

# The Floras of the Outlying Islands of New Zealand and their Distribution.

BY

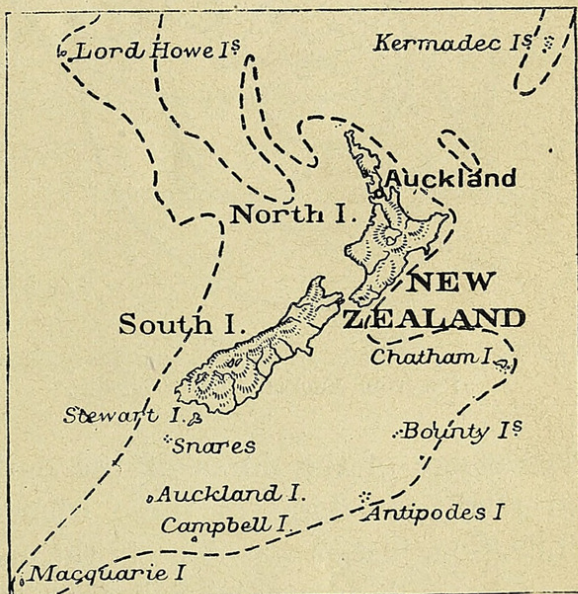
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With two Maps and twenty-one Tables in the Text.

IN this paper I shall deal chiefly with the smaller islands that lie at some distance from New Zealand, but on the same submarine plateau, especially with the Kermadecs, Chathams, and Aucklands, following up the work on the taxonomic distribution of the New Zealand flora given in a series of preceding papers (6 to 11). In one of these (8) I have already shown that one may prophesy, with the aid of age and area, that the plants that reach these islands will on the whole be the oldest, and therefore the most widespread, in New Zealand, and find, on examination of the facts, that the prophecy is completely borne out.

My authority for the floras continues to be in the main Cheeseman's New Zealand Flora (2), supplemented by his later lists in Chilton's 'Subantarctic Islands' (3), and by Cockayne's lists (4). As I have already pointed out, the detailed completion of a flora makes but slight differences in the final result. This was very strikingly shown in the additions to the Ceylon flora made in a short paper subsequently published (13), and in those to the flora of Stewart Island given in the appendix to my last paper (11). In neither instance was any serious difference made by the addition in the one case of 110, in the other of 71, further species. By

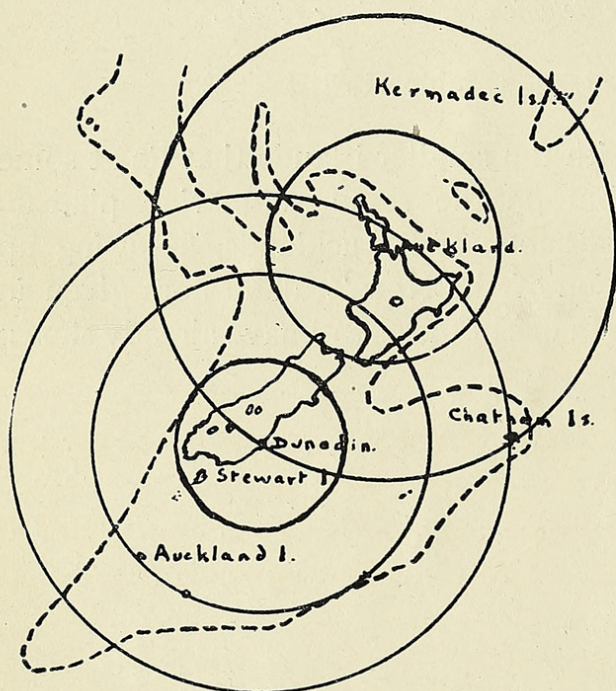


New Zealand and outlying islands. The dotted line is the 1,000 fathom limit.



keeping to the larger floras and papers it must not be forgotten that I gain the very considerable advantage of dealing with a flora worked up by one or by a few persons, and consequently one which is fairly uniformly treated in its conception of specific forms, &c.

The second map-diagram of my last paper, reproduced here, represents an imaginary distribution of the plants of the northern and southern invasions of New Zealand already dealt with, and supposed, for the sake of simplicity, to centre in Auckland (city) and Dunedin. A very brief consideration of it shows that while on the whole the plants of Stewart Island will be older in New Zealand itself than the general average of the plants of New Zealand, those of the outlying islands will be on the whole at least as old,



New Zealand and islands to show imaginary distribution from Auckland and Dunedin.

and in most cases probably older, as they would have to start very early from New Zealand to reach the islands before they were cut off. The Kermadecs and Aucklands, however, having been to some extent in the track of invasions, may of course contain species which arrived there too late to reach New Zealand at all, or only just reached it at the last minute before it was cut off. The Chathams, on the other hand, must clearly have received all, or nearly all, their flora by way of New Zealand; no invasion can have passed that way. We shall start from this conception of the great

relative age of the floras of the outlying islands as a fundamental fact, and study the floras of these islands by the method of prediction and verification, just as was done in the case of Stewart.

One will expect to find that there is what one may perhaps term a selection list (the Scottish term 'short leet' exactly expresses it) of the (in New Zealand) older families, from which Stewart as the nearest island will select practically all, while the more outlying islands will have fewer of them. But the families of these islands should be all included in the Stewart list, unless they be the later arrivals of the northern or southern invasions, or families which have their maximum development in the centre of New Zealand, from which it is less distance to the Chathams than to Stewart.



Now if Natural Selection were the determinant, one would hardly expect, when one considers the extremely different climatic, geological, and other conditions of these widely separated islands, that they would, so to speak, choose their floras from just the same families. One would anticipate finding considerable differences between them, and that more of the other important families of New Zealand would occur, or that the islands would contain relicts belonging to some of the less important families in New Zealand.

(1) We shall therefore expect to find that the islands have *proportionately* more in common with Stewart in the matter of families than with New Zealand proper.

TABLE I.

<i>Occurring in</i>	<i>Aucklands.</i>	<i>Chathams.</i>	<i>Kermadecs.</i>	
	3 <sup>2</sup>	4 <sup>8</sup>	37	} of 91 New Zeal. fams.
	35 %	52 %	40 %	
	3 <sup>2</sup>	4 <sup>1</sup>	28	} of 60 Stewart fams.
	53 %	68 %	46 %	

Thus all the islands, even the Kermadecs, contain a considerably higher percentage of Stewart families than they do of New Zealand families. All the Auckland families occur in Stewart, 41 out of 48, or 85 per cent., of the Chatham families, and even 28 out of 37, or 75 per cent., of the Kermadec families.

(2) We shall expect to find that a large part of the families in the different islands are the same, and that most of them are selected from the Stewart list. The following table gives, in ordinary type, the 60 Stewart families, with the islands in which they occur. Those not occurring in Stewart are printed in capitals.

TABLE II.

<i>Fam.</i>	<i>Spp. in Stewart Island.</i>	<i>Fam.</i>	<i>Spp. in Stewart Island.</i>
Ranunculaceae	10 A C	Droseraceae	4 A
Magnoliaceae	1 —	Haloragidaceae	13 A C K
Cruciferae	3 A C K	Myrtaceae	4 A C K
Violaceae	6 C K	Onagraceae	13 A C
Pittosporaceae	1 K	CUCURBITACEAE	— K
Caryophyllaceae	4 A C	Ficoideae	3 C K
Portulacaceae	2 A	Umbelliferae	14 A C K
Elatinaceae	1 —	Araliaceae	7 A C K
Hypericaceae	1 —	Cornaceae	1 C
Malvaceae	2 C	Rubiaceae	17 A C K
Linaceae	1 C	Compositae	54 A C K
Tiliaceae	4 —	Stylidiaceae	4 A
Geraniaceae	4 A C K	Goodeniaceae	1 K
RUTACEAE	— K	Campanulaceae	3 A C K
RHAMNACEAE	— C	Ericaceae	2 —
ANACARDIACEAE	— C K	Epacridaceae	10 A C
Coriariaceae	2 C K	Primulaceae	1 A C K
LEGUMINOSAE	— C K	Myrsinaceae	4 A C K
Rosaceae	7 A C K	Apocynaceae	1 —
Saxifragaceae	3 —	Loganiaceae	1 —
Crassulaceae	2 A C	Gentianaceae	4 A C



TABLE II (continued).

<i>Fam.</i>	<i>Spp. in Stewart Island.</i>	<i>Fam.</i>	<i>Spp. in Stewart Island.</i>
Boraginaceae	3 A C	Loranthaceae	1 —
Convolvulaceae	3 C K	Euphorbiaceae	1 C K
SOLANACEAE	— C K	Urticaceae	1 A C K
Scrophulariaceae	13 A C K	Orchidaceae	21 A C K
MYOPORACEAE	— C K	Iridaceae	2 C
Lentibulariaceae	1 —	Liliaceae	12 A C K
Labiatae	1 C	Juncaceae	8 A C
Plantaginaceae	3 A	PALMAE	— C K
Illecebraceae	1 —	TYPHACEAE	— K
Chenopodiaceae	2 C K	Naiadaceae	4 C
Polygonaceae	3 A C K	Centrolepidaceae	2 A
PIPERACEAE	— C K	Restionaceae	2 C
Chloranthaceae	1 K	Cyperaceae	44 A C K
Thymelaeaceae	3 C	Gramineae	35 A C K

Thus of the 60 Stewart families, 49 (or 81 per cent.) occur in the other islands, while of the 31 families that occur in New Zealand and do not occur in Stewart, only 10 (or 32 per cent.) occur in the islands. Of these 10, Rutaceae, Rhamnaceae, Anacardiaceae, Cucurbitaceae, Myoporaceae, Piperaceae, Palmae, and Typhaceae, are enumerated in the list of the northern invasion given on p. 356 of 10, and Solanaceae is given as probably belonging to that invasion, so that only Leguminosae remains. This is represented in the Kermadecs by *Canavalia*, a genus that does not occur in New Zealand, and in the Chathams by *Sophora tetraptera*, a species which should in all probability be found on Stewart.

It is thus clear that the prophecy made above is borne out by the facts. A mere glance at the table suffices to show how many of the families occur in two or more groups of islands, and we have seen that most of them also occur in Stewart.

(3) As we have already seen, in dealing with Stewart Island, the largest families (in a given country) will on the whole be the oldest (in that country). We may therefore predict that the families that reach all three groups of islands will on the whole be the largest, both in New Zealand as a whole, and in Stewart. Those reaching two groups will be next in size, and then will follow those reaching only one, and those reaching none. An examination of the facts gives us

TABLE III.

<i>Reaching</i>	<i>The families contain (in New Zealand as a whole),</i>
3 islands.	221, 119, 113, 113, 61, 57, 47, 22, 22, 20, 19, 17, 17,    11, 11, 9, 8, 8, 1.
2 „	50, 31, 31, 26, 25, 25, 20, 17,    15, 12, 10, 10, 5, 4, 3, 3, 2, 2, 1, 1.
1 island.	19,    15, 13, 7, 7, 7, 6, 6, 5, 5, 3, 3, 3, 3, 2, 2, 2, 2, 1, 1.
No islands.	10, 8, 6, 6, 6, 6, 4, 4, 4, 4, 3, 3, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1.

The mark || is placed at the position of the average size of family in New Zealand (15.2 species).

A similar comparison for Stewart Island shows that the size of the families in that island, according to the number of groups they reach, is :



TABLE IV.

<i>Reaching</i>	<i>Size of Families in Stewart Island.<sup>1</sup></i>
3 islands.	54, 38, 30, 21, 17, 14, 13, 13, 13, 10, 7, 7, 4, 4, 3, 3, 3, 1, 1.
2 „	12, 10, 10, 8, 6, 4, 4, 3, 3, 3, 2, 2, 2, 1.
1 island.	4, 4, 4, 3, 3, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1.
No islands.	4, 3, 2, 1, 1, 1, 1, 1, 1, 1, 1.

A mere glance at these figures is enough to show that the prophecy is borne out by the facts; but we may put it in tabular form thus :

TABLE V.

<i>Reaching</i>	<i>New Zealand Families.</i>			<i>Stewart Families.<sup>1</sup></i>		
	<i>Fams.</i>	<i>Spp.</i>	<i>Average size.</i>	<i>Fams.</i>	<i>Spp.</i>	<i>Average size.</i>
3 islands	19	896	47.1	19	256	13.4
2 „	20	293	14.6	14	70	5.0
1 island	20	112	5.6	16	34	2.1
No island	32	91	2.8	11	17	1.5

(4) Just as we predicted in the case of Stewart that the New Zealand families omitted would be on the whole the smallest, so here we may predict that the missing Stewart families will on the whole be the smallest, a prophecy which is clearly borne out by the facts in Tables IV and V.

(5) One will expect the Aucklands to contain many of the families of the southern invasion—they contain all but Naiadaceae. One will expect the Chathams also to contain many; and on the whole to lack the smaller ones. The smallest, those with less than 11 species, are Portulacaceae, Droseraceae, Stylidiaceae, Plantaginaceae, and Centrolepidaceae, and it is exactly these which are missing in the Chathams. The bulk of the invasion, if not all of it, is missing in the Kermadecs.

(6) One will expect the Chathams to contain many of the families of the northern invasion, and perhaps the Kermadecs also, but, as we have already seen (10, p. 358), they do not seem to have lain in the track of the main invasion. Examination of the facts shows that the Chathams contain only 9 of the 33 families, and the Kermadecs 11, while Stewart itself only contains 8 and the Aucklands 3. It is thus evident that old though it was, the northern invasion did not in general get very far south. This may have been due to the species reaching their climatic boundary, in some cases at any rate, though my experience of the surprising degree of cold which many 'tropical' species bear in southern Brazil, and the fact that so many tropical species go very far south in New Zealand, makes me hesitate to say that a species has reached its climatic limit. Given slow enough progress, a species may travel into climates to which it would seem quite unsuitable.

<sup>1</sup> Note the much greater proportion of the Stewart families reaching islands, even three islands. The Stewart families are on the whole older.



(7) One may also predict that the outlying islands will have proportionately many more families in common with one another than they have with New Zealand.

TABLE VI.

	<i>Kermadecs.</i>		<i>Chathams.</i>		<i>Aucklands.</i>		<i>New Zealand.</i>	
Kermadecs in common with	—	—	31	64 %	19	59 %	37	40 %
Chathams „ „ „	31	83 %	—	—	27	84 %	48	52 %
Aucklands „ „ „	19	51 %	27	56 %	—	—	32	35 %

Even the Aucklands have a greater proportion in common with the Kermadecs than any of the islands but the Chathams have with New Zealand.

(8) We may now go on to deal in the same way with the genera, and may begin by predicting that they will be chiefly selected from the list of genera found in Stewart Island. The result of testing this prediction is given in the following table, which gives the Stewart list, with the number of species in Stewart, and the islands in which the genera are found. The genera that occur in the islands and New Zealand and have not been found in Stewart are printed in capitals.

TABLE VII.

Clematis	1	—	Tillaea	2	A C
Ranunculus	8	A C	Drosera	4	A
Caltha	1	—	Haloragis	4	A K
Drimys	1	—	40 Myriophyllum	4	—
Cardamine	1	A C K	Gunnera	4	C
Lepidium	2	A C	Callitriche	1	A C K
Viola	2	C	Leptospermum	1	C
Melicytus	2	K	Metrosideros	2	A K
Hymenanthera	2	—	Myrtus	1	—
10 Pittosporum	1	K	Epilobium	11	A C
Stellaria	1	A C	Fuchsia	1	A
Colobanthus	2	A C	SICYOS	—	K
Spergularia	1	—	Mesembryanthemum	1	C K
Claytonia	1	—	50 Tetragonia	2	C K
Montia	1	A	Hydrocotyle	5	C K
Elatine	1	—	Azorella	1	A
Hypericum	1	—	Actinotus	1	—
Plagianthus	2	C	Apium	1	A K
Aristotelia	3	—	Oreomyrrhis	1	C
20 Elaeocarpus	1	—	Crantzia	1	C
Linum	1	C	Aciphylla	1	C
Geranium	3	A C K	Ligusticum	3	A
Pelargonium	1	C	DAUCUS	—	C
OXALIS	—	K	60 Aralia	1	—
MELICOPE	—	K	Panax	4	A K
POMADERRIS	—	C	Schefflera	1	—
CORYNOCARPUS	—	C K	Pseudopanax	1	C
Coriaria	2	C K	COROKIA	—	C
SOPHORA	—	C	Griselinia	1	—
30 Rubus	3	—	Coprosma	13	A C K
Geum	1	A	Nertera	3	A
Potentilla	1	C	Asperula	1	—
Acaena	2	A C K	Lagenophora	2	A C K
Donatia	1	—	70 Brachycome	2	—
Carpodetus	1	—	Olearia	8	A C
Weinmannia	1	—	Celmisia	7	A



TABLE VII (continued).

	Gnaphalium	4	A	C	K		PARIETARIA	—		K
	Raoulia	3			—		Dendrobium	1		—
	Helichrysum	4	A	C			Earina	2		C
	Cassinia	2	A				Sarcochilus	1		C
	Craspedia	1			—		Thelymitra	2	A	C
	SIEGESBECKIA	—			K		Microtis	1		C K
	BIDENS	—			K	140	Prasophyllum	1	A	
80	Cotula	4	A	C	K		Pterostylis	3		C
	Abrotanella	2	A				ACIANTHUS	—		C K
	Erechtites	6	A	C			Lyperanthus	1	A	
	Senecio	6		C	K		Caladenia	2	A	C
	Microseris	1			—		Chiloglottis	1	A	C
	Taraxacum	1			—		Corysanthes	5	A	C
	Sonchus	2	A	C	K		Gastrodia	1		C
	Phyllachne	2	A				Libertia	2		C
	Oreostylidium	1			—	150	Rhipogonum	1		C
	Forstera	1			—		Enargea	1		—
90	Selliera	1			—		Cordyline	1		K
	Pratia	1	A	C			Astelia	3	A	C
	LOBELIA	—		C	K		Phormium	2		C
	Wahlenbergia	2		C	K		Bulbinella	2	A	
	Gaultheria	2			—		Arthropodium	1		—
	Pentachondra	1			—		Herpolirion	1		—
	Cyathodes	2	A	C			ROSTKOVI	—	A	
	Leucopogon	1		C			Juncus	7	A	C
	Archeria	1			—	160	Luzula	1	A	C
	Dracophyllum	5	A	C			RHOPALOSTYLIS	—		C K
100	Samolus	1	A	C	K		TYPHA	—		K
	Myrsine	4	A	C	K		Triglochin	1		C
	Parsonsia	1			—		Potamogeton	2		—
	Mitrasacme	1			—		Zostera	1		—
	Gentiana	3	A	C			Centrolepis	1		—
	Liparophyllum	1			—		Gaimardia	1	A	
	Myosotis	3	A	C			LEPYRODIA	—		C
	IPOMOEA	—			K		Leptocarpus	1		—
	Calystegia	2		C	K	170	Hypolaena	1		—
	Dichondra	1		C			Eleocharis	3		C
110	SOLANUM	—		C	K		Scirpus	7	A	C K
	Glossostigma	1			—		Carpha	1	A	
	Veronica	5	A	C	K		Schoenus	3		C
	Ourisia	5			—		Cladium	3		C
	Euphrasia	2			—		Gahnia	1		—
	Utricularia	1			—		Oreobolus	2	A	
	MYOPORUM	—		C	K		Uncinia	9	A	C
	Mentha	1		C			Carex	15	A	C K
	Plantago	3	A			180	Ehrharta	1		
	Scleranthus	1			—		Microlaena	2	A	
120	RHAGODIA	—			K		Agrostis	1	A	
	Chenopodium	1			—		Hierochloe	2	A	C
	Atriplex	1		C			OPLISMENUS	—		K
	SALICORNIA	—		C			Deyeuxia	5	A	C K
	POLYGONUM	—		C			Dichelachne	1		C
	Rumex	1	A	C	K		Deschampsia	2	A	C
	Muehlenbeckia	2		C			Trisetum	1	A	C
	PIPER	—		C	K		Danthonia	6	A	C
	PEPEROMIA	—			K	190	Arundo	1		C
	Ascarina	1			K		Agropyrum	1		K
130	Pimelea	1		C			Poa	8	A	C K
	Drapetes	2			—		Atropis	1	A	
	Loranthus	1			—		Asprella	1		—
	Euphorbia	1		C			Festuca	2		C
	Urtica	1	A	C						

Thus we find, on summing up, that while New Zealand as a whole has 329 genera, of which 169 occur in Stewart and 160 do not, 114 of the



former, or 67 per cent., occur in the islands, while of the latter only 26 (the genera in capitals) occur, or 17 per cent., an enormous difference. The prophecy made above is thus fully borne out by the facts.

Further, of the 26, 11 occur only in New Zealand and the Kermadecs, 7 in the Chathams, 7 in both Kermadecs and Chathams, and one only (*Rostkovia*) in the Aucklands and the South Island of New Zealand. This was probably a late arrival of the southern invasion. 15 of the 26 genera belong to families enumerated in the northern invasion (10, p. 356), and all but *Rostkovia* are distinctly northern types, most of which probably took part in the northern invasions.

(9) Just as with the families, we may predict that those genera will on the whole be the largest in number of species, whether in New Zealand as a whole, or in Stewart Island, which reach three of the outlying groups of islands. Then will follow those reaching two islands, one island, and no islands at all. Testing this we find :

TABLE VIII.

<i>Reaching</i>	<i>Gen.</i>	<i>Spp. in Stewart.</i>	<i>Average.</i>	<i>Spp. in N.Z.</i>	<i>Average.</i>
Stewart and 3 groups	17	78	4.5	293	17.2
„ „ 2 „	39	132	3.3	396	10.1
„ „ 1 group	58	99	1.7	294	5.0
„ „ no „	55	74	1.3	162	2.9
Neither Stewart nor other islands	133			204	1.5
Other islands, but not Stewart	27			43	1.5

(10) Just as with the families, one may predict that the islands will have proportionately more genera in common with one another than they have with New Zealand.

TABLE IX.

	<i>Kermadecs.</i>	<i>Chathams.</i>	<i>Aucklands.</i>	<i>New Zealand.</i>
Kermadecs in common with	—	32	21	62
Chathams „ „ „	32	32 %	30 %	19 %
Aucklands „ „ „	51 %	—	44	98
	21	44	64 %	29 %
	33 %	44 %	—	68
				20 %

Again the facts bear out the prophecy.

(11) One may predict that the genera which occur in Stewart and do not occur in the islands will on the whole be the smaller genera of Stewart. The average number of species in a genus in Stewart is 2.2, and of the 55 genera that do not occur in the islands 44 have one species in Stewart Island, six have 2, and the others 3, 3, 3, 4, and 5, or an average of 1.3 species per genus.

(12) We may now go on to the actual species, and predict that these will also be largely selected from the Stewart list. It would occupy too



much space to give the whole list over again (cf. 11, p. 27), but of the 382 species so far recorded from Stewart, no fewer than 153, or 40 per cent., are found in the islands, whereas of the 1,301 species found in New Zealand as a whole, only 199 occur on the islands, or 15 per cent. Thus there are only 46 species on the islands, other than local endemics or species which do not occur at all in New Zealand, which do not occur in Stewart, against 153 which do.

(13) We may predict that the families which occur in Stewart but have no species on the islands will on the whole be small (in Stewart). The average size of a family in Stewart is 6.3 species, and those families that contain no species on the islands contain in Stewart 4, 3, 2, 1, 1, 1, 1, 1, 1, 1 species, or all below the average size in Stewart.

(14) We may also predict in this connexion that the islands will have very many species in common between themselves, and this also proves to be the case. The Kermadecs have a total flora of 71, of which 19 occur nowhere else, leaving 52, of which 30 occur in the Chathams and 5 in the Aucklands. The Chathams have a total flora of 152, of which 27 occur nowhere else, leaving 125, of which 30 occur in the Kermadecs, and 32 in the Aucklands. The Aucklands have a total flora of 119, of which 44 do not occur in New Zealand, leaving 75, of which 32 occur in the Chathams and 5 in the Kermadecs.

(15) We may predict that the species in common between the islands, or between the islands and Stewart, will show a greater proportion of wides (which on the whole are older than endemics), the more the islands on which the species occur.

TABLE X.

	<i>Wides.</i>	<i>Proportion.</i>	<i>Endemics.</i>	<i>Proportion.</i>
3 islands and Stewart	4	80 %	1	20 %
2 " " "	27	64 %	15	36 %
1 " " "	43	41 %	61	59 %
No " but "	57	24 %	174	76 %
Not even reaching Stewart	170	18 %	749	82 %

The proportions decrease and increase, respectively, with regularity.

(16) We may now go on to some slightly more general predictions, and say that as on the whole the islands were probably cut off earlier than Stewart, their plants will on the whole be older, and should therefore show a greater proportion of families to genera and genera to species.

TABLE XI.

	<i>Families.</i>	<i>Genera.</i>	<i>Gen. per fam.</i>	<i>Species.</i>	<i>Spp. per gen.</i>
Islands	55	130	2.3	199	1.5
Stewart	60	169	2.8	382	2.2
New Zealand	91	329	3.6	1392	4.2

(17) We may make the same prediction with regard to the islands as the second made with respect to Stewart on p. 34 of 11, that on the whole



the more genera in a family the older the family will be, and therefore the better represented.

TABLE XII.

<i>Fam. repres. in N.Z. by</i>	<i>In N.Z.</i>	<i>In Stewart.</i>	<i>In islands.</i>	<i>Not there.</i>
1 genus	36	16	15 41%	21
2 genera	15	7	10 66%	5
3 „	15	13	10 66%	5
4-5 „	10	10	10 100%	—
6-10 „	9	8	8 90%	1
over 10 „	6	6	6 100%	—

(18) Similarly we may repeat the prediction (3) on the same page, and say that the same thing will be true with regard to the genera. This also proves to be the case, the proportions of genera that occur being 21, 35, 58, 55, 66, 68, and 80 per cent., a progressive table, save for the one slight drop from 58 to 55 in the middle.

(19) We may go on to predict that the plants reaching 3 groups of islands, New Zealand, and Stewart, 2 groups, 1 group, Stewart only, and the main islands of New Zealand only, should show a progressive decrease in the average size of families and genera.

TABLE XIII.

<i>Reaching</i>	<i>Aver. size of fam.</i>	<i>Aver. size of genus.</i>
3 islands	88	6 <sup>1</sup>
2 „	42	13
1 „	29	7.8
Stewart only	18.5	6.8
N.Z. as a whole	15	4.2
N.Z. only	2.9	1.5

(20) All the predictions we have made with regard to the flowering plants should also hold in the case of the ferns, and a very cursory examination shows that they do, so that it would be a work of supererogation to go into details; but we may predict that as the ferns are on the whole an older group than the flowering plants, those of the flora of Stewart will be on the whole better represented. Examination shows that no less than 64 per cent. of the ferns of Stewart are represented on the islands, against only 40 per cent. of the species of flowering plants.

There are other predictions that might be made with regard to families, genera, and species, but we must go on to other more general features, and may begin with the species endemic to the islands only, which are fairly numerous.

(21) Upon the hypothesis of Natural Selection one might expect that some of these endemics at any rate would be relicts. If this were so, one might surely expect to find some of them occurring upon two of the groups of islands and not in New Zealand; they might have spread to these

<sup>1</sup> Only 5 genera with 30 species, too small a number for a reliable result.



islands in early times, and have since been killed out in the more crowded main islands of New Zealand. But in actual fact we find that there are none with such a distribution; all that occur in the Kermadecs and Chathams, or Chathams and Aucklands, occur also in New Zealand, as would be expected on the hypothesis of age and area. There are a good many which occur in the Aucklands and some of the other islands in the same stretch of sea (Campbells, Antipodes, and Macquarie), but none that occur in two of the main groups of islands and not also in New Zealand.

(22) One will expect the endemics to belong on the whole to the oldest, i.e. in general to the largest, families and genera in New Zealand. They belong in fact to Ranunculaceae, Caryophyllaceae, Geraniaceae, Rosaceae, Umbelliferae, Cornaceae, Rubiaceae, Compositae, Epacridaceae, Myrsinaceae, Gentianaceae, Boraginaceae, Scrophulariaceae, Plantaginaceae, Chloranthaceae, Urticaceae, Liliaceae, Juncaceae, Palmae, Cyperaceae, and Gramineae, 21 families, which contain in New Zealand and the islands as a whole 939 species, or 44 species per family, whilst no endemics occur in the other 70 families of the New Zealand flora, with 453 species (average 6.4 per family), except in the genera *Scaevola*, *Homalanthus*, and *Boehmeria*, which occur in the Kermadecs, but not in New Zealand.

Grouping all the families of New Zealand in order of size, we find that 52 endemics occur in 8 of the first 10 families, 10 in 5 of the second 10, and 3 in the other 2 families which are above the average size, or 65 endemics in all in families which are above the average in size, whilst 8 only occur in all the 68 other families which are below the average in point of size.

In the same way, 60 endemics belong to 25 genera which are above the average, and 13 to 11 genera which are below it.

(23) Being, on our supposition, very old genera, all the genera which contain endemics confined to the islands, unless possibly some of the later ones of the invasions, should occur in Stewart. Three genera occur in the Kermadecs only, and are not found in New Zealand, so that they may be looked upon as genera which arrived in those islands from the north too late to reach New Zealand, and three are endemic genera of the islands. All the remaining genera, except *Corokia* and *Rostkovia*, that contain island endemics, occur in Stewart. *Corokia* is a distinctly northern type, and the endemic occurs in the Chathams; *Rostkovia* probably a late arriving southern type, whose endemic occurs in Campbell.

It is thus clear that, just as in Stewart Island, the endemics of the islands belong chiefly to the 'successful' families and genera of New Zealand. The families are given above, and the actual genera are *Ranunculus* (4 endemics), *Stellaria*, *Colobanthus*, *Geranium*, *Geum*, *Azorella*, *Aciphylla* (2), *Ligusticum* (3), *STILBOCARPA*, *Pseudopanax*, *Corokia*, *Coprosma* (4), *Olearia* (4), *PLEUROPHYLLUM* (3), *Celmisia* (2), *Cotula* (3), *Abrotanella* (2), *Senecio* (2), *Sonchus*, *Cyathodes*, *Dracophyllum*, *Myrsine* (3), *Gentiana* (5),



*MYOSOTIDIUM*, *Veronica* (4), *Plantago*, *Ascarina*, *Urtica*, *Bulbinella*, *Rostkovia*, *Carex* (2), *Imperata*, *Hierochloe*, *Deschampsia* (2), *Poa* (7), *Festuca* (2). Those which have no number against them are represented by one species only, and those in capitals are endemic genera of the islands only. No one can look over this list of genera, and honestly suggest that it represents a set of relicts. Many are genera of world-wide distribution, and all are common, except the three endemic genera, with 5 species, which represent most of the species which might perhaps be looked upon as relicts.

(24) We have seen (10, pp. 358, 361) that the northern invasion of New Zealand was nearly all tree-like, the southern herbaceous. We shall therefore expect the proportion of trees to be greatest in the endemics of the northern islands, of herbs greatest in the southern. In actual fact, the Kermadecs have 7 endemic shrubs and trees and 2 herbs (both Monocotyledons), the Chathams have 13 shrubs and trees and 12 herbs (4 Monocotyledons), and the Aucklands 3 shrubs and trees only against 27 herbs (7 Monocotyledons), whilst in the Campbells there are 3 shrubs, in the Antipodes 1, and in Macquarie none. This bears out the prophecy completely, and it may also be pointed out that the three endemic genera of the islands are composed entirely of herbs (*Stilbocarpa*, *Pleurophyllum*, *Myosotidium*), a fact which does not harmonize well with Prof. Sinnott's suggestion that endemics are relicts and herbs the youngest forms.

It is clear, from the success of the 24 predictions above given, that, just as in the case of Stewart Island, it is hardly conceivable that the outlying islands should have received their floras by casual transport across the intervening seas. There must have been connexion by land at some time. When one works out their species one by one, it is fairly clear that a few—at most hardly exceeding, if they even equal, 10 per cent.—may have been carried by water or by birds, but the great bulk must undoubtedly have arrived by land. In no other way could the great similarities between the islands, or between the islands and Stewart, have come about. No casual transport could give results like those above, nor would it occur that the island endemics belonged almost solely to the larger families.

#### THE KERMADEC ISLANDS.

We must now go on to consider in brief some of the relations of the islands to one another, and to New Zealand and its probable invasions of plants (10, p. 355). Let us begin with the Kermadecs. They have altogether, according to Cheeseman, a flora of 71 species, made up thus:

TABLE XIV.

Dicotyledons	31 families	47 genera	56 species
Monocotyledons	6 „	15 „	15 „



Of these 62 genera and 71 species, there do not occur in New Zealand at all, in addition to the local endemics of the islands (belonging to genera of New Zealand), no less than 8 genera and 8 species, viz. *Canavalia obtusifolia* (cosmotropical), *Ageratum conyzoides* (cosmotropical), *Scaevola gracilis* (Kermadecs only), *Aleurites moluccana* (trop. Asia), *Homalanthus polyandrus* (Kermadecs only), *Boehmeria dealbata* (ditto), *Panicum sanguinale* (cosmotropical), *Cenchrus calyculatus* (Polynesia). Besides these there occur in these islands *Metrosideros villosa* (Polynesia), *Coprosma petiolata* and *acutifolia* (endemic), *Myrsine kermadecensis* (ditto), *Ipomoea biloba* (cosmotropical), *Ascarina lanceolata* (endemic), *Cordyline terminalis* (Polynesia, Indomalaya), *Rhopalostylis Baueri* (Norfolk I.), *Imperata Cheesemanii* (endemic), *Eleusine indica* (trop. Asia), and *Poa polyphylla* (endemic), 10 genera in all with 11 species, the genera, but not the species, occurring in New Zealand.

Now as these species, which do not occur in New Zealand proper, are either endemic to the Kermadecs, or common to the Kermadecs and Polynesia, it would seem probable that the Kermadec Islands received part of their flora not by way of New Zealand, but by way of the ridge which runs north from these islands to Tonga and Fiji, or at any rate from some part of Polynesia.

Subtracting these from the total of the Kermadec flora leaves only 52 species found there which actually occur in New Zealand, and it is of interest to trace out their distribution there. Twenty-five belong to Class 1 in order of rarity, ranging New Zealand (including Stewart) from end to end, and of these no less than 20 reach the Chathams also, and 5 the Aucklands as well. It may be noted that the 5 which have not been recorded from the Chathams are *Meliccytus ramiflorus* (tree), *Haloragis alata*, *Tetragonia expansa*, *Apium prostratum*, and *Agropyrum scabrum* (herbs). A further 13 belong to Class 2, ranging from North Cape to Foveaux Strait, and of these only 6 reach the Chathams, a much smaller proportion, corresponding to the generally lesser age. With regard to these species, 38 in all, it seems to me almost impossible at present to make any safe deductions as to whether they reached New Zealand by way of the Kermadecs, or vice versa.

There remain 14 species with less range, all of which range northwards to North Cape. Several of these belong to genera which are otherwise unrepresented in New Zealand, e. g. *Piper excelsum* (Polynesia, Class 3) *Corynocarpus laevigata* (K. and N. Z. only, Class 4), *Oplismenus undulatifolius* (K. and N. Z. only, Class 4), *Sicyos angulata* (Polynesia, Class 5), *Acianthus Sinclairii* (K. and N. Z. only, genus New Caled., Class 5), *Rhagodia nutans* (Australia, Class 6), *Siegesbeckia orientalis* and *Bidens pilosa* (palaeotropical, Class 7), *Peperomia Endlicheri* (Lord Howe Island, Norfolk Island, Class 7). These species it would seem justifiable to regard as having entered New Zealand by way of the Kermadecs.



There remains one species in Class 9, *Ipomoea palmata*, which ranges about 80 miles from North Cape. The only other species of *Ipomoea* in this region, *I. biloba*, occurs only in the Kermadecs. It is fairly clear from the very short range that *I. palmata* probably did not reach New Zealand from the Kermadecs by land. It is more probable that it has only comparatively lately, so to speak, arrived, and by water carriage. There are hundreds of miles of the northern coast on which it would in all probability be equally at home.

It is thus fairly evident that while a large part of the flora of the Kermadecs was in all probability derived from New Zealand, it is at least extremely probable that some of it was derived directly from some part of Polynesia, probably by way of the Tonga-Fiji ridge. This supposition is confirmed by the behaviour of the ferns, already pointed out (9, p. 341). A number of Polynesian ferns appear to have entered New Zealand by way of the Kermadecs, and in New Zealand only range part of the length of the islands.

When we come to compare the Kermadec flora with that comprised in the northern invasion (10, p. 356), and find that 22 of the 33 families are missing, it seems hardly possible, in view of what we now know about the rarity of dying out among flowering plants at any rate, that the northern invasion passed by way of the Kermadecs. On the other hand, we have seen that the only members of Anacardiaceae, Cucurbitaceae, and Piperaceae, three of the 33 families enumerated in it, probably passed to New Zealand by way of the Kermadecs. It would seem therefore probable that these three families should be excluded from the list of the northern invasion proper, and should be classed, together with the other plants mentioned above (*Siegesbeckia*, &c.), as a second northern (Kermadec) invasion.

From the extreme regularity of the distribution of the Kermadec plants in New Zealand (except the conspicuously different *Ipomoea palmata*), one is obliged, it seems to me, to conclude that there was at one time a land bridge connecting the two.

We also know (10, p. 358) that the northern invasion was mainly (84 per cent.) trees and shrubs. Examination of the Kermadec flora, however, shows that it contains 45 herbs and only 26 shrubs and trees. The latter thus form only 36 per cent. of the flora, a very different proportion from that in the northern invasion proper.

Of the 26 shrubs and trees, 12 are confined to the Kermadecs, or at least do not reach New Zealand, and 5 of the other 14 range from end to end of New Zealand, the mean range of the whole 14 being represented by the figure 3.0. Of the 45 herbs, 7 only are not found in New Zealand, 20 range New Zealand from end to end, and the mean range is represented by the figure 2.2. These facts are inclined to suggest, though they offer no



proof, that herbs may range more rapidly than trees and shrubs, as indeed one is inclined to think must necessarily be the case. Eight of the 14 shrubs and trees reach the Chathams also, and only 17 of the 38 herbs, a fact which also points in the same direction, as it gives one to suppose that the former were opposite to the Chatham connexion at an earlier period than the latter.

(25) Finally, many Kermadec species also reach the Chathams, as we have seen. Now if age be the chief determinant in distribution, we shall expect (cf. map-diagram 2) that those of these forms which belong to the chief northern invasion, supposed to centre in Auckland, will also reach Dunedin to the south, while those which do not may cease at a less distance from the North Cape. Examining the facts, we find that of the 29 species which the Kermadecs have in common with the Chathams, 26 range to Dunedin or farther south, whilst *Piper excelsum* reaches only to Banks Peninsula and Okarito, *Corynocarpus laevigatus* to Banks Peninsula and Westland, and *Acianthus Sinclairii* to Dun Mountain and Westport. All of these, we have seen above, may very probably be regarded as having entered New Zealand in the Kermadec invasion; and it is also noteworthy that *Corynocarpus* is a tree, which might have been early enough to reach the Chathams without perhaps travelling sufficiently fast to have reached so far south as some of the other forms also common to the Kermadecs and Chathams. There are 16 other Kermadec species which reach as far south as *Corynocarpus* and do not reach the Chathams; 13 of these are herbs, *Melicytus ramiflorus* and *Panax arboreum* are trees, and *Coprosma Baueri* is a shrub.

#### THE AUCKLAND ISLANDS.

Turning now to the southern end of New Zealand for a while, let us look at the flora of the Aucklands and their surrounding islands (the Antipodes, Campbell, and Macquarie). The first thing that strikes one is that though the Aucklands are subantarctic and the Kermadecs subtropical, the former have a much larger flora recorded, 119 species against 71. Of these 44 do not occur in New Zealand proper.

As regards constitutional habit, the Aucklands contain only one tree (*Metrosideros lucida*), 11 shrubs, and 107 herbs. The last named thus form 90 per cent. of the total, against only 64 per cent. in the Kermadecs.

Another feature of interest is the great proportion of Monocotyledons. To deal properly with this feature, we must briefly consider the distribution of Monocotyledons in New Zealand itself, though complete details must be left for subsequent papers. If we divide the main islands of New Zealand from north to south into zones of 100 miles, as has already been done upon several occasions (cf. 6, p. 444), and tabulate the species that occur in them, we get for the Monocotyledons:



TABLE XV.

	-100 m.	-200	-300	-400	-500	-600	-700	-800	-900	-1000	-1080
Wides reaching islands	21	21	23	23	24	26	26	26	26	29	26
Wides (N.Z. only)	71	68	85	84	83	80	76	69	62	56	27
Endemic N.Z. and islands	22	22	23	25	27	31	31	30	31	31	30
Endemic N.Z. only	56	63	71	81	80	100	98	98	104	86	39
	<hr/> 170	<hr/> 174	<hr/> 202	<hr/> 213	<hr/> 214	<hr/> 237	<hr/> 231	<hr/> 223	<hr/> 223	<hr/> 202	<hr/> 122

It is clear that the centre of the Monocotyledons as a whole is in the South Island. But the numbers do not run with perfect regularity to a maximum at one zone, and this leads one to suspect, what indeed seems probable when one realizes (10, p. 355 seq.) that there have been at least two invasions of New Zealand, that the group really entered partly in one, partly in the other, invasion. The southern invasion of Monocotyledons was, as we shall see, so much the larger that its figures all but swamp those of the northern.

If we now examine the Monocotyledons genus by genus, we soon find that they divide into two main groups, one commencing at the north end of New Zealand and ranging to a greater or less distance south, the other commencing at the south end and ranging to a greater or less distance north. It is very striking how few species there are which have intermediate ranges, among the wides—the endemics of course have every possible range. The only wides that do not reach one or the other end of the two main islands of New Zealand are given in the table below (I have counted those wides that only reach the southern end of the narrow peninsula at the extreme north as reaching the north end of New Zealand, this peninsula being so entirely different from the rest of the country, and so small in area).

TABLE XVI.

Prasophyllum rufum	Uncinia Sinclairii
Pterostylis mutica	tenella
Hypoxis pusilla	Carex acicularis
Juncus scheuchzerioides	lagopina
Triglochin palustre	leporina
Potamogeton palustre	Brownii
Zannichellia palustris	Imperata arundinacea
Lepilaena Preissii	Stipa setacea
Centrolepis strigosa	Alopecurus geniculatus
Lepyrodia Traversii	Agrostis parviflora
Eleocharis acicularis	

A mere glance at this list, for any one who is familiar with Cheeseman's Flora, is sufficient to show that it includes, as is usual in lists of species that behave irregularly (as regarded from the point of view of age and area), the bulk of the doubtful determinations, species of possible recent introduction, &c. The three orchids might possibly have been brought by the aid of the wind in comparatively recent times. There are only perhaps 8 of the 21



which can be regarded as probably in reality ranging short of either end of New Zealand, and which are not either wrongly named or probably introduced, whilst it is obvious that any further discoveries of these species in new localities will go to make the original contention, that the wides in general range to one or the other end of New Zealand, nearer and nearer to the exact truth. In any case, as there are 179 Monocotyledon wides, it is clear that an 'error' of 8 is nothing very marked.

Beginning with the orchids, we may probably regard as northern genera (inasmuch as their wides, where they do not range completely along New Zealand, usually begin at the north end) *Dendrobium*, *Bulbophyllum*, *Earina*, *Sarcochilus*, *Spiranthes*, *Thelymitra*, *Orthoceras*, *Microtis*, *Caleana*, *Acianthus*, *Cyrtostylis*, *Calochilus*, and *Gastrodia*. Similarly we may regard *Cordyline* and *Astelia* in Liliaceae, *Rhopalostylis* in Palmae, *Freycinetia* in Pandanaceae, *Kyllinga*, *Cyperus*, *Mariscus*, *Fimbristylis*, *Scirpus*, *Schoenus*, *Cladium*, *Lepidosperma*, and *Gahnia* in Cyperaceae, and *Imperata*, *Zoysia*, *Paspalum*, *Isachne*, *Oplismenus*, *Spinifex*, *Sporobolus*, *Dichelachne*, *Amphibromus*, *Bromus*, and *Agropyrum* in Gramineae, as northern types. If now we take the zonal distribution of the species of these genera, and add them up, we get:

TABLE XVII.

	-100 m.	-200	-300	-400	-500	-600	-700	-800	-900	-1000	-1080
Wides reaching islands	14	14	14	14	14	15	15	13	13	13	10
Wides (N.Z. only)	36	32	32	30	25	21	17	11	5	3	3
Endemic N.Z. and islands	13	13	13	14	14	14	14	12	12	12	11
Endemic N.Z. only	28	27	29	31	24	23	19	16	14	10	6
	91	86	88	89	77	73	65	52	44	38	30

tapering markedly from north to south. If now we subtract this table from Table XV, we get:

TABLE XVIII.

	-100 m.	-200	-300	-400	-500	-600	-700	-800	-900	-1000	-1080
Wides reaching islands	7	7	9	9	10	11	11	13	13	16	16
Wides (N.Z. only)	35	36	53	54	58	59	59	58	57	53	24
Endemic N.Z. and islands	9	9	10	11	13	17	17	18	19	19	19
Endemic N.Z. only	28	36	42	50	56	77	79	82	90	76	33
	79	88	114	124	137	164	166	171	179	164	92

These figures clearly show that the supposition of two chief invasions of Monocotyledons is supported by the facts; and it is probable that when our detailed knowledge of distribution in New Zealand reaches comparative perfection, we may be able to go into even greater detail. As it is, one or two genera, e.g. *Scirpus* or *Schoenus*, have wides beginning at both the north and the south ends of New Zealand, and ranging part way along the islands to the south or to the north. If these genera were regarded as having entered by



both invasions, and their species divided between them, the slight irregularities shown in the tables above would be removed.

(26) The southern invasion of Monocotyledons being thus much larger than the northern, we shall expect the Aucklands to show a larger percentage of this group in their flora than do the Kermadecs, and we shall expect the Chathams to show an intermediate percentage.

TABLE XIX.

	<i>Aucklands.</i>		<i>Chathams.</i>		<i>Kermadecs.</i>	
Monocotyledons	54	45 %	49	31 %	15	21 %
Dicotyledons	65	55 %	106	69 %	56	79 %

(27) It follows incidentally from what has been said that Stewart Island should show a greater proportion of Monocotyledons in its flora than New Zealand as a whole. This comes out in

TABLE XX.

	<i>New Zealand as a whole (including islands).</i>		<i>Stewart.</i>	
Monocotyledons	348	27 %	130	34 %
Dicotyledons	954	73 %	252	66 %

or, to put it in another way, 37 per cent of the New Zealand Monocotyledon flora occur in Stewart, and only 26 per cent. of the Dicotyledon flora (neglecting in each case the few Stewart endemics). The whole makes a very awkward problem for the supporter of Natural Selection; why are Monocotyledons so much better suited to Stewart and the Aucklands than to the Kermadecs, and why are the Chathams intermediate in the proportion they bear? But if we simply recognize that the proportions are merely due to the size and time of the invasions of New Zealand by plants, we get a perfectly simple and straightforward explanation.

(28) Examination of map-diagram 2 will show that if we draw a circle with its centre in the Auckland Islands, passing through the Chathams, it will also pass through Auckland City. We shall therefore expect that in general (unless of course there was not direct land communication in either of these directions), species which reach both the Aucklands and the Chathams will also reach Auckland City. Examination of the facts shows that of the 32 species that these groups of islands have in common, 26 are found at least as far north in New Zealand as Auckland City. Of the other 6, 2 are wides, both South American species, *Tillaea moschata* and *Veronica elliptica*, reaching, the one to the northern side of Cook's Strait, the other to West Wanganui and Cape Foulwind, in South Island. *Coprosma foetidissima* reaches to the Thames goldfields, and *Deschampsia caespitosa* to the lower Waikato, so that these two reach within a very short distance of Auckland. *Tillaea moschata* and *Rumex neglectus* are



coast species, which may have reached the Chathams by water, and *Urtica australis* finally, which only reaches the small islands in Foveaux Strait, is also probably a water-carried species. The prediction is thus borne out by the facts as well as can be expected. Even if all the six species be considered as exceptional, the prediction is within 20 per cent. of accuracy.

Both the southern invasion, and the floras of the Aucklands, Campbell, &c., contain a large number of South American forms, and the question has been much discussed as to how they have reached New Zealand, or whether indeed they did not reach South America from New Zealand. Guppy (5, p. 294) discusses the possibilities of water carriage, and shows that seeds drifted from South America could only reach the extreme north of New Zealand. But an examination of the New Zealand forms with South American affinities shows that those which do not range the entire length of the islands are mainly concentrated in the south. The only ones with northern location are *Sicyos angulata* (range 0-540), *Mesembryanthemum aequilaterale* (360-500), *Gratiola peruviana* (0-940), *Cyperus vegetus* (60-500), and *Scirpus sulcatus* (80-700, Tristan da Cunha, not South America proper). Of these we have seen that the first probably entered from the Kermadecs, it also occurring in Polynesia and Australia, and the last may have been drifted by water from Tristan. *Mesembryanthemum* and *Gratiola* also occur in Australia, so that there remains only *Cyperus vegetus*, and it is permissible to suppose that this may have arrived by water carriage, perhaps when the Lord Howe I. bank was dry land.

Water carriage, however, will hardly explain how the others reached New Zealand from South America, and there remains the possibility that the transport was the other way, and that these species reached South America from New Zealand. Guppy shows that transport is possible from the south of New Zealand to Chili. The genera involved are mostly so cosmopolitan that one cannot argue from the generic distribution, and must take other matters into consideration. The great argument against this supposition, to my mind, is based upon age and area. These species, in South America, mostly reach not only Chili, but also Fuegia, the Falkland Islands, South Georgia, &c., and in some cases also Kerguelen and other islands of the Antarctic Ocean. It is, therefore, clear that they must be enormously old in South America, and if they had gone there from New Zealand they must be yet older in that island, and should therefore be very widely distributed there, which is exactly what does not occur. Their distribution shows clearly that they must be older in South America, and must therefore have gone *to*, not from, New Zealand.

Or again, we may take single examples. It would seem very strange if *Ranunculus biternatus* spread from Macquarie to South America (it does not occur in New Zealand), or *Cardamine glacialis*, found only in the Aucklands, Campbell, Macquarie, and South America, or other species



found only in limited areas in the South Island. The South American wides are no commoner, in fact slightly rarer (less distribution area) in New Zealand than the Australian wides, and it may also be noticed that those South American wides that also reach Australia are very widespread indeed in New Zealand.

There seems therefore some reason to suppose that the affinity between New Zealand and South America is really due to the fact that at one time there was land connexion, complete or nearly complete, between them, though a few species, especially those with northern range in New Zealand, may owe their presence to water carriage. The equatorial current from the west coast of South America passes by way of the Kermadec and Chatham Islands.

As to the position and direction of the land bridge, it is very difficult to come to any definite conclusion in the present state of our knowledge. In general we may perhaps imagine that it went by way of the Antarctic continent, perhaps all the way to South Georgia, or perhaps by way of Juan Fernandez to Chili, though this seems unlikely. But a land connexion seems to me to be indicated by the facts of distribution.

As so many Australian and Tasmanian forms are included in the plants of the southern invasion, it would seem probable that this land connexion extended also to Australia and Tasmania.

Whether the South American and the Australian plants arrived by the same route from the south it is difficult to say. The general facts seem to me to indicate—it is impossible to put it into words without a vast amount of detail—that it is quite possible, if not probable, that the land joining New Zealand to the Antarctic continent was more or less broken up by water areas. It is, for example, noticeable that a number of species which occur in Kerguelen, the Crozets, Marion Island, &c., are found only in Macquarie, though of course this is quite possibly due to water carriage.

The next question is, Did this connexion with Antarctica pass through any of the groups of islands that we are now considering? As even the Aucklands only possess 39 out of 127 wides of the southern invasion, and Campbell, the Antipodes, and Macquarie progressively less, it may be inferred that it did not pass directly through any of them, and that it was probably nearest to the Aucklands.

The average rarity in New Zealand of the Auckland wides as a whole is 2.7, while that of the wides of the southern invasion is 3.1. This is little to go upon, but at least it tends to show that on the whole the arrivals of wides in the Aucklands were fairly early.

There are a considerable number of South American genera which occur in New Zealand but not in the Aucklands, another fact which goes to show that the southern invasion, or some of the invasions, if there were more than one, did not pass directly through these islands.



In Campbell, the Antipodes, and Macquarie we find in general the Auckland flora, in less and less proportion, so that on the whole these islands must probably have received their floras by the same invasion. It would lead too far to go into greater detail.

#### THE CHATHAM ISLANDS.

To turn lastly to the Chathams, it is obvious that they could never have formed part of a bridge from New Zealand to anywhere else, the water on their eastern side being almost the deepest in the world, so that their flora, except in so far as it may have been brought by currents, must have come through New Zealand. Even if the whole area shown in the map as above the depth of 1,000 fathoms were dry land, a species beginning between the Chathams and Antipodes would as a rule have also reached New Zealand by the time that it had reached both groups of islands.

The Chathams are fairly opposite to the middle of New Zealand, and connected by shallower water with the South than with the North Island, so that one will expect their flora to be fairly rich, unless they were cut off very early indeed, a matter as to which we have no information. As a matter of fact they have the richest flora of the outlying island groups, composed of 106 species of Dicotyledons and 49 of Monocotyledons, the proportion of the latter being, as we have seen, intermediate between that in the Kermadecs and that in the Aucklands.

(29) We shall expect that on the whole the families missing in the Chathams from the Stewart list, which is likewise old, will be the smaller families of that island, i. e. on the whole those which have been the latest in arriving there. If we omit all those with one species, we omit Magnoliaceae, Pittosporaceae, Elatinaceae, Hypericaceae, Linaceae, Cornaceae, Goodeniaceae, Primulaceae, Apocynaceae, Loganiaceae, Labiatae, Illecebraceae, Lentibulariaceae, Chloranthaceae, Loranthaceae, and Euphorbiaceae. Primulaceae must certainly occur in the Chathams, as the only species in the family occurs in both Kermadecs and Aucklands. Leaving this out, the only other families in this list which are recorded from the Chathams are Linaceae, Cornaceae, Labiatae, and Euphorbiaceae. The other Stewart families not recorded from the Chathams are Portulacaceae (2 species), Tiliaceae (4), Saxifragaceae (3), Droseraceae (4), Stylidiaceae (4), Ericaceae (2), Plantaginaceae (3), and Centrolepidaceae (2), but we have already seen that (prediction 5) we must expect the Chathams not to contain the very small families of the southern invasion. This excludes from this list Portulacaceae, Droseraceae, Stylidiaceae, Plantaginaceae, and Centrolepidaceae, leaving only three families of the Stewart flora that might be expected and have not been recorded, and four recorded that would hardly be expected, as being families with only one species in Stewart. The seven families that occur in the Chathams and do not as yet appear to have been recorded



from Stewart, Rhamnaceae, Anacardiaceae, Leguminosae, Solanaceae, Myoporaceae, Piperaceae, and Palmaceae, are all northern except perhaps Leguminosae, which is the largest New Zealand family not yet recorded from Stewart.

(30) In the same way, we shall expect the smaller genera of the Stewart flora to be those that are chiefly missing, and on examination we find that of those represented in Stewart by one species 57 are not found in the Chathams, and 31 have been found, while of those represented by two or three species 19 have not been found, and 26 are present, in the Chathams.

(31) One may, by the aid of age and area, go a good way towards a prediction of the whole flora of the Chathams (cf. that of the flora of Stewart in 11, p. 27). If one first predict that they will contain the Kermadec species that reach Dunedin, this gives 38 species of which 26 reach the Chathams; then adding that they will contain the Auckland species that reach Auckland city gives about as many more. If now one add to this that the bulk of the rest of the flora will likely be made up from the species which range the whole length of New Zealand (for those that ranged less distance would as a rule be too young to reach the Chathams at all, unless they ranged beyond New Zealand to the Kermadecs or Auckland), one obtains almost all the remaining flora, except the local endemics, which we have already seen may be to some extent predicted as likely to belong to the oldest families in the Chathams, that is to say, to the families represented by the most species in New Zealand (see above, p. 270). Of course this prediction that the Chatham\* flora will be selected almost entirely from Classes 1 and 2 (6, p. 449) of the New Zealand flora brings in also a great many other species belonging to those classes, but which do not occur in the Chathams. We have as yet no means of deciding which are the oldest species in a given class, and it will only be the oldest, in general, which will reach the Chathams. The fact remains, however, that by this prediction we cover all of the Chatham flora but 14 species and the local endemics, and we have seen that we can more or less closely predict the families and genera to which these belong. These unpredicted species are:

*Pomaderris apetala*: a special case, see 8, p. 332.

*Corynocarpus laevigatus*: see above, p. 279.

*Tillaea moschata*: a coast species.

*Epilobium insulare*: lowland swamps.

*Coprosma foetidissima*: see above, p. 284.

*Helichrysum filicaule*: dry grassy places.

*Veronica elliptica*: a coast species.

*Piper excelsum*: usually near the coast.

*Urtica australis*.

*Pterostylis australis*: cf. 11, p. 39.



*Acianthus Sinclairii*.

*Rhopalostylis sapida*.

*Lepyrodia Traversii*: doubtful determination, see Cheeseman.

*Deschampsia caespitosa*: see above, p. 284.

Thus several are doubtful determinations, or coast forms, which may have been brought by the currents. But it is only among these few species that one can look for exceptions to age and area; all the remainder of the flora of the Chathams—155 species in all—is easily explained by the simple operation of this law, and no other assistance is needed to explain it.

(32) We may predict that the Chathams should have proportionately more species in the higher classes of width of distribution than the Kermadecs or Aucklands, where more recent arrivals may occur, as these islands have been nearer to the tracks of the invasions.

TABLE XXI.

The Chathams have	155	species, of which	77	are Class 1,	30	Class 2
„ Kermadecs „	71	„ „	22	„ „	16	„
„ Aucklands „	119	„ „	35	„ „	6	„

The proportion (and the totals) in the Chathams is by far the greatest.

One might give other predictions about the floras of these islands, but these will suffice to show that in a well-defined area like New Zealand and its surrounding islands one can without hesitation draw upon the hypothesis of age and area to make predictions about the taxonomic distribution of the flora, and find that the predictions are justified by the facts. I have now used the hypothesis to make no fewer than 67 predictions (32 in this paper), every one of which has proved to be correct. In several cases the exactness with which the prediction has been borne out by the facts has been positively astonishing, and in all cases the result has been as near to accuracy as can reasonably be expected in a biological subject, and especially in one so complex as geographical distribution, where changes in the configuration of the land and sea may be continually going on, and in a very complicated way. It seems to me, therefore, that the hypothesis of age and area, having been successfully used to make so many predictions, may now perhaps be regarded as being fairly well established as one of the chief (if not the chief) positive factors in geographical distribution, while the action of barriers, which may be of many kinds—seas, rivers, mountains, ecological barriers, changes of climate, &c.—may be regarded as the chief negative factor, and other things, such as the action of man, are also of very great importance indeed.

If this position be regarded as reasonable, it is evident that we must now state the hypothesis in rather more clear and definite terms than those in which it was first formulated, e.g. in 6, p. 438. After careful



consideration of the various papers that have been written on the subject, and after devoting much time to further work upon it, I am inclined to word the hypothesis thus:

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.

In other words, age and area is the chief positive, the action of barriers the chief negative, factor in plant distribution, while in recent times the action of man has become of greater importance than either.

It is clear that in general this law also covers the case of a genus of more than a very few species, for a genus is in general a group of allied species, though it is becoming every year more clear (cf. 1 and 12, p. 446) that many genera are based upon too few characters, and are in reality polyphyletic.

The acceptance of this hypothesis will involve various changes in our methods of handling problems of geographical distribution, and in further papers I shall go on to indicate some of these.

#### SUMMARY.

In this paper the chief attention is devoted to the islands outlying around New Zealand, especially the Kermadecs, Chathams, and Aucklands, and the following points are indicated, chiefly by the method of prediction and subsequent verification, which is here used successfully no fewer than 32 times. It is first shown that the floras of these islands must be very old, from their far outlying position, and is then indicated that—

1.<sup>1</sup> The islands have proportionately more families in common with Stewart, whose flora is also old, than with New Zealand proper (Table I).

2. The great proportion of the families in the different islands are the same, and most are selected from the Stewart list (Table II).

3. The families reaching three groups of islands are on the whole the largest (oldest), those reaching two next, and then those reaching one or none (Table III). The same is true for the Stewart families (Table IV), and the total result is summed up in Table V.

4. The Stewart families that are missing in the islands are on the whole the smallest.

5. The Aucklands and the Chathams contain most of the families of the southern invasion, and those that are missing in the Chathams are the smallest, numerically, of that invasion.

<sup>1</sup> Predictions numbered as in text above.



6. The Chathams contain many families of the northern invasion.
7. The outlying islands have proportionately more families in common with one another than they have with New Zealand (Table VI).
8. The genera of the floras of the outlying islands are chiefly selected from the Stewart list (Table VII) ; only 26 out of 140 do not occur there, and are mostly northern genera.
9. The genera that occur in the islands are on the whole the largest in number of species, both in Stewart and New Zealand (Table VIII).
10. The islands have proportionately more genera in common with one another than they have with New Zealand (Table IX).
11. The Stewart genera which are missing are on the whole the smallest.
12. The species in the islands are also to a very large extent indeed selected from the Stewart list.
13. The Stewart families that have no species in the islands are on the whole very small in Stewart.
14. The islands have very many species in common among themselves.
15. The species in common between three islands (the oldest) show the largest proportion of wides (the oldest forms), then those of two islands, one island, and those reaching none (Table X).
16. The plants of the islands show a greater proportion of families to genera and genera to species than those of Stewart and New Zealand (Table XI).
17. The more genera in a family in New Zealand, the older on the whole is the family in New Zealand, and the better represented in the islands (Table XII).
18. The same thing shows in regard to the genera.
19. The plants reaching 3 groups of islands, New Zealand and Stewart, 2, 1, Stewart and New Zealand only, and New Zealand only, show a progressive decrease in the average size of families and genera (Table XIII).
20. All these predictions are also true of the ferns, and the fern flora of Stewart, as on the whole older, is better represented in the islands than the flowering plants.
21. The species endemic to the islands only do not occur on two of the chief groups without occurring in New Zealand, as one might expect were they relicts.
22. The endemics of the islands belong on the whole to the largest (i.e. on the whole the oldest) families of New Zealand.
23. Practically all the genera of the island endemics, being old, occur in Stewart.
- Just as in Stewart, the island endemics belong mainly to the 'successful' families and genera of New Zealand.
24. The proportion of trees is greatest in the northern islands, least in the southern, intermediate in the Chathams.



The islands must have had connexion by land with New Zealand.

The Kermadecs contain a number of species which do not occur in New Zealand, but occur in Polynesia; it therefore seems probable that they received part of their flora direct from Polynesia.

The distribution of the Kermadec species in New Zealand is considered, and it is shown that it does not agree with any hypothesis but that of a land bridge between the two.

The Kermadecs probably were not in the track of the main northern invasion of New Zealand, but were upon the route of a minor invasion from Polynesia.

25. The Kermadec species which reach the Chathams also reach in general as far south in New Zealand as Dunedin.

The Aucklands show a great proportion of Monocotyledons, and the distribution of this group in New Zealand is briefly considered, it being shown that it probably took part in both invasions.

The wides of New Zealand nearly all range to one or the other end of the islands, if not to both. Those which do not (Table XVI) include the doubtful determinations, species of probable recent introduction, &c.

26. The proportion of Monocotyledons is greatest in the Aucklands, least in the Kermadecs, and intermediate in the Chathams.

27. Stewart Island shows a greater proportion of Monocotyledons than New Zealand.

28. Species reaching both Aucklands and Chathams reach also in general to Auckland city.

The evidence is against the probability of carriage by water of South American forms to New Zealand, or of New Zealand forms to South America, though there are a few that may have been so carried, and favours the former existence of a land bridge, which probably passed to New Zealand nearer to the Aucklands than to the other southern islands.

29. The families missing in the Chathams are the smaller families of the Stewart list, in general; (30) similarly the smaller genera.

31. A great part of the Chathams' flora can be predicted by aid of age and area.

32. The Chathams have more species in the highest classes (widest distribution in New Zealand) than the Kermadecs and Aucklands.

The hypothesis has now been successfully used to make no fewer than 67 predictions, which have proved to be correct on examination of the facts, and increase of area with age may thus perhaps be considered as being the chief positive factor in determining the distribution of plants about the globe, the chief negative factor being the presence of barriers.

Finally, a restatement of the hypothesis is made.



LITERATURE QUOTED.

1. BOWER : Natural Classification of Plants (Hooker Lecture), esp. p. 119. Journ. Linn. Soc. (Bot.), xliv, 1918, p. 107.
2. CHEESEMAN : Manual of the Flora of New Zealand, Wellington, 1906.
3. ——— : Islands to the S. of New Zealand, in Chilton's Subantarctic Islands of New Zealand, ii. 389, Wellington, 1909.
4. COCKAYNE : Botanical Survey of Stewart Island, Wellington, 1909.
5. GUPPY : Plants, Seeds, and Currents in the West Indies and Azores, 1917.
6. WILLIS : Distribution of Species in New Zealand. Ann. Bot., xxx, p. 437, 1916.
7. ——— : Relative Age of Endemic Species. l. c., xxxi, p. 189.
8. ——— : Distribution of Plants of the Outlying Islands. l. c., xxxi, p. 327.
9. ——— : Further Evidence for Age and Area. l. c., xxxi, p. 335.
10. ——— : Sources and Distribution of the New Zealand Flora. l. c., xxxii, p. 339.
11. ——— : The Flora of Stewart Island. l. c., xxxiii, p. 23.
12. ——— : Studies in the Morphology of the Podostemaceae. Ann. R. B. Gardens, Peradeniya, i, p. 267, 1902.
13. ——— : The Endemic Flora of Ceylon : A Correction. Proc. Roy. Soc., B., lxxxix, p. 257.





Willis, J. C. 1919. "The floras of the outlying islands of New Zealand and their distribution." *Annals of botany* 33, 267–293.

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