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CHAPTER III

Endemism in Southern Europe

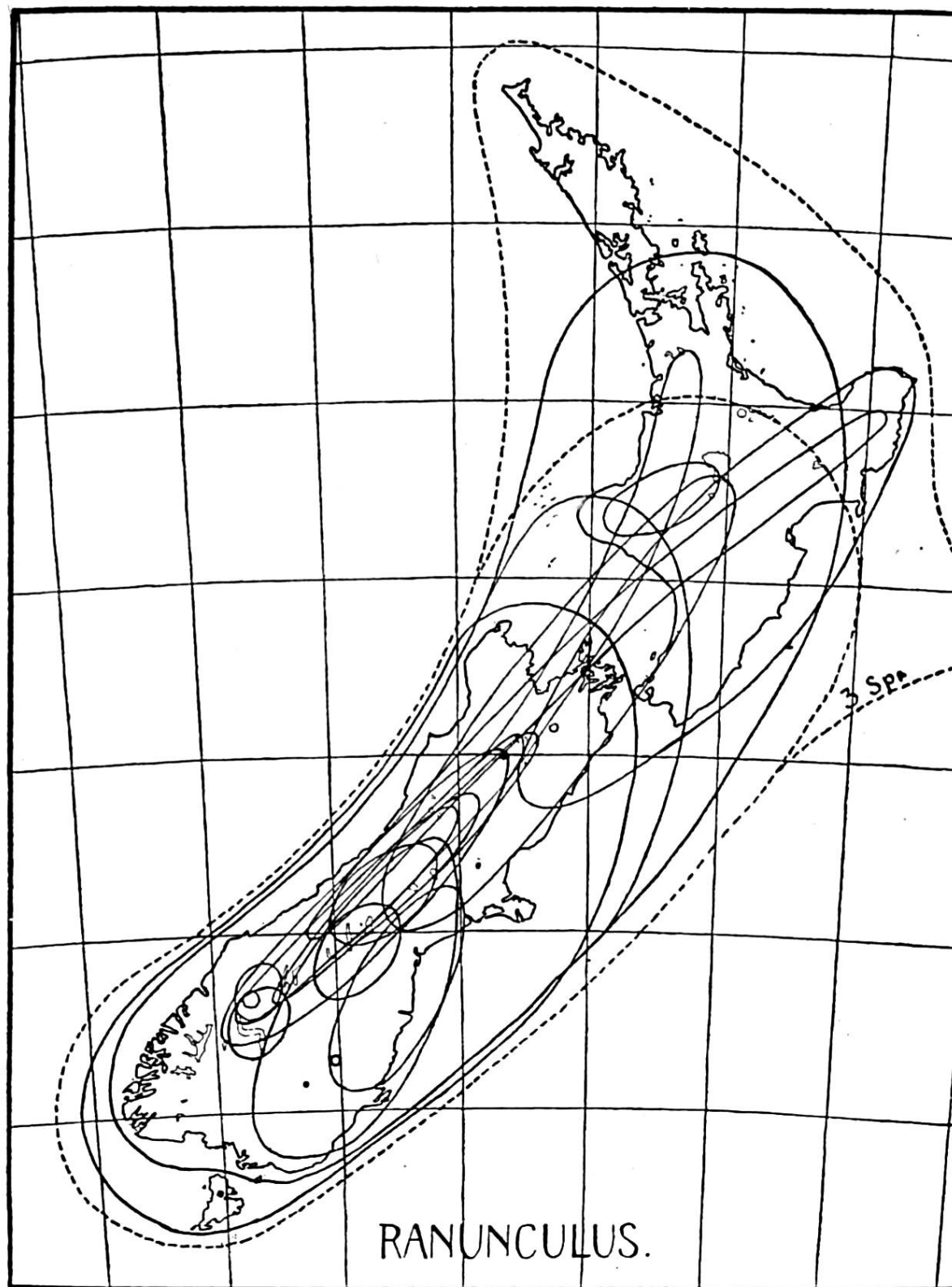
Endemics, both species and genera, as we have seen, appear in crossing EUROPE, and become abundant around the MEDITERRANEAN, which in pre-Darwinian days was termed a "centre of creation", and might now be called a centre of evolution, as there are a great number of genera of from one to twenty species found only in that region. In the north endemics are but few, and in the far north are mainly circumpolar. The question of what they really are, and why and how, and where and when, they were formed, has caused endless discussion and controversy, for no explanation of distribution that does not explain them is of much value. Under selection one expects to find in many places the relics of species defeated in the struggle for existence; its supporters, therefore, found the harmless endemics a perfect godsend, as apparently fulfilling these conditions. They being especially common upon islands and upon chains of mountains, these places gradually became recognised as refuges for the defeated, though how these reached them was left unexplained. They would have to undergo some adaptation in doing so, and if so, why could they not become adapted to meet the competition in their old homes? It became customary to say that the competition was less severe on islands or on mountains; but the average number of competitors in any one place (six) is the same in both, and the widespread ("successful") species are if anything commoner on the islands or the mountains (lower parts).

Another popular view, also almost purely speculative, was that endemics were not relics, but were things that had

become adapted to some peculiar local conditions, in which they flourished as successes. As no evidence could be found to support either of these contradictory explanations, it is clear that real knowledge was still to seek. Both were continually met by insoluble difficulties, but such was the glamour of selection that these were pushed to one side, or ignored, a proceeding bound sooner or later to lead to trouble.

The writer has devoted much time to the study of endemism, and it may be said at once that while there are many genuine relics, within range, for example, of the coming of the ice, and while it is clear that any species, surviving and reproducing in any place, must be suited, or adapted, to that place in order to survive, there is no doubt that the dispersal of endemics by area follows in general the same kind of curves as other distributions. There is nowhere that one can draw any line to distinguish between endemics and non-endemics, any line that is actually drawn depending entirely upon the personal preference of him who draws it, for some would keep endemics to the very bottom of the curve, others would go higher up.

As this type of arrangement was universal, the writer proposed (in earlier papers, and in *Age and Area*, 1922) to regard endemics in general, whether species or genera, as young beginners that had not yet had the time, and sometimes of course the opportunity, needful to enable them to spread to great distances. The area actually covered was simply a rough indication of their age as compared with allied forms, for barriers, or differences in adaptation to conditions would affect some more than others. The first deductions made are given in *Age and Area*, p. 65. The facts go in so mechanical a way that some mechanical explanation is needed, and age is far more reasonable as such than is youth, under which the things of small area would be relics. The objections to the latter are dealt with in some detail (*l.c.* pp. 88-100), and no answer has been given, so far as I am aware. Positive proof has also been given by the success of all predictions based upon these mechanical laws, already considered in Chap. I. The real objection to them is that they are contradictory of the Darwinian hypothesis which founded evolution upon the natural selection of structural adaptational improvement, thus seeking to explain as



Ranunculus in New Zealand (by courtesy of the Editor, Annals of Botany). Wides... Endemics —.

adaptational the structural changes that mark evolution. It is hardly fully realised that adaptation to local conditions involves living in those conditions, and that distribution to great distances from them involves having plenty of time to get there by easy stages, acquiring local adaptation to each set of conditions in turn. Time thus becomes the all-important factor in dispersal, and its effects completely override those of the vital factors that are so important at any one place or time.

Endemism begins in the OLD WORLD chiefly at the great mountain barrier that runs from east to west, while in AMERICA, where the mountains run north and south, and in the southern hemisphere, with its more broken area, there is not so close an approximation to a limit of endemism. In and south of the barrier, endemism is well marked, probably primarily because the genera have been longer upon the ground (and the ground is more varied and broken) than in the colder north. In the mountains one finds representatives of genera that came from the north, or down the mountains, in the cold periods, and then, as the warmth grew, were driven upwards and northwards, till they acquired a discontinuous distribution, as shown by such a plant as *Diapensia*, with species in the HIMALAYA and in the arctic regions. Many endemics in NEW ZEALAND or in SOUTH AMERICA are as near the pole as north-central EUROPE.

This probable fact, that *Diapensia* and other things were caught in the south by the returning warmth, and *killed out there*, only having at the present time survivors at high levels in the mountains, or in the arctic regions, goes to show that a change of conditions may actually kill out the organisms that become subject to it, whether this was done directly (as by increasing warmth) or indirectly (as by the encouragement by that warmth of the growth of plants that too much overshadowed the first, or in some other way). We do not of course know exactly what happened, nor how far north the *Diapensia* had actually gone, but the fact of its present discontinuous distribution is due to the fact that it was near enough to them to reach two different refuges, while it is quite possible that had it been just a local thing on the TIBETAN plateau, the change of conditions might have been too quick for it to escape, and it might have been killed out altogether. Such a fate may have

been the origin of many of the very local fossils that are known.

Upon our theory of the origin of endemics, they must, as young beginners, have had parents in the same place as themselves, living under the same conditions, and these parents are not necessarily, or even probably, killed out. It is therefore unlikely that there should be any country showing 100% endemism, even when we remember that there are many genera, all of whose species in some single country are there endemic (this will be dealt with later). Between 80 and 85% is the highest proportion of endemics anywhere found, and only in such long isolated places as W. AUSTRALIA, the HAWAIIAN Is., &c, as have given time for many endemics to form without being able to get beyond the country.

The areas occupied by individual endemic species or genera vary greatly, from those of *Coleus elongatus* with a dozen or more plants on RITIGALA summit in CEYLON, *Ranunculus paucifolius* with only 44 individuals upon four acres in NEW ZEALAND (as Prof. F. T. BROOKS kindly informs me), or the whole genus *Sphagneticola* in the little LARANJEIRAS valley now forming part of RIO DE JANEIRO, upwards to whatever area one may select as the largest possible for an endemic (cf. *Age and Area*, pp. 151-161).

It was this great variety of areas occupied, with no break between larger and smaller, that first attracted the writer's attention, making him realise that an endemic was usually simply a young beginner. Their numbers were largest upon the smallest areas, and decreased upwards, forming curves with the maximum at the base. These curves show not only with the whole flora of a country, but with individual families, and even with individual genera that have more than about a dozen species (*AA*, p. 161). "It is clear that the distribution of endemics is only a special case of a wide general phenomenon—that there are, in any family or genus of reasonable size, a few species of wide dispersal, and others of less and less dispersal in increasing numbers, the increase being more rapid as one descends the scale, so that the curve produced is hollow". When, as in NEW ZEALAND, where there are many endemics, with their localities well worked out, so that one can draw a map (p. 65), one can see quite well how the smaller areas greatly

outnumber the large, and how they tend to centre at some region of NEW ZEALAND where the genus probably entered.

There are many endemics in southern EUROPE, especially, as usual, species, and those mainly in the larger genera. At first glance they seem to be a completely casual assortment, but studying them in detail, one finds their appearance to be just as much, and as regularly, governed by definite laws and principles as any other features of a scientific discipline. We shall see that the endemism of any one MEDITERRANEAN country bears a very definite relationship to that of any other, and at the same time shows a clear relation to the composition of the flora of BRITAIN or of other countries in northern EUROPE. There is little or no doubt that most of the flora of such a country as BRITAIN is due to migration from the south after the retreat of the cold. The first plants to follow the increasing warmth and the newly available land would be determined by various causes, such as (1) how old they were in the south, and (2) how far north they were already found, these two of course going very much together, and being modified by (3) suitability or adaptability to somewhat wet and cold conditions, (4) capacity for quick enough travel to arrive before the cutting of communications, though it is not unlikely that the retreat of the ice would be slow enough for perhaps most plants to follow, subject to the third condition, and (5) general presence or absence of great barriers like the sea or high mountain ranges.

BRITAIN has long been cut off by the sea, so that only those plants which arrived in good time would reach it, *i.e.* those on the whole that were oldest in the south. But upon my theory of divergent mutation (*Evol.*) these older forms would probably have had time enough in the south to give rise to new ones, which of course would be endemic there, not having had time enough to spread further. The same thing would be true of the MEDITERRANEAN islands. The great majority of Mediterranean endemics, thus, would belong to the largest and oldest families and genera there, and these would be the same on the whole as the largest and oldest in BRITAIN. The arctic element in the British flora is not large enough to disturb this seriously. Here is where the stipulation as to allied species comes in. A monospecific genus of

water plants, for example, meeting much more uniform conditions everywhere than is the case with land plants, might easily reach BRITAIN more quickly than a species of a large but woody genus of say *Leguminosae*, and the stipulation eliminates such difficulties. If on the other hand, all these endemics were relics, there would hardly be any *necessary* resemblance between those of one country and of another. One would be rather inclined to expect to find them in the smaller and less important local families and genera, which under Darwinism are supposed to be old and dying out, but upon my theories are simply locally younger.

Since families and genera with endemics in the south are probably older on the whole than those without, they should therefore, by the rules of ASA, be the largest and most widely dispersed southern families and genera, as well as the oldest. Let us take the recently worked up Balkan flora (126) as an example. Taking the Dicots, 55 of its families contain no endemics, but they are by no means the large or "successful" families, whose relics might have been killed out. They are the small and rare ones, only containing among them 114 genera and 287 species, while the 49 families with endemics have 625 genera and 5169 species, the *Compositae* alone containing 100 genera with 915 species, of which 323 are endemic, or more than all the species in all the small families. *Caryophyllaceae* have 175 endemics, *Labiatae* 153, *Scrophulariaceae* 128, *Umbelliferae* 106, *Leguminosae* 105, and so on. These six large families alone contain 990 out of the 1576 Dicot endemics of the BALKANS, or 63%, and incidentally contain 58% of the endemics in SPAIN, and 47% of those in the AZORES. For over 35 years the writer has been trying to bring home the fact that endemics chiefly occur in the large and "successful" families and genera, which would shrink to small dimensions if their endemics died out as relics. This fact clashes hopelessly with the Darwinian explanation of things, and little notice has been taken of it.

Endemism in the BALKANS shows a wonderful resemblance to that of SPAIN, as will be seen by looking at the table (Dicots only) that follows: —

Families in Spain and in the Balkans that show endemism

DICOTS				Spain	
Family	No. in other list	Species	Endemics	Percentage of Endemism	
1. Compositae	1.	646	217	33%	
2. Leguminosae	6.	477	137	27%	
3. Cruciferae	7.	300	112	37%	
4. Caryophyllaceae	2.	251	78	31%	
5. Scrophulariaceae	4.	200	78	39%	
6. Labiatae	3.	236	75	31%	
7. Umbelliferae	5.	217	61	28%	
8. Ranunculaceae	11.	143	31	21%	
9. Saxifragaceae	21.	60	31	51%	
10. Rubiaceae	9.	77	25	32%	
11. Borraginaceae	10.	85	24	28%	
12. Plumbaginaceae	19.	55	24	43%	
13. Cistaceae	38.	70	19	27%	
14. Campanulaceae	8.	53	16	30%	
15. Resedaceae	48.	23	15	65%	
16. Rosaceae	14.	23	15	12%	
17. Geraniaceae	27.	46	14	30%	
18. Dipsacaceae	12.	42	12	28%	
19. Euphorbiaceae	16.	58	12	20%	
20. Papaveraceae	23.	38	9	23%	
21. Valerianaceae	22.	31	9	29%	
22. Chenopodiaceae	44.	53	8	15%	
23. Crassulaceae	17.	43	8	18%	
24. Thymelaeaceae	49.	22	7	31%	
25. Malvaceae	39.	35	6	17%	
26. Primulaceae	20.	36	6	17%	
27. Fagaceae	—	22	5	21%	
28. Orobanchaceae	31.	33	5	15%	
29. Plantaginaceae	40.	31	5	16%	
30. Violaceae	13.	16	5	31%	
31. Gentianaceae	30.	33	4	12%	
32. Hypericaceae	15.	21	4	19%	
33. Polygalaceae	32.	15	4	26%	
34. Solanaceae	—	28	4	14%	
35. Caprifoliaceae	37.	11	3	27%	
36. Frankeniaceae	—	5	3	60%	
37. Lythraceae	—	8	3	37%	
38. Onagraceae	—	24	3	11%	
39. Polygonaceae	34.	42	3	7%	
40. Salicaceae	—	31	3	9%	
41-3. Convolv. (33), Eric. (—), Rhamn. (24), at 2 each		58	6	10%	
44-53 Berb., Cappar., Celastr., Dros., Gesn., Glob., Lentib., Lin., Santal., Urtic., at one each		61	10	17%	
		3859	1119	29%	

DICOTS

Balkans

Family	No. in other list	Species	Endemics	Percentage of Endemism
1. Compositae	1.	915	323	35%
2. Caryophyllaceae	4.	421	175	41%
3. Labiatae	6.	375	153	41%
4. Scrophulariaceae	5.	311	128	41%
5. Umbelliferae	7.	334	106	31%
6. Leguminosae	2.	548	105	19%
7. Cruciferae	3.	341	96	28%
8. Campanulaceae	14.	142	76	53%
9. Rubiaceae	10.	131	53	40%
10. Borraginaceae	11.	155	47	30%
11. Ranunculaceae	8.	196	37	19%
12. Dipsacaceae	18.	83	32	38%
13. Violaceae	30.	58	32	55%
14. Rosaceae	16.	187	23	13%
15. Hypericaceae	32.	52	22	42%
16. Euphorbiaceae	19.	77	20	26%
17. Crassulaceae	23.	59	16	27%
18. Linaceae	51.	39	14	35%
19. Plumbaginaceae	12.	39	13	33%
20. Primulaceae	26.	52	12	23%
21. Saxifragaceae	9.	45	9	20%
22. Valerianaceae	21.	38	7	18%
23. Papaveraceae	20.	50	6	12%
24. Rhamnaceae	43.	20	6	30%
25. Aristolochiaceae	—	13	5	38%
26. Asclepiadaceae	—	13	5	38%
27. Geraniaceae	17.	44	5	11%
28. Gesneraceae	48.	5	5	100%
29. Rutaceae	—	14	5	35%
30. Gentianaceae	31.	41	4	9%
31. Orobanchaceae	28.	41	4	9%
32. Polygalaceae	33.	16	4	25%
33. Convolvulaceae	41.	35	3	8%
34. Polygonaceae	39.	24	3	12%
35. Santalaceae	52.	17	3	17%
36. Aceraceae	—	10	2	20%
37. Caprifoliaceae	35.	17	2	11%
38. Cistaceae	13.	29	2	6%
39. Malvaceae	25.	30	2	6%
40. Plantaginaceae	29.	27	2	7%
41-9. Apoc. (—), Cappar. (45), Celastr. (46), Chen. (22), Glob. (49), Lentib. (50), Resed. (15), Tamar. (—), Thym. (24) at 1 each		127	9	7%
		5171	1576	30.4%

MONOCOTS

Family	Spain			
	No. in other list	Species	Endemics	Percentage of Endemism
1. Gramineae	2.	352	61	17%
2. Amaryllidaceae	6.	43	18	41%
3. Liliaceae	1.	121	15	12%
4. Cyperaceae	7.	108	8	7%
5. Iridaceae	4.	28	8	27%
6. Juncaceae	9.	39	2	5%
7. Potamogetonaceae	8.	21	2	9%
8. Araceae	5.	7	2	28%
9. Orchidaceae	3.	59	1	1%
10. Alismaceae	10.	7	1	14%
11. Hydrocharidaceae	15.	3	—	—
12. Scheuchzeriaceae	14.	3	—	—
13. Sparganiaceae	13.	3	—	—
14. Lemnaceae	12.	3	—	—
15. Typhaceae	11.	2	—	—
16. Butomaceae	18.	1	—	—
17. Dioscoreaceae	16.	1	—	—
18. Naiadaceae	17.	1	—	—
19. Palmaceae	+	1	—	—

+ not in the other list.

This is a very striking list, after studying which it is difficult any longer to believe that endemism is just a case of casual relicdom. It shows several interesting features, *e.g.* (1) the larger the family on the whole, the more endemics does it produce; (2) there is wonderfully close agreement between SPAIN and the BALKANS, though they are 1000 miles apart; (3) the agreement goes into the proportion of endemism, which decreases with the size of the family, as shown in the table at foot of following page; (4) families with many endemics in one country also show them in the other, as is shown by the figures of position in the other list given after each (*e.g.* *Compositae* is first in both lists, *Leguminosae*, second in the Spanish list, is sixth in the Balkans, and so on; most of the earlier families occur in both lists; (5) the first seven families are the same in both countries, and are the largest in EUROPE; (6) their proportion of endemics is 67% of the Spanish, 68% of the Balkan, a result one would not expect upon any theory of selection; (7) only 26 Spanish and 19 Balkan Dicot. endemics, out of the very large totals, are in families that have endemics in one of the countries only.

It is difficult to find any argument based upon selection for such close agreement of the two lists of Dicots and also

MONOCOTS

Balkans

Family	No. in other list	Species	Endemics	Percentage of Endemism	With endemics in Spain
1. Liliaceae	3.	252	93	36%	Sp.
2. Gramineae	1.	353	32	9%	Sp.
3. Orchidaceae	9.	99	14	14%	Sp.
4. Iridaceae	5.	62	14	22%	Sp.
5. Araceae	8.	12	4	33%	Sp.
6. Amaryllidaceae	2.	22	3	13%	Sp.
7. Cyperaceae	4.	140	2	1%	Sp.
8. Potamogetonaceae	7.	25	—	—	Sp.
9. Juncaceae	6.	39	—	—	Sp.
10. Alismaceae	10.	6	—	—	Sp.
11. Typhaceae	15.	6	—	—	
12. Lemnaceae	14.	5	—	—	
13. Sparganiaceae	13.	5	—	—	
14. Scheuchzeriaceae	12.	4	—	—	
15. Hydrocharidaceae	11.	4	—	—	
16. Dioscoreaceae	17.	2	—	—	
17. Naiadaceae	18.	2	—	—	
18. Butomaceae	16.	1	—	—	

All the families except the palms appear in both lists. The grouping of the families is very similar to that in the Spanish list. But the total of the seven large families with endemics is 940 species, 162 endemic, or only 17.2%.

the two lists of Monocots, with such different percentages. It has been suggested that it is due to a different rate of mutation, but we shall see in the SEYCHELLES that the figures go the other way there.

Figures of endemism (Dicots) in Spain and in the Balkans

Dicots	Total	Spain species Endemic	% endem.	Total	Balkans species Endemic	% endem.
First 7 families ¹	2327	758	32%	3245	1086	33%
Second ²	543	170	31%	952	300	31%
Third ³	361	86	24%	363	106	29%
Fourth	244	45	18%	183	39	21%
Fifth	155	29	18%	188	26	13%
Sixth	156	19	12%	123	12	9%

¹ The same in both.

² Four in common.

³ One in common.

The smaller the family on the whole, the smaller its proportion of endemism. In other words, local size of a family depends upon local age to a large extent (laws of ASA), and the older that it is there, the more likely is it to have many endemics, which are usually simply the species of younger development.

In case it is asked why ITALY is not included, its flora is constructed upon so different a standard of specificity that it would have required too much labour to equate them. But the proportions of endemism are much the same, and the genera with endemics also.

A still more striking feature in the table is that only 26 Spanish and 19 Balkan endemics, out of the large total of Dicots, belong to families that do not show endemism in both countries, though they are 1000 miles apart. Each list comprises about half the 100-odd Dicot families in the country, yet the two agree in all families with more than five endemics. Those that have them only in one list are marked (—) instead of with the number of the family in the other list, and these marks only begin at line 25. They comprise only 45 out of 2695 endemics, while the 43 families with endemics in both countries contain 2650, or 97% of the Spanish and 98% of the Balkan endemics.

A similar connection in endemism, but even more striking, as one would expect, is shown by CEYLON and the nearer parts of INDIA, the MADRAS PRESIDENCY, TRAVANCORE, and COCHIN. For a complete list of the species there endemic, a list which would have cost great labour to prepare, I am most deeply indebted to Mr C. E. C. FISCHER, joint author of the *Madras Flora* (41), and with the aid of this I have worked out the following statistics :

Dicot Genera with endemics		Endemic spp. in			
		S. India	Aver.	Ceylon	Aver.
129	in both countries	678	5.2	442	3.4
188	in Madras only	333	1.77		
99	in Ceylon only			157	1.58
<hr/> 416		<hr/> 1011		<hr/> 599	

Taking them on the whole, therefore, before any analysis is made, it is evident that the MADRAS genera are the older for those with endemics in both countries, as shown by their greater average, and even to a small extent, perhaps, for those with endemics in one only. Even though there are 188 MADRAS genera with no endemics in CEYLON, no fewer than 119 of them are represented there by wides, in decreasing order with size, 58 showing only one, 26 two, and so on. There are 69 left, of which 31 are confined to the INDO-MALAYAN region, and had not reached CEYLON in time. As in the MEDITERRANEAN region, they are small genera, none exceeding 25 species—any larger (older) than that have usually reached to greater dispersal. Five are endemic to the MADRAS region, all monospecific. Some are large tropical genera like *Mimosa* with 400 species, or *Jatropha* with 200, which had not yet reached CEYLON when it was cut off, and the rest mostly are palaeotropical, probably in the same conditions. It is not possible here to go into the details of the peopling of CEYLON with plants, though it is worthy of special notice that in the MADRAS endemics and in other features of the flora there is some definitive evidence that MADRAS was independently connected to FURTHER INDIA as well as round by CALCUTTA, for there are a number of genera of that region that do not occur in CEYLON, and other things.

The families with endemics only in SPAIN or only in the BALKANS are usually represented in the other country by a few non-endemics, which have evidently not been there long enough to give rise to local species. Indications like this, tending to show that some family or genus has reached A sooner than B, may prove useful in tracing migrations, and perhaps even in tracing regions of origin. *Resedaceae*, again, has 15 out of 23 endemic in SPAIN, and only one of eight in the BALKANS, so that it looks as if they had actually commenced in or near SPAIN, and spread eastwards. *Cistaceae* show somewhat similar phenomena.

All over the world, the large families show the largest numbers and proportions of endemics. Even in the HAWAIIAN ISLANDS, with perhaps the most remarkable endemic flora in the world, the bulk of it is found in *Campanulaceae*, *Caryophyllaceae*, *Compositae*, *Gesneraceae*, *Labiatae*, *Rubiaceae*, and *Rutaceae*. In the GALAPAGOS, it is chiefly *Amarantaceae*,

Boraginaceae, *Compositae*, *Euphorbiaceae*, and *Rubiaceae*, again large families, but indicating a somewhat different source or sources of origin. Similar facts are true of the genera. It is abundantly clear that endemism is not a casual phenomenon of relicdom, but is obeying definite laws, and is open to inductive study, which may lead to many useful results, even though it does contradict the theory usually known as Darwinism.

Another interesting fact is that the representation of the families in SPAIN and in the BALKANS is not altogether unlike. After each family in the tables on pp. 70-3 is given its place in the other list. Adding these numbers up in eights, the first eight adds to 39 in the Spanish list, 42 in the Balkans, seven out of the eight families being the same in both. The following eights give 167/144, 210/206, 220/291, and 286/333. The number of endemics in other words, shrinks fairly well with the size of the family. The top seven families, which are the largest families in EUROPE, have 57% of the BALKAN species and 62% of the SPANISH, and contain respectively 67% and 68% of the endemics, a close agreement. They contain a good half of the whole flora of most, or all, European countries. Their percentage of endemics is markedly higher than that of their species, which bears out what we have said about the greater proportion of endemics in the larger families.

If one look into the sizes of the genera in any MEDITERRANEAN (or other) flora, one finds a striking difference between those that do, and those that do not, contain endemics. On the principles here employed, it is clear that the endemics should be in the larger (older) genera. Probably, of course, there will be exceptions, with various reasons behind them. One will not expect biological phenomena to occur with deadly exactness. But one will expect that even though the two sets of numbers overlap, those with endemics will be mainly towards one end of the scale, those without towards the other. Supposing that we examine the *Compositae* in the BALKANS and in SPAIN, we find

Proportions of endemics in Spain and in the Balkans in genera of the Compositae of different sizes

SPAIN

Size of genus	Number of gen.	With endemics	Without	% with	Total endemics	% of endemics
1 species	49	7	42	14.2%	7 spp.	3.2%
2-3	42	13	29	23.8%	14	6.4%
4-6	22	18	4	81.8%	30	13.7%
7-12	12	11	1	91.6%	31	14.2%
Over	8	8	0	100.0%	135	62.2%
	<hr/> 133	<hr/> 53	<hr/> 80	<hr/> 40.0%	<hr/> 217	<hr/>

Average per genus 1.6

BALKANS

1 species	32	2	30	6.6%	2 spp.	0.6%
2-3	25	8	17	32.0%	11	3.4%
4-6	16	10	6	62.5%	20	6.1%
7-12	9	8	1	88.0%	23	7.0%
Over	18	18	0	100.0%	268	82.4%
	<hr/> 100	<hr/> 46	<hr/> 54	<hr/> 46.0%	<hr/> 324	<hr/>

Average per genus 3.24

The greater the size of the genus, the more endemic species has it, in proportion, and upon the whole. The Balkan genera show a higher percentage of endemism, in the large genera especially, which goes perhaps to show that the *Compositae* are older in the BALKANS than in SPAIN. But full taxonomic investigation is absolutely needed, especially as the Spanish flora recognises more genera than does the Balkan.

An approximate count of the whole Balkan flora goes to show that the number of "ones" with endemics is 14, against 259 without, of twos 17 against 79, of tens 9 against 5 (note order reversed), while above 20 species there are 58 genera, ranging up to 171 species, and of these only two, *Salix* with 24 and *Medicago* with 29, are without endemics.

If now we take the Spanish and Balkan genera that contain the largest numbers of endemics, we get :

Spanish and Balkan genera with largest numbers of endemic species

DICOTS			Spain	
	Position in other column		Endemic species	Spp. in world
1. Centaurea	(1)	Comp.	49	600
2. Hieracium		Comp.	37	750
3. Saxifraga		Saxi.	31	325
4. Genista		Legum.	29	90
5. Linaria		Scroph.	28	100
6. Ononis		Legum.	22	75
7. Ranunculus		Ranun.	21	325
8. Galium	(11)	Rubi.	19	250
9. Armeria		Plumb.	17	60
10. Senecio		Comp.	16	2000
11. Teucrium		Labi.	16	180
12. Thymus	(4)	Labi.	16	100
13. Ulex		Legum.	15	20
14. Arenaria		Caryo.	15	100
15. Dianthus	(2)	Caryo.	15	250
16. Iberis		Cruc.	14	30

360

Average (world) 327

DICOTS			Balkans	
1. Centaurea	(1)	Comp.	112	600
2. Dianthus	(15)	Caryo.	63	250
3. Verbascum		Scroph.	57	210
4. Thymus	(12)	Labi.	56	100
5. Campanula		Camp.	50	300
6. Silene		Caryo.	46	400
7. Viola		Viol.	32	400
8. Astragalus		Legum.	30	1600
9. Stachys		Labi.	30	200
10. Asperula		Rubi.	29	80
11. Galium	(8)	Rubi.	25	250
12. Trifolium		Legum.	23	290
13. Hypericum		Gutt.	22	300
14. Crepis		Comp.	21	240
15. Euphorbia		Euph.	20	750
16. Achillea		Comp.	19	115

635

Average (world) 380

Families with genera/endemic species

1. Compositae (1)	3/102	Compositae (1)	3/152
2. Leguminosae (2)	3/66	Leguminosae (2)	2/53
3. Caryophyllaceae (3)	2/30	Caryophyllaceae (3)	2/109
4. Labiatae (4)	2/32	Labiatae (4)	2/86
5. Scrophulariaceae (5)	1/28	Scrophulariaceae (5)	1/57
6. Rubiaceae (6)	1/19	Rubiaceae (6)	2/54
7. Saxifragaceae	1/31	Campanulaceae	1/50
8. Ranunculaceae	1/21	Violaceae	1/32
9. Plumbaginaceae	1/17	Guttiferae	1/22
10. Cruciferae	1/14	Euphorbiaceae	1/20
<hr/>		<hr/>	
Total spp. Spain	360	Balkans	635

Numbers in brackets give position in other column. The first six are the same in each.

All these 28 top genera are British, as would be expected by the laws of ASA. They are all near the top of their families, nine being actual leaders. They contain 995 out of a total of 2695 endemics of SPAIN and the BALKANS, or 37%. In each case they belong to ten large families, the top six of which are the same in both, with 24/788 gen./spp. against 8/207 in the other four. The average world size of these genera is very large indeed. These facts are repeated all over the world, and there seems to be no possibility of maintaining the thesis that endemics are relics, except in special cases. *Alyssum*, with 21 endemics in all, is the largest non-British genus, but there are many British genera that surpass this figure, up to *Centaurea* with 112 in the BALKANS alone.

Roughly speaking, the great majority of those genera that have many endemics have some in both countries, and what reason should there be for this if these genera were relics. Much more probably, it is they that are the oldest in the MEDITERRANEAN region, and have therefore spread to the widest dispersal there, and therefore are most likely

to be found also in the British flora. On the other hand, genera with very small numbers of endemics are usually found to show them only in SPAIN, or in the BALKANS, not in both, and to be rare, if found at all, in BRITAIN.

These tables provide many queries for the selectionist. Why should *Centaurea* have so many "relics" in the MEDITERRANEAN region, and none in BRITAIN, where there would seem to be less competition? Why is BRITAIN not a refuge? Why should *Verbascum* have 57 relics in the BALKANS with 25 widely dispersed species, and only 5 with 12 in SPAIN—the proportions reversed? Were some of the wides killed out in the fight with the endemics? Why has it only one relic in CRETE, close to the BALKANS, and an island, usually supposed to be a good refuge? Why should *Asperula* and *Galium* have 28 and 25 relics in the BALKANS, and only 5 and 19 in SPAIN, while *Senecio* has 17 in one and 16 in the other? There is no end to the awkward questions that may be brought up, and that are quite insoluble by the aid of the theory of adaptational structural selection, but which show that endemism is a subject that follows definite rules, and that will repay inductive study. There is still ample opening left for those who, in HOOKER's words, "find it far easier to speculate than to employ the inductive process".

The flora of Sardinia. Let us now consider one of the MEDITERRANEAN islands, further from the mainland than BRITAIN, and with deeper water between, probably sooner isolated. One may predict that the bulk of the flora will belong to the same families as in BRITAIN, the older, as usual, being the better represented. Taking the 14 families with more than ten genera, we find them, with one exception, the same as the largest families in BRITAIN; *Ericaceae* there replaces *Borraginaceae*. They have 379 genera out of 571, or 66%, while in BRITAIN they have 287 out of 475, or only 60%. The only families in SARDINIA that are not found in BRITAIN are 14 small ones with 20 genera among them. The proportion of endemism is not so high as one might expect, for what reason is not evident, but that of the Dicots is double that of the Monocots; there is a greater proportion in the larger genera, and the average world-size is greater :

Flora of Sardinia to show local and world sizes of genera, and British relationships

Size in Sardinia	Genera	DICOTS		Genera	MONOCOTS	
		Proportion British	World Size		Proportion British	World Size
8 or more species	31	100%	318	8	100%	243
4, 5, 6, or 7 species	71	84%	129	28	85%	84
2 or 3 species	122	58%	57	35	77%	41
One only	218	39%	42	58	48%	34
Total	442			129		

Arranging the families with and without endemics in parallel rows by their numbers of species in SARDINIA, we get :

Sardinian families with and without endemics

With endemics 183, 179, 77, 66, 58, 57, 52, 40, 35, 34, 26, 25, 21, 19, 18, 16, 16, 16, 13, 10, 9, 6, 4, 2/3.
 Without 29, 21, 16, 12, 12, 11, 10, 9, 8, 8, 8, 8, 7, 7, 6, 6, 6, 5, 5, 5, 5, 4, 4, 4, and 12/2, 19/1.

This very striking feature about endemism shows everywhere except in a few places where there are a few endemics and those undoubted relics, mainly places where they came under the influence of the cold in the glacial period.

The larger genera in SARDINIA are all British, but the proportion decreases down to the ones, where it is below 50%. This arithmetical phenomenon, of which the writer has published numerous examples, is inexplicable by aid of selection or of adaptation. There is here the effect of a definite factor, which has already been sufficiently shown to be mere age, that allows time for the resultant of all the active factors to work, and we must fully understand these mechanical effects before we can properly study those of the vital factors.

The figures show that the larger a genus or family is in SARDINIA, the better is its chance of appearing in BRITAIN. *Compositae* head the list by a large margin, followed by *Cruciferae*, *Labiatae*, *Leguminosae*, *Scrophulariaceae*, *Umbelliferae*, *Borraginaceae*, and *Euphorbiaceae*, all families that have already figured high in our lists. Just as in going northwards, and especially at great barriers like mountains

or sea, the smaller families and genera are those chiefly dropped out, so are they dropped out in the formation of endemics, which is more and more rapid the larger the family (hollow curve). The older or larger families and genera are those that have had the most time, whether to travel northwards, to evolve many species, or to form others (which begin as endemics) from those already present ("to him that hath shall be given").

The other MEDITERRANEAN islands may be passed over in a few words, as all show the same phenomena as SARDINIA. CRETE presents a point of interest. The average local size of a Dicot genus in the BALKANS (including CRETE) is 7 species, but of the 400 out of the total of 739 that actually reach CRETE, it is 11, while of the 191 Cretan genera that also reach BRITAIN, it is 18. The laws of ASA are very important in distribution, and practically dispense with any need to call in adaptation.

If we compare the endemism of SARDINIA and the BALEARICS with that of SPAIN or the BALKANS, we find that a great part of the genera that show endemism in the islands also show it on the mainland. They belong mainly to the genera that on the whole are the oldest, and therefore the most widely dispersed in the MEDITERRANEAN region.

The seniority of the Dicots in the MEDITERRANEAN area is so marked that one may with some confidence make the further prediction (150 p. 87) that in the CANARIES, which are very old as islands, and are upon the extreme edge of the MEDITERRANEAN region, one will find the position of the Monocots, as regards endemism, to be even lower than in SARDINIA. This is strikingly borne out by the facts, for while the CANARIES have 418 species of Dicot endemics, which would lead one to expect about 105 Monocot endemics (four to one, *cf.* AA. p. 22), they have in reality only 27.

Relationships between southern endemism and the composition of the British flora. If, as we have seen good reason to believe, dispersal is chiefly regulated by the three laws of ASA, the large and old families, with many endemics in the south, will be the largest and oldest in BRITAIN. A glance at the table on p. 70 shows that all Spanish families with endemics are British, excepting three with one endemic each—*Capparidaceae*, *Gesneraceae*, and *Globulariaceae*. In the Balkan list six families, all small, do not occur in BRITAIN

—*Asclepiadaceae*, *Gesneraceae*, *Rutaceae* with five endemics each, *Capparidaceae*, *Globulariaceae*, and *Tamaricaceae* with one each. Even here, three of them also occur in SPAIN.

As the endemics are mainly in the larger genera, one may make about as good a prediction by picking these out as most likely to be found in BRITAIN. There are 96 with at least 15 species, and all but nine occur in the British flora. One may even make more predictions, for example that the British single genera (one only in the family) that have endemics in both SPAIN and the BALKANS will be larger in BRITAIN than those with endemics only in one of these countries. They actually show (in British species) 37, 26, 21, 16, 8, 8, 8, 2 against 5, 3, 2, 1, 1, 1, 1. Or again, one may predict that the larger genera of BRITAIN will usually have endemics in south EUROPE; this is the case for 93% of the Dicots, but for only 79% of the Monocots, again a difference in favour of the former. We may even expect that the most widely dispersed in BRITAIN will show the most southern endemics, and we find that those with one species only and with a dispersal in BRITAIN not more than 56 have southern endemics of 43% of their number, 56-112 of 61%, while the twos have 118%, threes 170%, fours and fives 188%, sixes to tens 196%, and larger 226%. These are again simple arithmetical relations, which help to make the support of the idea of relicdom rather precarious.

Range of dispersal in Britain. There are 101 Dicot species, in 71 genera, which range over all the 112 vice-counties of BRITAIN. Placing the families by the numbers that they contain, we get the table that follows. The first eight families contain the first seven of the lists of Spanish and Balkan families on pp. 70-3. *Rosaceae* displaces *Ranunculaceae* from the top eight of the Spanish list and *Campanulaceae* from the Balkan list. Of the 71 genera these families contain 46, and of the 101 species 62. They also receive more additions at 111, 110, &c. Smaller and smaller families come in as one goes down the list. These eight top families also contain 179 of the 347 British Dicot genera, or more than half, and 69% of the endemics of SPAIN and the BALKANS. There are 20 families with endemics that have no species reaching 112 in BRITAIN, but they only contain among them 202 endemics in the BALKANS, and the last five families, that have no species in BRITAIN at all, have only 17 endemics

Dicot families, any of whose members reach a dispersal of 112 vice-counties in Britain, in order of the number of genera that do so

Family	Place in Spain and Balkans	British Genera	No. with at least one species 112	Extra spp. 112	Total 112-105	Endemics in Spain	Endemics in Balkans	Total Endemics
Comp.	(1, 1)	43	14	4	30	217	323	540
Caryo.	(4, 2)	12	6	2	12	78	175	253
Labi.	(6, 3)	18	6	1	11	75	153	228
Legum.	(2, 6)	17	5	2	14	137	105	242
Crucif.	(3, 7)	24	4	1	9	112	96	208
Rosac.	(16, 14)	15	4	1	14	15	23	38
Scroph.	(5, 4)	13	4	5	16	78	128	206
Umbell.	(7, 5)	34	3	—	9	61	106	167
Ranunc.	(8, 11)	11	2	5	8	31	37	68
Rubi.	(10, 9)	4	2	2	6	25	53	78
Polygon.	(39, 34)	3	2	3	10	3	3	6
Eric.	(42, —)	11	2	—	3	2	—	2
Betul.	(—, —)	4	2	—	3	—	—	—
		209	56	26	145	834	1202	2036
15 fams. with one gen. 112 ¹		48	15	4	32	103	174	277
		257	71	30	177	937	1376	2313
Percentage of Brit. Dicots		74 %						

¹ Aral., Borag., Caprif., Chenop., Dips., Euphorb., Geran., Lin., Onagr., Oxal., Plantag., Primul., Urt., Valer., Viol.

among them. Of the genera with a dispersal in BRITAIN of 112-109, 76.9% have endemics, dispersal 108-101 63.6%, and 100 or less only 48% have endemics.

A good illustration of the way in which the endemics in the different MEDITERRANEAN countries agree in belonging only to the larger genera or families, and very commonly to the same ones in countries far apart, was given as Table XXVII on p. 89 in (150).

So closely are the arithmetical laws of ASA that we have been illustrating followed, that we may even take single families or large genera to show them. Of the *Compositae*

of SPAIN and the BALKANS, 74 genera show endemics there. Twenty-seven with endemics in each country show 442 endemics in all, and have an average world size of 215; while 47 show endemics in only one of the two countries, have 82 endemics in all, and an average world size of 30 only. Of the 27,85% are British, while of the 47 only 19% are.

If the British flora owed its dispersal and composition to adaptation, one could not do any prediction from the floras of southern EUROPE, whereas we have seen that most of the larger genera, and other features, can easily be predicted. Mere size or age of families and of genera has had an enormously greater influence than anything else in determining the composition of a flora, and the proportions of endemics contained in it in the countries where it is oldest.

Monocotyledons. So far we have dealt only with Dicots, not because they show better results, but to save space, and because the Monocots, while showing results that are essentially the same, yet show them in such different degree that there is evidently a hitherto unnoticed difference between the two groups. The table of numbers of species and of endemics, was given above.

This table offers points of interest. It shows clearly how the larger families have endemics in both countries, and that the smaller have endemics in one, or none in either. A noteworthy feature is the much smaller percentage of endemism than in the Dicots (14 and 15% against 32 and 33%). This at once suggests that the Monocots are later arrivals on the whole. It has been suggested that they are slower in mutation, but this does not explain cases where the figures go the other way. The differences between individual families are also very marked. Careful and detailed work upon such figures as are given here should ultimately teach us much about dispersal, but much more work is needed yet, and more mathematical skill than is usually possessed by the biologist, including the writer. It should also lead to results which will be useful in geological and other investigations.

Endemic genera. Most endemics are species in large genera, but there are also many genera that may be classed as endemic as they are very local. There are a number of these in south EUROPE, though often overlapping into AFRICA or ASIA. They behave like the species, *e.g.* in belong-

ing to the larger families. *Umbelliferae* with 38 and *Cruciferae* with 34, both well-known Mediterranean families, head the list in EUROPE, *Compositae* and *Gramineae* with 24 each following, these four families thus having nearly half the total number of about 250 in that area. Not only so but they belong to existing sub-families, usually the most important. For example, more than half the *Umbelliferous* genera belong to the *Apioideae-Ammineae*, the largest division of the family. Only very rarely indeed, in any part of the world, does one find endemic genera as instances of very discontinuous distribution, or belonging to out-of-the-way groups.

If in conclusion we sum up the statistics, we get :

*Proportions and distribution of Spanish and
Balkan endemics*

DICOTS

British genera	Genera	Species (Spain)	No. per genus	Species (Bkns)	No. per genus	World size	No of 112s
Endemics in both	119	737	6.1	1098	9.1	172	83
Endemics Spain only	53	141	2.7	—	—	57	9
Endemics Bkns. only	34	—	—	88	2.6	69	8

Non-British genera

Endemics in both	37	66	1.8	149	3.9	—	—
Endemics Spain only	100	176	1.7	—	—	—	—
Endemics Bkns. only	76	—	—	194	2.6	—	—

MONOCOTS

British genera

Endemics in both	15	72	4.8	73	4.8	154	6
Endemics Spain only	19	32	1.6	—	—	53	9
Endemics Bkns. only	11	—	—	63	5.7	32	1

Non-British genera	Genera	Species (Spain)	Nº per genus	Species (Bkns)	Nº per genus	World size
Endemics in both	3	3	1.5	16	5.3	—
Endemics Spain only	10	12	1.3	—	—	—
Endemics Bkns. only	8	—	—	10	1.4	—
Total Dicots						
British	206	878	4.2	1186	5.7	126
Non-British	213	242	1.1	343	1.6	—
Total Monocots						
British	45	104	2.2	136	3.0	81
Non-British	21	16	0.8	26	1.3	—

The percentage of endemics in genera that appear in BRITAIN is fairly closely the same as the actual percentage of the whole number of species that belong to them. This fact shows in nearly all the larger families, and is an almost full denial of the supposition of relicdom. One can hardly imagine relics formed in proportion to the number of species. One or two families appear as if they might to some extent be polyphyletic, especially *Borraginaceae*.

The phenomena of endemism clearly show themselves in such a way that it is evident that they are determined by the action of law; it would be impossible that relics should behave in such a manner. This view might probably have been accepted long ago, had it not been that in this acceptance is involved the destruction of the Darwinian theory of the operation of evolution, that it proceeds by the selection of advantageous variations, and little by little. Endemism is clearly a normal accompaniment of the composition of any flora that has reached a certain age in the place where it is growing, especially, it would seem, if that locality be rather isolated, or mountainous, or otherwise broken, or when the plants there perhaps come under the influence of certain stimulants to a greater extent than usual, a fact which, upon the working hypothesis which I have used since 1907 (p. 96) would be likely to stimulate a rearrangement of the nucleus, most often only to such an extent as to produce a new species, but at times going far enough to produce a new genus.