.	Total of first two.	Total of last two.
Dicotyledons . .	1004	396	623	1400	1019
Monocotyledons .	504	96	186	600	282

The widespread Dicotyledons which have reached Ceylon are accompanied in Ceylon and Peninsular India by more endemic species than their own number, the Monocotyledons by merely 65 per cent. of their own number. Or we may better put it that the Dicotyledons of Wide and of Indian distribution have given 44 per cent., the Monocotyledons 31 per cent. of their own number, of Ceylon endemic forms.

On the whole, then, the evidence is in favour of the greater age of the Dicotyledons in Ceylon, though of course no great stress can be laid upon it. At least, however, it does not go against that hypothesis.

The Value of "Adaptations."

In cases where we get two large and well-defined groups in a family, we may compare their degrees of rarity, when the difference between them is what is usually looked upon as an adaptation. For example, in the Rubiaceae it is usually supposed that the sections with fleshy fruits are more recent than those with dry. But on the other hand the former is supposed to be an adaptation to enable the seeds to be easily dispersed, which should tend to make them more common, and one would expect them to be on the whole at least as common as the dry fruited species, whereas on the theory here enunciated, if the dry fruit be really the older, it should be the commoner. In actual fact the figures show :

TABLE XXIII.

	Number.	Marks.	Rarity.
Dry fruit.	62	218	3·5
Fleshy	76	285	3·7

Or, taking only the Ceylon endemic forms—

TABLE XXIV.

	Number.	Marks.	Rarity.
Dry fruit	30	124	4·1
Fleshy	41	182	4·4

It is evident that the fleshy fruit has not proved of any special value to its possessors, and is probably a more recent development. There are many other so-called adaptations in many other families which can be dealt with in the same way. Always the figures go to show that evolution of forms is on the average indifferent, and that these so-called adaptations are of no special advantage to their possessors.

Possible Size of Mutations.

Many of the advocates of mutation hold to the view that mutations must of necessity be what they call "small," or such differences as are, for example, exhibited by the small species into which JORDAN divides the Linnean species *Draba verna.* This seems to me to be an unnecessary handicap to the theory of mutation, and I propose that it should be replaced by the hypothesis that no specific change is too great to appear in one mutation.

In the first place, we have no criterion to go by, by which to affirm that a certain specific difference is "small" and another "large." We have no right to say, for example, that if a leaf of one species is simple and of another compound, this is a larger difference than if one is pinnatifid, the other pinnatipartite. We have not the least idea whether the changes in internal construction of the nucleus necessary to form Jordanian species are in any way different from, or smaller or larger than, those necessary to give Linnean species.

The differences between many of the very rare endemic Ceylon species are large, and these species are accepted as well-marked Linnean species by both TRIMEN and Sir JOSEPH HOOKER. Even in an endemic genus this is the case, as, for instance, in Doona or Stemonoporus, where a great number of species are very rare, and only represented by a few plants each. When we reflect upon the facts that have been brought forward in this paper it is clear that we have no right to invoke extensive killing out of intermediate forms.

It is a great deal more difficult to define the difference between a Linnean and a Jordanian species than one is at first inclined to imagine. In such a plant as *D. verna*, where the Linnean species is made by drawing a line round a number of forms at the point of their greatest separation from allied forms, it is comparatively simple ; but all the Linnean species are not like this, as we have just pointed out in the cases of Doona and Stemonoporus.

The species in which Jordanian splitting can be applied are just such species as *D. verna*, common species of wide distribution. This we have just seen to imply considerable age, and it is just as probable that there was originally a single well-separated form to which the name *D. verna* could be applied, which subsequently broke up into many forms, as not. We must simply take account of all definite and hereditary differences, whether we consider them large or small. Every one appears to imply a mutation, but whether some mutations are large and others small, we have no idea, for we do not know in what a mutation really consists.

It seems to me better to adopt the hypothesis that any specific difference may appear at one step, whether it be large or small. But we may go further than this, and claim that even "larger" differences than any we have as yet discussed may also arise at one step. For instance, the endemic *Coleus elongatus* on the top of Ritigala differs so much from all other Colei in its equally toothed calyx, and raceme-like inflorescence, as well as in other points, that it must probably be regarded as almost, if not quite, subgenerically distinct. Yet the whole species is confined to the summit of this one mountain and exists there as about a dozen individuals, a number which can never have been much exceeded, if at all ; and it must in all reasonable probability have arisen there at one step.

But even with the formation of a sub-genus the possibilities of single mutations do not cease. Of the Ceylon endemic genera no less than 17 out of 23 have only one species each, and these have a rarity of 3·7, showing that on the whole they are probably older than the endemic species as a whole. But as there is only one species in the genus, this species must presumably have arisen at one step, forming the genus at the same time. We are thus led to suppose that the distinction between genus and species is really more or less artificial, depending upon our ideas as to what are large and what are small changes.* The distinction is extremely useful, and so long as further mutations, or turns of the kaleidoscope, do not interfere with those characters which we regard as generic, or impose upon them new "generic" characters, the descendants of the first species will continue to belong to its genus. In the case of the Ceylon endemics we seem to have caught most of the genera still in the stage of one species each, but a few have two or three, and two, Doona with 11 species, and Stemonoporus with 15, have gone a stage beyond this.

The fact that in widely separated islands, such as the Hawaiian, the proportion of endemic genera is larger, though the number of endemic species is not so large, would suggest that perhaps "generic" differences sometimes arise by the superposition of specific differences affecting the same character. The fact that in Ceylon there are six families, five with one species each, and one with two species, with all species endemic, goes to show that it is possible for all representatives of a family to become endemic. When we turn to the genera in the other families we find quite a number in which all the species are endemic, which give the following Table :—

Table XXV.

VC . . .	3	RR . . .	33
C . . .	24	R . . .	34
RC . . .	31	VR . . .	44

Total 169 species, with mean rarity 4·20, or slightly more common than the endemic species as a whole. The number of genera with one species only is 63, with two 10, with three 6, with five 5, with seven 3, with nine 1, and with thirteen 1.

There is a marked difference in rarity between those genera with few, and those with many, in these cases with all the species in a genus endemic. When the genus contains one or two species only, the rarity is 4, when it contains more than two the rarity is 4·3. This is exactly what we found in the endemic genera, and would also suggest that genera may perhaps tend, after a certain period, to break up into many species.

It would also appear to follow that there is no evidence that the same mutation must go on appearing in order to establish itself.† Many of the Ceylon endemics in the VR class, *e.g.*, *Coleus elongatus*, on the summit of Ritigala, are represented by only a very few individuals, and cannot so far as one can conceive ever have had more. Whether a species begins as one solitary individual one cannot say; more probably, perhaps, it begins as the seeds of one individual, which may come to nothing, or may give rise to one or many individuals of the new species. But there appears no reason to suppose that the same mutation must appear in several

* Or, more correctly, what are more, and what less, permanent changes.

† *Cf.* de Vries, 'Mutation Theory,' English edition, p. 208.

successive generations in order to become established, though, of course, in that case its chance of becoming established will be greatly increased.

Evolutionary History of a Species.

We may now go on to consider the light which these observations throw on the probable evolutionary history of a species. Mutations being granted as the only available method of origin, the species must have sprung directly from some other species, and natural selection being reduced to very secondary importance, there is no reason why this other species should be killed out.

As the numbers of endemic species increase from VC to VR, this would indicate that they began at one or other end of this scale, and not somewhere in the middle. Now it is highly improbable that they began at the VC end, for this would indicate that they are now dying out, and it would seem a most remarkable thing if species actually developed in Ceylon should not even have enough local adaptation to be able to survive there. It is far more probable that they began at the VR end of the scale, and this is a view strongly supported by the fact that there are amongst them a great number of species confined to one mountain top or to some very small area. No fewer than 108 species* are thus confined to one mountain top or to small areas in the mountains. Many of these only occur, as, for instance, those on the top of Ritigala,† as a very few individuals; they must have been evolved on the mountain top where they are found, as I have shown elsewhere; and they can never have existed as many more individuals than at present.

Each species then, we may suppose, began as VR, *i.e.*, as one or a few individuals in some very limited area. In the case of *C. elongatus*, which is confined to Ritigala summit, the whole plant, so far as I could discover, is represented by a few individuals (not more than a dozen or so), and as there are several other endemic forms on this mountain top, whilst the area of ground suited to the Coleus is very limited, there cannot ever have been many more.

Beginning thus, the species, we may take it, either spread, just held its own, or died out. We may represent what occurs, perhaps, by such a diagram as that on p. 333.

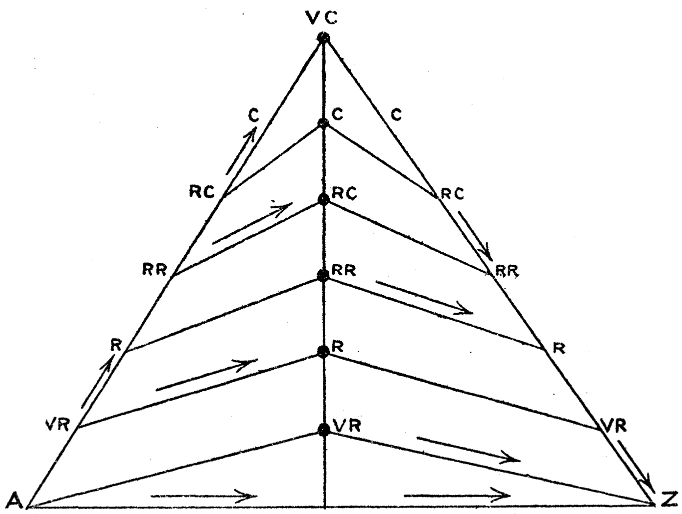
If the species appears first as several individuals (a dozen or more), then the line through VR should be the horizontal one.

Some of the new species developed will probably be so much worse adapted to the local conditions (which are the only ones that matter for a long time), or will meet with such unfavourable chances, that they will die out, and their progress will be indicated by the straight line AZ. Others will be able to creep up in the direction of VC. How far they will get on this line will depend not only on the degree of local adaptation with which they set out, but also on numerous such chances as, for

* "Floras of Hilltops in Ceylon," 'Ann. Perad.,' vol. 4, p. 131 (1908).

† "Flora of Ritigala: a Study in Endemism," *loc. cit.*, vol. 3, p. 271 (1906).

example, the arrival of a disease to which they may be more than usually subject. The first species of a group starting in a new country will perhaps mostly be able to reach a greater degree of commonness than they would now reach, whilst the least common of them, which would then be described as VR, would perhaps be about as common as those now called R. Each new arrival would perhaps find it harder to reach VC, and take longer to do it.



(Appearance of new species) (Extinction of old species)

Now, of the species that thus start to climb, it cannot be said that they begin with the certainty of reaching any definite point, such as RC, for as they climb they may come under the influence of new factors which may make great differences. A species that looked as if it was going to reach C may be compelled to stop at RR. The element of chance must be enormous, though natural selection is probably the ultimate deciding factor in the position finally reached.

Ultimately, however, each species will reach a maximum height on the curve. It may stay there a long time, or may go up or down with the appearance on the scene of new factors affecting it. But as a good many of the newer species which come into being and climb the curve will tend to be a little better adapted* than those that preceded them, we may take for granted that in the great majority of cases the species, however high it may have climbed, will ultimately begin to descend.

Now, if the zenith reached has only been VR, which, we may take it, will be the case with about a sixth of the species—whether owing to poor degree of adaptation, or simply to ill chance, or late arrival on the scene—the species will always be in a precarious position. For example, a serious fire on the summit of Ritigala, or a forest clearance for planting on the summit of Hinidunkanda, in Ceylon, would in all likelihood exterminate four or five species. How many have thus been

* On the average perhaps half will be better, half worse, adapted than the average of their forerunners.

exterminated we have no means of knowing, but it does not seem *a priori* probable that it must have been many, as we may infer from the figures in this paper that species increase or decrease in commonness at a very slow rate under natural conditions, and we have also seen that there is probably little difference in adaptation to local conditions amongst them. But the point is, that while at VR or below it, either on the upward or downward journey, the species is liable to extinction.

Species that have reached the stage R will be much safer from this liability to extinction, and those that have got to RR safer still, and so on in increasing certainty up the series of stages. But in all likelihood a number of good species, well enough adapted to have reached above the average, will be exterminated at the stage VR on their upward path.

Reaching its zenith on the curve, then, and remaining there for a longer or shorter time, a species will sooner or later begin to descend on the other side, and ultimately will reach VR.* Now, if there has been nowhere any serious lack of local adaptation, or serious local mischance, the species will, as it descends the scale, tend to more or less shrink its area in such a way as not to leave unoccupied gaps therein. But if it is, for example, VC in several countries, and R or VR in one or two countries lying among these, then, if the same causes of descent are operating in all, it may tend to disappear sooner in some than in others, and so give a disjointed area.

Once the species reaches VR or below that point, it runs the risk of being any day exterminated, just as it did when passing that point on the upward curve, and sooner or later, in the case of a descending species, it will die out.

The killing out of the species at the stage of VR or below it, with the death of those which are so badly suited to the local conditions that they go along the line AZ, will tend to widen the gaps between the survivors, so that at last not only will genera (in some cases) be formed, but also families, and larger groups. But as we have already pointed out, these, or, at any rate, genera, may also be formed by single mutations on the upward curve.

Instead of the old view that the ancestral forms of the now existing species are all extinct, we must now take the view that there is no very particular reason why they should not exist on the earth at this present moment. As to which species is the ancestor of which we can only sometimes hope to be able to give a definite well-founded opinion, but there can be little doubt that we shall someday find out the principles on which evolution works, sufficiently well to be able to commence breeding new species.

The adoption of this view renders the time necessary to evolve some of the families of plants at present existing distinctly less than on the old theory, and the new view has this additional point to recommend it. As most of the families of plants now existing occur in both hemispheres, they are probably very old. But they were not

* In a subsequent paper it will be shown that there is little evidence that any species are dying out.

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then necessarily families ; that has perhaps come about by superposition of mutations, and dying out of types.

Geographical Distribution in General.

We may now go on to point out what is one of the most important bearings of the facts that have been brought forward, and which are so striking and consistent that they demand some explanation, even if that which I have given be not accepted. In a paper published over seven years ago,* I pointed out the effect upon the current theories of geographical distribution which an acceptance of mutation without natural selection would have. I then chose the Dilleniaceæ for no other reason than that it was the first order in HOOKER'S Indian Flora with distribution less than world-wide. In the present place I take the Menispermaceæ because the monograph in ENGLER'S 'Pflanzenreich' happens to be lying on my table. Nearly all families have the same general type of distribution.

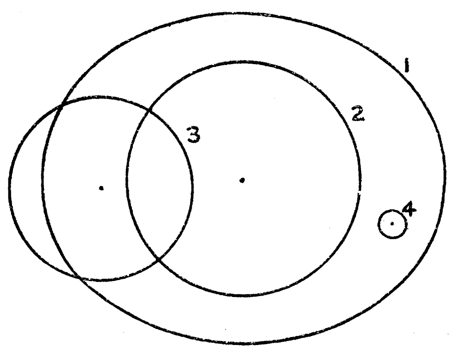
In the paper referred to, I pointed out that there was no particular reason why the whole tree of descent of a family should not exist on the earth at the present moment, and I suggested that all the Dilleniaceæ might be descended from Tetracera, the most widely distributed genus in the family. This idea that the most widely distributed genera are the most primitive, rather than necessarily the best adapted, receives great support from the facts which have been brought forward in the present paper.

It is true that these facts have chiefly been used to show that local commonness, on the whole, increases with age, but as the commonest species are those of wide distribution, the next commonest those developed somewhere in Ceylon and Peninsular India, and the least common those confined to Ceylon, we may take it as extremely probable that wide distribution also goes with commonness, and therefore with age. It hardly needs pointing out that quite possibly some of the species that are now of wide distribution originated in Ceylon in very early times. The Ceylon endemics have not yet nearly reached the stage of average distribution ; only, perhaps, when they have become so old that the difference in age between them and the other species has become negligible, will they do so. The facts of distribution would seem to indicate that the time still required to reach average dispersal would be at least as long as the average time between the arrival of the widely distributed species and those also found in Peninsular India, whatever time that may have been. As the Ceylon endemics climb the scale some of the widely distributed species will be forced to descend.

One may, perhaps, imagine that the various species that occur in Ceylon will all the time be becoming more and more accustomed to the local conditions, by natural selection acting on fluctuating variation, but in any case this cannot amount to much, or cause any structural differences between them.

* "The Geographical Distribution of the Dilleniaceæ, as Illustrating the Treatment of this Subject on the Theory of Mutation," 'Ann. Perad.,' vol. 4, p. 69 (1907).

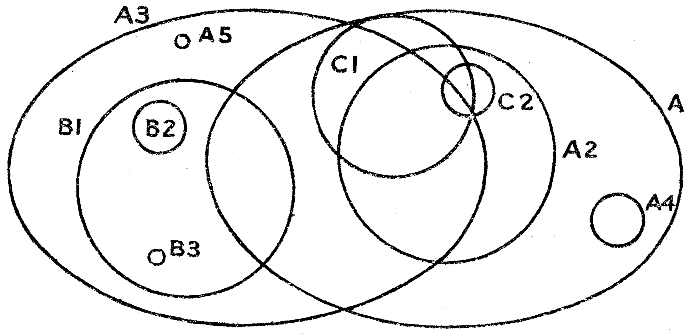
It being, then, assumed that not only, on the whole, do age and commonness go together, but also age and wide distribution, we may now proceed to follow out the probable course of development of the different systematic groups. According to the hypothesis proposed in my former paper, taken together with the interesting facts which have been set out in the present contribution, a species probably starts on a small area as one or more individuals, and from that area spreads by aid of its dispersal mechanism. Under the influence of natural selection, modified very much at first (*i.e.* in the earlier stages) by chance, but less in proportion later, the species will spread, gradually occupying a larger and larger area of the earth's surface, so long as there remain places suited to it within reach. Sooner or later, in perhaps a large proportion of the cases, it will give rise somewhere or another to another species, which again will commence as a single one or as a few individuals in a definite spot. If this spot were always near the centre from which the original species started, we should on the average, after some time, get a series of concentric circles, representing the various species developed, the largest circle representing the oldest species. But in actual fact we know that new species may develop, as they must have developed in Ceylon, near to the margin of the area occupied by the parent species. Further, while each new species on the average will be at approximately the same degree of adaptation as its forerunners, this will rarely happen exactly in any individual case, nor will the effects of chance be the same, so that the size of the area occupied will, in comparatively few cases, indicate the exact age of the species as compared with others of the same genus or family.* It will generally happen that no two species are exactly alike, and consequently that while the "circle" of species 2 will for a long time be enclosed in that of species 1, it may sometimes exceed it all round, or overlap it at one place, where the conditions of life suit 2 but not 1. Also, obviously, as the circles spread, the mere effect of climate will tend to make them spread more to east and west than to north and south. We may thus presently get a distribution diagram something like the following :—



We have seen above that the origin of genera appears to be similar to that of species, and in the gradual dispersal of a family it is obvious that that of the

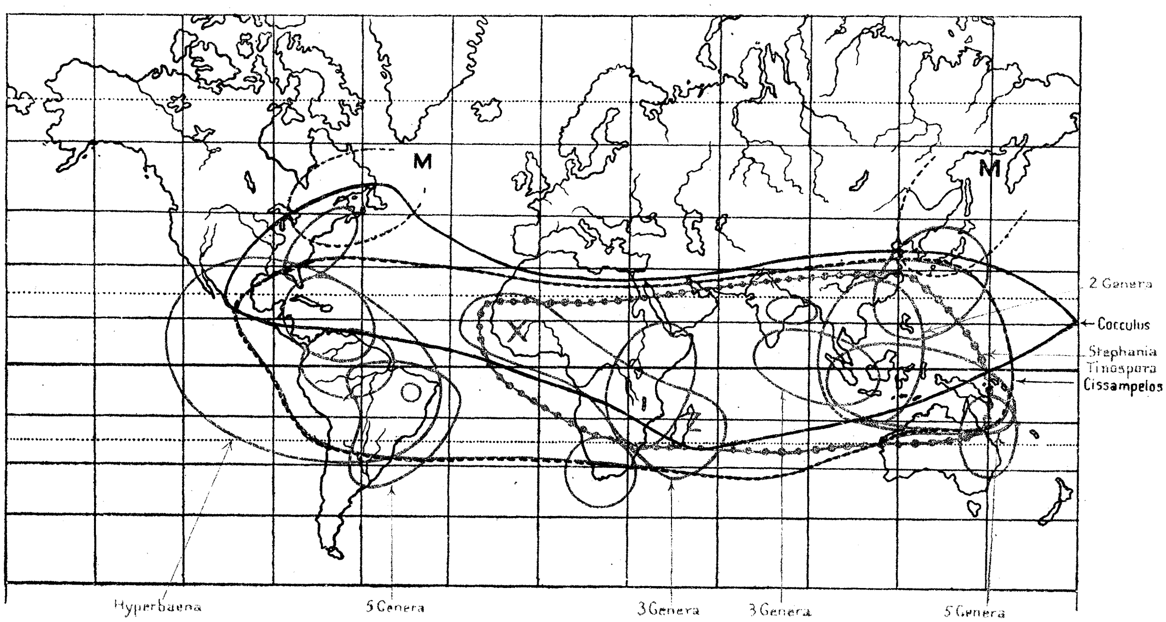
* And, of course, a species will some day occupy a maximum area beyond which it will not go.

genera* will follow the same rule as that of the species, so that, after a time, the family, now supposed to contain three genera, may show such a distribution as the following :—



Of course, in actual fact, the dispersal will not be so simple. Even in one country, the climate and other conditions will vary from place to place, so that the actual distribution can very rarely be a circle or even an ellipse, unless just at the start in such a flat country as Russia. As the forms spread, their dispersal will be altered by geographical obstacles such as chains of mountains, arms of the sea, etc., and geological changes will also affect it. But the underlying principle will remain the same.

Now, when one comes to examine the distribution of almost any order, one finds that it may be very well explained on such principles. I have here taken the Menispermaceæ, but the distributions already given of the Dilleniaceæ and Podostemaceæ, etc., in other papers agree perfectly well with it, and, in fact, so do most orders. The following rough map gives sufficient to show the general outline of the dispersal of this family.



Geographical Distribution of Menispermaceæ in outline.

At **X** (West Africa) 12 genera. At **Z** (Madagascar) 5 genera. M = Menispermum.

* Genera will obviously tend to follow the age and area rule more closely than species.

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The map here given shows that two genera, Cocculus and Cissampelos, have a distribution which is almost exactly that of the order, though each overlaps the other to some slight extent in some places. One or other of these genera, on my hypothesis, is to be regarded as the original ancestor of the existing Menispermaceæ; it is noteworthy that they both belong to the same tribe, the Cocculeæ, and are chiefly distinguished in their respective sub-tribes by a mere difference in the number of the carpels, a matter which might easily be the subject of an early and simple mutation.

These genera, and probably Menispermum, which occurs on the eastern sides of Asia and North America, as do so many genera, must have commenced when there was still a possibility of reaching both the great land masses. Later, or at least not in time to spread from one of the great continents to the other, came the genera Stephania and Tinospora in the eastern, and Hyperbæna in the western, continent, and, subsequent to these again, the groups of genera which are roughly indicated on the map, *e.g.*, three genera occurring from West Africa to Madagascar, five genera in the Malay Archipelago, five in Brazil, and yet later the groups of genera that are confined to one locality, *e.g.*, 12 in West Africa, 5 in Madagascar, 1 in North East India, and so on.

There is nothing surprisingly new about these views, but in 1907 was the first time, to my knowledge, that they were put forward in so many words, and a proper understanding of them will make a great difference in the handling of problems of geographical distribution. Hitherto, we have assumed that the distribution of a genus was largely determined by its degree of adaptation, and, still more important, we have assumed that the appearance of two or more new genera has meant the disappearance of ancestral forms, so that it became a matter of extraordinary difficulty to trace the history and distribution of any family. But if we admit that one species or genus may arise directly from another by means of mutation, and also admit that natural selection has but little value, so that there is no reason why the parent form should be killed out (almost a necessity with the old theory), we simplify enormously the dealing with the problems of geographical distribution, and get a standpoint for treatment which will greatly help us in determining the relationships of species, genera and other groups.

I hope to follow this paper with others, in which I shall deal at greater length with various problems which have only been touched upon here, and especially with adaptation. This paper, it seems to me, makes a step upon the road to a sound common-sense non-teleological theory of evolution. It is very difficult to escape from teleology and even now far too much stress is laid upon adaptation. The figures given in this paper, showing that all families are much alike, will help to check this. When one comes to look into it, there is really very little special adaptation in plants, and once that a plant has specialised into root, shoot, leaf, inflorescence, and flower, further specialisation goes for very little, except in special cases. Xerophytes are more or less specialised for dry climates, hydrophytes for wet places, but the vast majority of plants are mesophytes, and within the range of temperature to which they are suited, one will do about as well as another in any given place, provided both come from somewhat similar climates, etc.

The present paper goes to show for the first time that evolution itself, as has already happened to breeding, can be brought within the range of arithmetic, and that the processes that accompany the dispersal of species and genera about the globe can be expressed in simple terms, without serious complications arising from different "adaptations." In a later paper I hope to bring forward the tentatives towards a theory of evolution which are suggested by the work in this paper and in a previous one upon lack of adaptation in Podostemaceæ.

Summary.

Ceylon contains 149 families, 1027 genera, and 2809 species of flowering plants; 91 families and 324 genera (of which 23 are endemic) contain 809 endemic species. Six families with 7 species have all species endemic; 4 families with 91 species out of 102 have over 75 per cent., and 14 with 255 out of 435 have over 50 per cent. of their number endemic.

Trimen divides these according to rarity into six classes: Very Common, Common, Rather Common, Rather Rare, Rare, Very Rare (Table II). Marking these from 1 to 6, the mean rarity is 3·5. Dividing the flora into three groups: Ceylon (809 sp.), Ceylon-Peninsular India (492), and of wider distribution (1508), Table III shows that the endemics increase in number from 19 VC to 233 VR, and have rarity 4·3, while the "wides" go in the other direction, with rarity 3. The Ceylon–Indian species are fairly evenly grouped, with rarity 3·5. Multiplying by factors to reduce to one level of commonness (Table IV) under each head of VC, etc. (or taking percentages), brings this out very clearly indeed.

Thus the rarest plants in Ceylon are the local endemics, the next most rare those also common to Peninsular India, and the commonest those of wider distribution.

The rarity of the endemics as a whole is not due to special rarity of any one family. Taking groups of not less than 14 species, it is wonderfully uniform, ranging only from 3·9 (above the average for the whole flora) to 4·9 (Table VI). There is little to choose between one family and another on the average of a reasonable number of species.

This is also shown by comparing the rarities of the whole list of families containing over 20 species, which, with one exception, the Dipterocarpaceæ (47 species out of 48 endemic), runs only from 2·9 to 4·1, or equal distances on either side of the mean. The families with the greater rarity have most endemics, and allowing for this the range of commonness goes over a less distance.

The comparison may also go into the genera. Adding up the species of those that contain species of all three types of distribution (Table IX) we find rarities 4·2, 3·4, and 2·8; in the 47 genera that contain one endemic and one non-endemic species, the rarities are 4 and 2·7 (Tables XII, XIII); in the genera with one species of each

distribution, of which there are seven only, the rarities are 4·8, 3·2, and 3·2. The rule comes out with the regularity of MENDEL's law.

Incidentally, a comparison of the species that occur in the dry zone, in the wet zone, or in both, shows that the two former have rarities of 3·8, the latter of 2·3.

From these interesting figures one may conclude that the local endemic species have not been developed in any kind of advantageous response to local conditions. They are much rarer than those species which are also common to Peninsular India, and these again than those of wider distribution. The endemics increase in number to VR, the species of wide dispersal towards VC. There has been ample time to become VC if really adapted to local conditions, yet only 19 out of 809 have done so. The endemic species in families that have many are rarer than in families that have few. Natural selection requires that many forms shall modify in the same direction, and this cannot have been the case with many of these forms, which only occur as a very few individuals in a very restricted area.

The endemic genera (23 in number) have 52 species with a mean rarity of 4·5, or greater than that of the endemic species as a whole (Tables XVII–XIX). The genera of one species among them are the commonest, while Doona with 11 species shows a rarity of 4·6, and Stemonoporus, with 15, one of 5·4. These facts cannot be explained on any theory of adaptation.

Table XX shows these facts summarised, and goes in the exact reverse direction all through to what it should follow if the theory of natural selection could be relied upon.

The second conclusion drawn is that on the average the commonness of a species depends upon its age from the time of its arrival in, or evolution in, the country. The commonness of any individual species will, of course, also depend upon its degree of adaptation to local conditions, and upon many things which can only be regarded as chance, such as the sudden appearance of new factors, like diseases, etc., in the problem.

In other words, on the average, species are developed quite indifferently to local conditions, though it is possible that they may be developed because of those conditions.

As examples of the possible use of these statistical methods, it is then shown that the evidence on the whole favours, so far as Ceylon is concerned, the theory of the greater age of the Dicotyledons than of the Monocotyledons, and that the Rubiaceæ with fleshy fruit are rarer than those with dry fruit, from which they are usually supposed to have been derived, and that consequently their "adaptation" to dispersal by animals has proved of no value to them except in special cases.

The possible size of mutations is then considered, and it is proposed as an hypothesis that no specific difference is too "large" to appear as a single mutation. There is no reason to suppose that the well-separated species of the Ceylon genera with many endemics owe their separation to the destruction of intermediate types.

Sub-genera and genera may apparently arise in the same way as species by one step, and the distinctions drawn between Jordanian and Linnean species, sub-genera, genera, etc., seem to be to a large extent artificial, though in the highest degree convenient in practice.

There seems to be no evidence that the same mutation must go on appearing in order to become established. Many of the Ceylon endemics are represented by a very few plants, and cannot ever have had more.

It is probable that species first appear as one or a few individuals by a sudden mutation, in a very restricted area.

The diagram on p. 333 gives an indication of the subsequent history of a species. It may progress straight to extinction, or may rise to one of the stages VR, R, etc. But ultimately better adapted forms will come into competition with it, or other chances will affect it, and it will begin to go downwards on the curve. Finally, it will reach VR, and then or shortly afterwards will become extinct.

Species do not, so far as we can tell, appear in any sort of advantageous response to local conditions, which are the only conditions that matter when they first appear.

Having appeared, a species will, or will not, spread, according to its suitability to local conditions. But this will be enormously affected by chance, especially at the first. However well a species may be locally adapted, it will be very liable to extermination until it has got beyond the degree of commonness represented by VR.

In each locality the ultimate commonness of a species will depend upon its degree of adaptation to the local conditions, and, to a large extent, on chance. But most species can thrive in a considerable variety of conditions, and there is not the slightest reason to suppose that many Ceylon endemics would not thrive over wide areas of the earth's surface, like the very local species *Cupressus macrocarpa* which is now perhaps the commonest Conifer in the sub-tropics.

But the commonness of a species in a given place at any previous period will mainly depend upon its age. There is no evidence that local species are specially adapted to local conditions.

Having reached the maximum height that it is going to reach, a species will ultimately descend, and will sooner or later be extinguished, though there is no evidence that as yet many, or any, species are on the downward road. These disappearances of species will tend to widen the gaps between the survivors, which may also be widened by the superposition of mutations upon one another.

The bearing of the facts here brought up upon the hypothesis of geographical distribution under mutation and without natural selection that I proposed some years ago is then considered. They support very strongly the hypothesis that the whole tree of descent of a family may exist on the earth at the present moment, and that the area occupied is in general an indication of the age of the species or genus, if it has not already attained its maximum.

The Menispermaceæ are taken as an example, as were the Dilleniaceæ, Tristichaceæ, and Podostemaceæ in previous papers, and it is suggested that the family is descended from Cocculus or Cissampelos, the most widely distributed genera which it contains, and whose distribution is very much that of the whole order.

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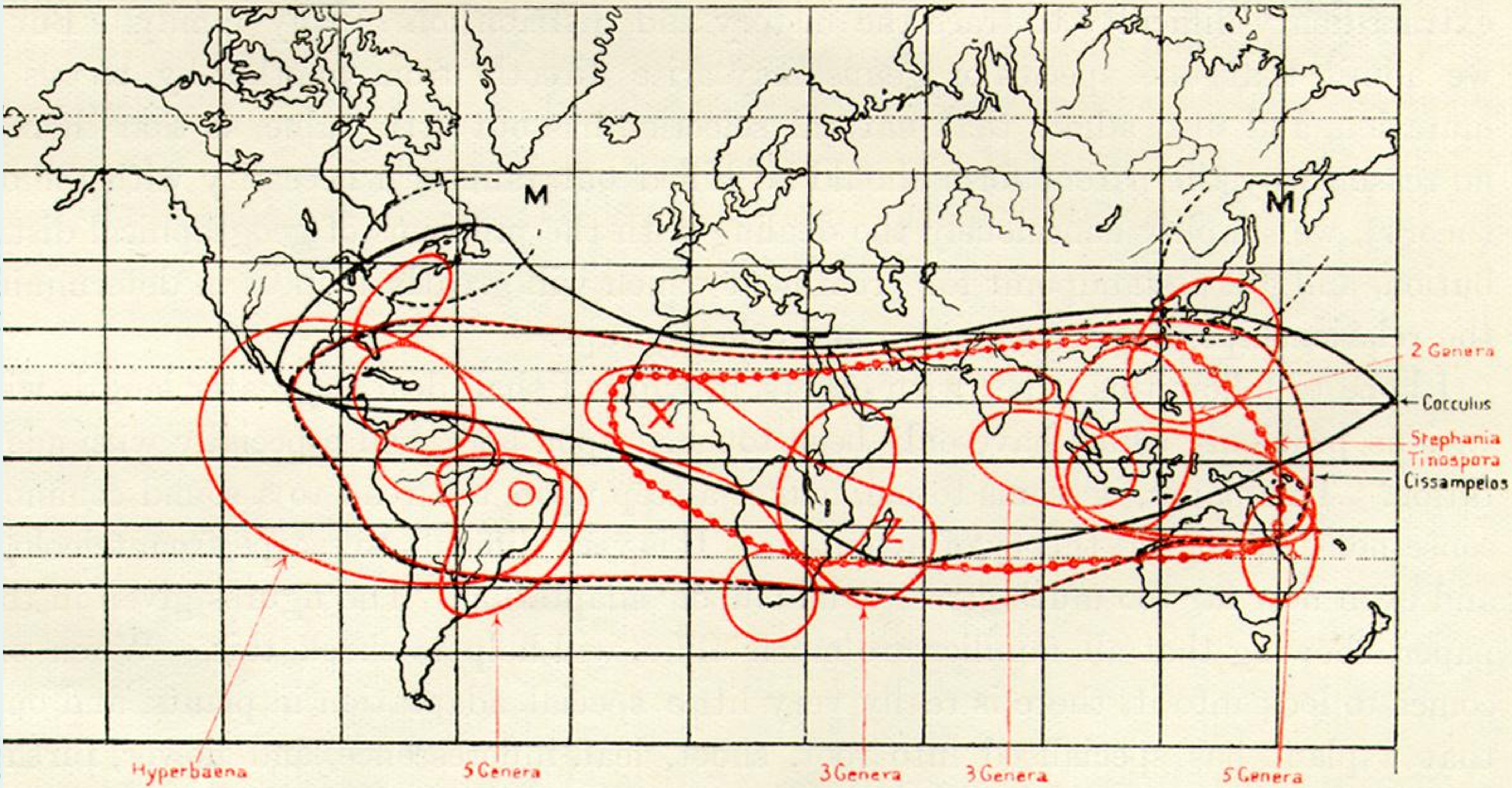

Geographical Distribution of Menispermaceæ in outline.

At X (West Africa) 12 genera. At Z (Madagascar) 5 genera. M = Menispermum.

* Genera will obviously tend to follow the age and area rule more closely than species.

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