Some General Principles of Plant Distribution as illustrated by the South African Flora.

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INTRODUCTION.

THE geographical distribution of plants, which has been described by Darwin (20), in one of his letters to Sir Joseph Hooker, as 'that grand subject, that almost keystone of the laws of creation', has been studied from many different standpoints, and, with the increasing interest in plant ecology, is now attracting more and more attention. Darwin's own position is summarized in a single sentence in the 'Origin of Species' (16, p. 360): 'If the difficulties be not insuperable in admitting that in the long course of time all individuals of the same species, belonging to the same genus, have proceeded from one source, then all the grand leading facts of geographical distribution are explicable on the theory of migration, together with subsequent modification and the multiplication of new forms.' The general progress of the study of plant distribution since the publication of the 'Origin of Species' has been dealt with by Thiselton-Dyer (20), from whose paper a few extracts will be taken. 'If Darwin laid the foundations, the present fabric of botanical geography must be credited to Hooker. It was a happy partnership. The far-seeing generalizing power of the one was supplied with data and checked in conclusions by the vast detailed knowledge of the other.' Hooker's views were given in the 'Introductory Essay to the Flora of Tasmania' (27) and in the 'Distribution of Arctic Plants'—publications which were, according to Thiselton-Dyer, 'only less epoch-making than the "Origin" itself'. After Darwin, Wallace carried on the task of investigation, and his views are given in his well-known work 'Island Life' (35) and as late as 1911 in 'The World of Life' (36).

Both Wallace and Darwin objected to invoking geographical change as a solution of every difficulty. They believed in the general stability and permanence of our continental areas, while admitting 'wonderful and repeated changes in detail' (35, p. 101). Their views in this respect received great support as the result of the *Challenger* expedition, which furnished proof that the floor of the ocean basins has no real analogy

among the sedimentary formations which form most of the framework of the land. Hooker, however (27), was much more inclined than either Darwin or Wallace to find a way out of difficulties by supposing great geographical changes. In explaining the connexions between the isolated southern floras, he says, 'The most conspicuous characters that extra-tropical Africa presents in common with Australia are the abundance of the species of the following orders: Proteaceae, Compositae, Irideae, Haemodoraceae, Buettneriaceae, Polygaleae, Restiaceae, Ericaceae, Epacrideae, Decandrous Papilionaceae, Rutaceae, Thymelaeaceae, Santalaceae, Anthospermous Rubiaceae. . . . With regard to the natural orders enumerated, their genera are almost unexceptionally different in the two countries. . . . The many bonds of affinity between the three floras—the Australian, Antarctic, and South African—indicate that these may all have been members of one great vegetation, which may once have covered as large a southern area as the European does a northern. To what portion of the globe the maximum development of this southern flora is to be assigned it is vain at present to speculate, but the geographical changes that have resulted in its dismemberment into isolated groups over the Southern Ocean must have been great indeed.'

In contrast with this, I quote one more paragraph from Thiselton-Dyer (20, p. 303): 'Darwin objected to "continental extensions" on geological grounds, but he also objected to Lyell that they do not "account for all the phenomena of distribution on islands, such, for example, as the absence of Acacias and Banksias in New Zealand". He agreed with de Candolle that "it is poor work putting together the merely possible means of distribution". But he also agreed that they were the only practicable door of escape from multiple origins. If they would not work, then "every one who believes in single centres will have to admit continental extensions", and that he regarded as a mere counsel of despair, "to make continents as easily as a cook makes pancakes".'

Coming now to Thiselton-Dyer's own views and those of Guppy, who has contributed probably more than any one else to the detailed study of plant migration in recent times (24–26), we find that these authors are agreed that a theory of southward migration is the key to the interpretation of the geographical distribution of plants. Even with regard to the *Glossopteris* flora, Thiselton-Dyer says, 'I confess it would not surprise me if fresh discoveries in the distribution of the *Glossopteris* flora were to point to the possibility of its also having migrated southwards from a centre of origin in the northern hemisphere'. Guppy's earlier views were similar to those of Wallace. He sought to explain all the phenomena of distribution by migration. Later he was inclined to hesitate. As Thiselton-Dyer says, 'Guppy's heart failed him when he had to deal with the isolated case of *Agathis*, which alone seemed inexplicable by known means of transport'.

In his latest book (26), however, Guppy accepts Thiselton-Dyer's own views. He also elaborates the 'theory of differentiation', applying it first to families which, he states, tend to fall into two groups, the primitive and derivative, the first world-ranging, and the second restricted in their area. Differentiation and decrease of range go together. He goes on to apply the same principle 'in the tribe, in the genus, in the species, and in the local race or variety'. He takes the Geraniales, Geraniaceae, Geranieae, *Geranium*, sections of the genus *Geranium*, as examples, and quotes the work of Andrews on the development of the families Myrtaceae (1) and Leguminosae (2) in Australia.

Guppy further points out that, 'if the differentiation hypothesis is correct, no natural order could have been developed on the lines implied by the Darwinian theory, which, as interpreted in recent works, begins with the variety and terminates with the order, a process that reverses the usual methods of Nature'. 'Yet such a process', he says, 'as is there implied is common enough in the plant world, but it accounts not for the natural orders but for the oddities of plant forms.' 'It is here termed a specializing process in contrast with that of differentiation; but it is the differentiating process that has been the principal determining cause of diversification in plants'. There is probably much truth in this theory, though, taking into consideration the palaeontological record, it is doubtful whether it contains all the truth.

Guppy goes on to state that the differentiation theory could of itself explain distribution, if the land areas of the world were continuous and not affected by unstable climatic conditions, and he deals with the factors that modify its operation.

The theory of southward migration favoured by Thiselton-Dyer and Guppy permits of postulating the permanency of the general configuration of the land-masses of the earth's surface, and is so far in agreement with the views of Darwin and Wallace. The southern end of South Africa is a 'cul-de-sac into which the species have poured and from which there is no escape', hence the extraordinary congestion of species there. Again, as Guppy remarks (26), 'if it can be shown, as undoubtedly the general trend of the facts of distribution does show, that the divergence of plant types responds to the divergence of land-masses from the north, and that dissimilarity is intensified with distance from that pole, any evidence for a Tertiary Antarctic centre for the flowering plants would be discounted in advance'. Thiselton-Dyer and Guppy agree that the centrifugal dispersion of species from the north, which all acknowledge took place during the last Ice period, has been repeated often during the course of geological time.

'At a time when a genial climate prevailed over the northern or land hemisphere, the plants now represented in type in the warmer latitudes occupied the regions beyond the Arctic Circle. When this period gave

place to cooler conditions, the retreat to the south began; and the plants, as the diverging continents pulled them more and more asunder, became more and more distinct from each other. . . . When the warmer conditions returned, the plants advancing northwards met again in the common gathering ground around the Pole, but modified by their different experiences in southern regions lying oceans apart. There they mingled together, the eastern and the western floras, and when, with the next climatic change, they began again to retreat to their ancient home in the warmer latitudes of the south, the east had borrowed from the west, and the west from the east. The secular changes of climate have therefore tended in this way to mix together the floras of the globe.'

Recently, Willis, in a series of papers (37-44), has developed what he calls the 'age and area' law, which is based on the fact that endemic species in any country tend, on the whole, to have a narrower range than non-endemic species. The older a species in any country, the wider is its range. In South Africa, where the climatic conditions are very diverse and very mixed even in comparatively small areas, the action of this 'age and area' rule is greatly modified, yet, in a general way, it seems to hold and it fits in with Guppy's theory of differentiation. 'Differentiation and decrease of range go together.' The theories of Guppy and Willis have been applied very successfully by Small (32), in his detailed monograph on the Compositae.

Most botanists since Darwin have followed him in dismissing the possibility of multiple origins. The most prominent exception is Engler, who argues in favour of polyphyletic, as he calls it (21). Drude (18) also accepted the possibility of multiple origins for major groups. Clements (15) has discussed the matter fully, and he should be consulted for further references to the literature on the subject. He says, 'The idea of polyphyletic as advanced by Engler contains two distinct concepts: (1) that a species may arise in two different places, or at two different times, from the same species, and (2) that a genus or higher group may arise at different places or times by the convergence of two or more lines of origin'. Clements accepts Engler's views and proposes that the term 'polyphyletic' should be restricted, as its meaning would indicate, to the second concept, and that the term 'polygenesis' (first suggested by Huxley in the sense of polyphyletic) should be used for the first.

Clements regards the occurrence of different 'habitat forms' of the same species, e.g. of *Galium boreale* or *Aster levis*, in different areas, but obviously related to the area of the parent form, as proof of polygenesis, and he finds further convincing evidence in de Vries's mutations. 'The evidence is conclusive that the same form may arise in nature or in cultivation, in Holland or in America, not merely once, but several or many times.' 'In the presence of such confirmation, it is unnecessary to accumulate proofs.' Clements also considers that de Vries's work proves the

possibility, not merely of the polyphyletic of genera and higher groups, which, since the appearance of Engler's work, has been very generally accepted by botanists, but also for species. 'De Vries found that *Oenothera nanella* arose from *O. lamarckiana*, *O. laevifolia*, and *O. scintillans*; *O. scintillans* arose from *O. lata* and *O. lamarckiana*; *O. rubrinervis* from *O. lamarckiana*, *O. laevifolia*, *O. lata*, *O. oblonga*, *O. nanella*, and *O. scintillans*, &c.' Numerous similar examples could be applied from the recent literature of genetics.

If the polygenesis of species, particularly, is to be accepted as an established fact, the difficulties of explaining the distribution of many poly-genetic species at once disappears; but, of course, there has been no intention on the part of any one of asserting that all species originate in this way. It will be shown later that in the case of certain South African endemics a polygenetic origin is at least extremely probable.

Schönland (29) has summarized some of the facts and theories concerning the origin of the angiospermous flora of South Africa, and he remarks at the outset that 'the question of the origin of our flora having been approached almost entirely by European botanists, who were naturally influenced by the leading features of the development of the floras of the northern hemisphere, it has sometimes greatly suffered through forced interpretation of facts and supposed facts (compare, e.g., Thiselton-Dyer, 1878)' (19). Schönland contends that the data for an adequate treatment of the subject are absent even to this day, and that there is need for caution in dealing with the whole question. Nevertheless, though he kept in mind Wallace's warning that it is 'so easy and pleasant to speculate on former changes of land and sea with which to cut the Gordian knot offered by anomalies of distribution', Schönland, after considering the facts of distribution in a number of separate families, found himself forced to the conclusion that in late Mesozoic times, possibly even up to the Cretaceous period, there was still a direct land connexion between Australia and South Africa and, possibly even in Tertiary times, between tropical Africa and America.

Recently Schönland (30) has given a summary of the distribution of the genera of South African flowering plants with special reference to those found in the divisions of Uitenhage and Port Elizabeth without discussing further the question of origins.

The axiom that the present is the key to the past has been accepted ever since the time of Lyell, at least theoretically, but biologists have not always been willing to use it as much as they should in practice. Not only should it be applied to geology and biology, but also to climatology. Until we know as much as can be known about present-day tendencies, it is well to be cautious about dealing with the past, but I agree with Schönland that, so far, all the evidence goes to show that the climate of South Africa,

though it is subject to extreme fluctuations, has not altered, materially at least, since Upper Cretaceous times. I have pointed out elsewhere how tree-veld in South Africa has not, as has often been supposed, replaced more mesophytic forest (9), and how our extensive grasslands, though they often give way to forests (11), yet must have existed for a very long period of time, since most of our mammals in South Africa are adapted to grassland conditions (7, p. 150). In a word, present-day conditions, in a general way, as regards the main types of vegetation, must have existed for a very long period of time.

It is the object of the present paper to consider chiefly present-day tendencies in plant distribution in South Africa. The fact that these often do throw light on the past will be treated incidentally. Attention, therefore, is directed chiefly to the distribution and origin of species rather than to higher groups, a method which differs from that pursued by most plant geographers.

PRESENT-DAY CONDITIONS IN SOUTH AFRICA.

It is, of course, impossible, within the limits of the present paper, to give very full details regarding the distribution of the various types of vegetation in South Africa, nor is it necessary for our present purpose. It will be sufficient to recall the leading facts. Details have been given by the writer in various papers (4-13). There are many distinct climatic areas in South Africa, and there is a distinct advantage to be gained by arranging them in a series, beginning with the most adverse types and ending with the most favourable. Any great subdivision will not be attempted here, although, if small differences were taken into account, the series could be made a very long one. Even if space permitted, it is doubtful whether great subdivision is desirable, for the study of experimental plant ecology has shown that environmental differences as regards water content, humidity, light, or temperature have to be considerable to cause any distinguishable morphological adjustment in plants. They are, as Clements (15) has shown, much greater than the unit differences recorded by instruments. 'In short, the differences of habitats, as ascertained by thermograph, psychrometer, and photometer, are much greater than their efficient differences, and, with respect to their ability to produce modification, habitats fall into relatively few categories.' In South Africa, too, many species are so adaptable as to be able to inhabit rather widely different habitats, e. g. two or more of those given below. Though differences in soil conditions are efficient in causing changes, yet in South Africa the climatic factors are of more importance. The chief climatic areas, roughly arranged in order of increasing mesophytism, are the following:

(1) *Western region.* The Namib and stony or sandy desert areas of the western side. The rainfall is very irregular and small in amount.

What does fall is usually summer rainfall, but whole years may pass without any. The average temperatures are lower than at corresponding latitudes on the eastern side, owing to the absence of the warming influence of the Mozambique current. The region becomes moister and more tropical towards the north and east. The soil is mostly sandy or stony. Vegetation of scattered xerophytes in the driest parts, passing first into *Aristida-veld* and then into more mesophytic grass-veld and tree-veld in the moister eastern and northern portions.

2. *Central Karroo region.* The rainfall is small in amount (3–14 inches) but more regular, increasing in amount from west to east. General altitude from 1,800 to 2,500 ft., but the mountains which form the escarpment of the central plateau are from 4,000 to 8,000 ft. high, running from west to east. These have many species belonging to south-western or eastern genera. The temperature of the Karroo shows extremes of heat and cold, with frosts in winter. It forms a climatic barrier of considerable importance between south-west and east, and it would be still more important were it not for the mountains that cross it. The Karroo soils are hard-baked clay, very rich in salts. The vegetation is composed of dwarf shrubs and succulents.

3. *Cape or South-Western region.* Winter rains and dry, hot summers. Annual rainfall 20 to 40 inches. In places the rainfall amounts to 60 inches or more and the summer heat and drought is tempered by south-eastern mist-clouds. Temperatures, except during the summer months, fairly low, but actual frosts, except at high altitudes, are not common. Soils varied. Dominant vegetation of sclerophyllous shrubs with patches of eastern forest in moister situation. Flora shows affinities with South-West Australia, and also, to some extent, with the Mediterranean and Europe, though the species in nearly all cases are distinct.

4. *Sand-veld Region of the Kalahari.* Summer rainfall increasing from about 10 to 20 inches from west to east. Temperature considerably higher, becoming tropical towards the north. Sandy soil or sand-dunes with underground drainage. No surface water. Vegetation of grass-veld passing into tree-veld. Flora with close eastern or tropical affinities.

5. *Dry Thorn-veld (Low-veld) and Succulent Scrub Areas of the Eastern side.* Summer rainfall 20 to 30 inches. Great extremes of temperature. Very hot in summer, regular frosts in winter. Hot winds an important feature. Soils dry-baked clays, rich in salts (cf. the Karroo, which these areas resemble in many respects). Vegetation of grass-veld, tree-veld, succulent and thorny scrub.

6. *High-veld and Mountain Areas of the Eastern side.* Summer rainfall 30 to 50 inches and also mist-clouds. Temperature range (both daily and yearly) not so great as in the low-veld of the valleys, but frosts in winter are experienced outside the forests. Soils loose, deep, well-

aerated loams, or sometimes sandy, poor in plant food. Vegetation grass-veld, scrub, and forest.

7. *Coast-belt of the Eastern side.* Summer rainfall 30 to 40 inches. Temperatures uniformly fairly high, but not extreme. Frosts absent. Soils varied. Vegetation grass-veld, scrub, and subtropical forest. Flora with close tropical affinities (see Bews, 12).

WIDESPREAD SPECIES.

Species which belong to the climax plant communities in the western, south-western, and central regions often are found to belong also to early stages of the plant succession on the eastern side, so that the arranging of the climatic areas in an ascending series reproduces, to a certain extent, the various stages of plant succession in the higher types. Any species which, under favourable conditions, is able to oust another species is to be reckoned of a higher ecological type. The primitive ecological species tend to be widespread, the higher types more restricted in their ranges. For instance, if we consider the 320 species which are common to the Cape Peninsula and Natal, we find that, while they belong to widely different growth-forms and show no possible phylogenetic relationships, they practically all agree in belonging to early stages of the succession as ruderals in subseres or marsh and aquatic plants in the hydrosere, as litoral plants, or as xerophytic light-demanding species in the xerosere (13).

A little consideration will show why, in a country like S. Africa, widespread species usually belong to early stages of the succession. We have seen that South Africa shows a number of distinct climatic areas with increasing mesophytism in a general way from west to east, but with a south-western area, which, though it has a fairly high rainfall, receives that rainfall in winter instead of summer and is separated from the regions of summer rainfall by the dry Karroo. Nevertheless, traversing all the areas there are found primitive habitats, which are to a large extent uniform. They are :

1. Cultivated land, waste places, &c., with ruderal species.
2. Lakes, streams, marshes, with aquatic or semi-aquatic species.
3. The seashore habitat, mostly sandy, with widespread littoral or sand-dune plants.
4. To a less extent the mountain ranges which cross South Africa.
5. Drier areas in the (thorn-veld) river valleys, open rocky situations on steep slopes, &c., are common all over the eastern side and differ but little from the Karroo and western areas as a whole. They are occupied by primitive ecological types which are soon ousted by others in the east.

In addition to these primitive habitats, it should be remembered that South Africa lies south of a fairly uniform tropical region to the north,

where tropical species are able to cross the continent without encountering any barriers. This explains the connexions between the subtropical areas in the west and those in the east, but not the connexion between the Cape Peninsula and Natal.

THE ORIGIN OF NEW SPECIES AND VARIETIES.

Species which occupy any of these primitive or relatively primitive habitats listed above naturally have no difficulty in spreading all over South Africa, and a large number of them are thus widespread. Now, if a species which is adapted to extreme conditions in the course of its spread comes into contact with more mesophytic conditions it is, as a rule, rapidly ousted in the course of plant succession by more vigorous growing, more mesophytic species. But if the primitive species is capable of varying, it may give rise to a new variety or it may produce a new species capable of holding its own with other competitors. Many examples of this will be given later. The genus *Rhus*, e. g., has many species which have developed in this way.

It is a well-known fact among gardeners that the cultivation of a species often leads to variation or mutations. The same thing would appear to happen in nature when a species in the course of its migration comes into environmental conditions which differ from those which produced it. In South Africa this, as a rule, implies a change from xerophytic or hydrophytic to mesophytic conditions, since the former are widespread, the latter more local. That is why widespread species belong to early stages of the succession. Succession is usually towards the mesophytic. If, however, mesophytic conditions were widespread and xerophytic conditions local, the reverse might happen. A widespread mesophytic species in the course of its wanderings might give rise to one more xerophytic. This is of much less importance in South Africa at the present time, whatever it may have been in the past. However, another type is important, namely, when a tropical species which cannot withstand frosts gives rise to a temperate species which can. It has already been pointed out that to the north of South Africa tropical species are able to spread across the continent. Derived subtropical or warm temperate species invade South Africa at different points.

VARIOUS METHODS OF ORIGIN.

When we seek to apply the process just outlined to concrete examples, we find that these tend to fall into several different categories, and the process itself requires further analysis. If for 'species' we read 'varieties' in each case, the number of possible examples is, of course, enormously increased.

1. A species A, which is widely distributed, may give rise to a closely allied but much rarer, more mesophytic species B in Natal, another closely

allied species C in the northern Transvaal, and still another D, more xerophytic perhaps, in Namaqualand, &c. This is a very common type of occurrence, and in some of the larger genera numerous rare endemics can be grouped around a single widespread species in this way. Even in smaller and more uniform areas, such as the south-western region or Natal, the same thing can be shown to take place. In other cases, only two species are involved, the one widespread, the other usually more mesophytic and always more restricted in its range.

2. A species A is produced in or brought into a certain suitable climatic area and it spreads until it reaches the limits of that area. Then it gives rise to another closely allied species B, which spreads over the next climatic area, and the process may even be repeated with the production of a species C. Examples of this can be given, but it is hardly worth while speculating whether B could again produce A on the other side of B's own area. As long as one is only dealing with habitat varieties, no doubt this could happen, but with differences of specific rank the matter would be considered highly controversial and it would be impossible to prove in any particular case that A had not been distributed to the other side of B's area by ordinary methods of migration.

3. Several species A, B, C, &c., which are closely allied are often found to have more or less the same distribution. Different explanations of their origin are possible. Species A may have given rise to B and to C; or A may have given rise to B and then B to C, or, on the other hand, an ancestral species may have broken up into A, B, and C.

4. The same kind of thing may happen in the case of various species A, B, C, &c., which do not have the same distribution but whose areas overlap, though this category is hardly worth distinguishing.

5. *Polygenesis*. There are several examples to be given later of a widespread species A, and another closely allied species B, the latter having widely discontinuous distribution. B is often a subtropical species recorded only for the Natal coast-belt and the northern Transvaal, or for the north-western and again for the north-eastern side, while A is a tropical species widespread to the north. Or A may be a widespread species in one of the primitive habitats from Natal across the Karroo to the Cape, while B occurs only in Natal and at the Cape in mesophytic forest habitats. Now the usual assumption has been that B has migrated from one mesophytic habitat to the other, or from one subtropical habitat to the other, an assumption which of course it is difficult to disprove and probably is correct in many or indeed in the majority of the cases. Ordinary migration, of course, must explain things when B, as in the case of many forest trees, is an isolated species without any closely connected species A growing in between its mesophytic habitats. It is worth noting that, in such cases, the fruits or seeds are usually distributed

by birds. In other cases, where there is present the widely distributed and closely related species, polygenesis would appear to afford a much simpler explanation. It would appear, therefore, that we must admit at least the possibility of polygenesis, for, if it affords a simpler explanation than ordinary migration over enormous areas, then the onus of proof is on the side of those who deny the possibility of multiple origins. Personally, I would go farther and advocate its extreme probability. As we have seen, Clements regards it as definitely proved by the work of de Vries.

If now we extend the facts learned about the species to the genus, tribe, and family, we may take it for granted that the same methods will apply. We find widespread families like the Scrophulariaceae have given rise to families with a restricted distribution like the Selaginaceae, which is mostly S. African, with a few isolated genera to the north, or the Myoporaceae, which are mostly Australian, with isolated examples elsewhere as far apart as China and the West Indies, and one genus *Oftia* in S. Africa. Some authorities sink these families as tribes of the Scrophulariaceae, but this does not affect our argument. Again, in the Verbenaceae, Iridaceae, and other families we find the oldest tribes or sections of the family concentrated in the south-western region of South Africa, while other younger tribes or sections are eastern. All these facts are very significant. Instead of beginning with the whole world's flora and finding connexions between the Cape and Australia, for instance, we begin with a restricted area and study the origin of species. Then with caution our methods and observations may be extended to a wider area and the time lengthened from the present into the past, always keeping in mind that the only key to the past is to be found in the present.

THE EVIDENCE.

It may be well to anticipate one or two obvious objections which may be brought forward to accepting certain of the following examples as evidence supporting the above conclusions. The first is that our knowledge of detailed distribution in South Africa is still far from complete. Species which are now thought to be restricted or discontinuous in their distribution may very well subsequently be shown not to be so. This objection is valid, no doubt, in some cases, but it certainly cannot apply to them all. Its weight as an argument is in inverse proportion to the number of examples given.

The second objection is that the distribution in each example given can be explained by ordinary migration and its abundance or rarity by adaptation to environmental conditions. As regards the first part of the objection, it is, as already admitted, difficult to disprove in any particular case, nor do I seek to deny that it is usually a sufficient explanation, especially in the case of species distributed by birds. As regards the second part of the

objection, it would, in this case, be brought forward only to justify the first, since some explanation on the theory of migration would naturally be expected of one species being widespread and another closely allied species having restricted or discontinuous distribution. The objection as a whole applies chiefly to polygenesis as an explanation of discontinuous distribution. The case for polygenesis has already been sufficiently argued, and it is maintained that the onus of proof is on the other side. It is clearly as difficult to disprove polygenesis as to disprove migration, and the former, in many cases, is the simpler explanation. Some critics would admit that widespread species might produce closely allied but not identical species at two or more separate points, i.e. they readily admit No. 1 but deny No. 5 of our categories as given above. In reply to this, it might be asked, how often does it not happen that the systematist allows himself to be influenced by geographical distribution in deciding that two closely allied species are distinct? It makes him magnify minor differences which are not constant and it makes him sometimes see differences which do not exist. The result is clearly reasoning in a circle. Species are said to be distinct simply because they are widely separated geographically and the chances of migration are remote, and then it is denied that identical species can arise in separate geographical areas.

A third objection is that many of the examples quoted are not really distinct species, though they are so described in the 'Flora Capensis'. That probably in many cases is quite true, but it is not really an objection, for, though they may be considered merely varieties, the same evolutionary principles are involved. In fact, it has only been because it was thought unnecessary that the words 'or variety' were not repeated after 'species' in each case above. The 'Flora Capensis', too, has been the work of many different specialists, and it is unlikely that they all have erred in the making of too many species. The earlier work of Harvey more probably erred in the other direction, for he was not inclined to split species too much. In a large flora of about 13,600 species the mass of evidence to be sifted is so great that the presentation of it is a matter of considerable difficulty. Considerations of space prevent us from dealing with all the families. An effort has been made to make as varied a selection of examples as possible, and if any reader is still not convinced, he can read through the 'Flora Capensis' for himself and find many more. Our aim for the moment is to illustrate the method, and its bearing on other aspects of botanical study will be discussed later. Though the 'Flora Capensis' has been mentioned, it must be admitted that the earlier volumes are so incomplete as a record as to be of little use, though the later volumes are better. I have relied chiefly for details regarding distribution on the various local check-lists, supplemented in the case of Natal by my own various field investigations. The lists referred to are those by Bolus and Wolley-Dod for the Cape (14),

Medley Wood for Natal (45), Phillips for Basutoland (28), Eyles for Rhodesia (23), and Burtt Davy and Pott-Leendertz for the Transvaal (17), though the last mentioned does not give any localities or any information regarding relative abundance. Since most of the check-lists and the 'Flora Capensis' adhere to Bentham and Hooker's arrangement of the families, we shall also arrange those selected in the same order.

Ranunculaceae.

The genus *Clematis* is widely distributed through temperate countries, occurring in the tropics chiefly in mountainous regions. *Clematis Thunbergii* extends from Abyssinia to South Africa. *C. brachiata*, which is closely allied, is more distinctly South African, extending from the Cape to Natal and Rhodesia, but not farther north. This illustrates a species extending over one area and being continued in another area by a closely allied species. Other species of the genus differ in minor characters, and their distribution illustrates our principles extremely well. *C. Oweniae* differs from *C. brachiata* in its filaments and anthers. It is a rare species with discontinuous distribution at Inanda (Natal) and again in Zululand. Then again we have *C. glaucescens* in the Tugela district, Natal, *C. virona* in southern Rhodesia, *C. wightiana* at Chirinda, all allied to *C. brachiata* and all rare endemics, so that within the limits of this single genus we find examples of most of our above-named categories. Oliver, in 'The Flora of Tropical Africa', mentions other interesting points. *C. chrysocarpa* is recorded from the Nile and again from Angola on the west side, and is very closely allied to *C. trifida*, a Madagascar plant. *C. Kirkii*, Mozambique, is nearly related to *C. Bojeri*, Madagascar. *C. Stanleyi*, a suberect shrub (like *C. Kirkii* and *C. chrysocarpa*), is found in Angola and again in the Transvaal, but the record for Natal is doubtful. Some of the species of *Ranunculus*, being water or marsh plants, have spread all over South Africa. Other species of *Ranunculus* are more or less rare endemics, e.g. *R. capensis* at the Cape, *R. Meyeri*, King William's Town, Natal, and the Transvaal at isolated points, *R. Baurii* and *R. Cooperi* on the Drakensberg. *Anemone capensis* is confined to the south-western region. *A. caffra*, which belongs to the same section (*Pulsatilloides*) of the genus and is fairly closely related, occurs only on the eastern side. *A. Fanninii*, which again is allied to *A. caffra*, is a rare Drakensberg species, and three other species are recorded for the Transvaal.

Thalictrum rhynchocarpum is one of the most interesting species in the genus, having only a single carpel. It occurs from Natal to Abyssinia at the edges of bush and in sheltered places. It has no close ally, though the north-temperate *T. minus* also occurs in South Africa. The genus *Knowltonia* is exclusively South African. *K. vesicatoria* is the widespread species from the Cape to Natal. At the one end of its area, the Cape, it has *K. rigida*, *K. gracilis*, *K. hirsuta*, and *K. daucifolia* related to it; at the

other end of its area, in Natal, it has *K. brevistylis* (recorded only for Inanda and for Zululand). The Ranunculaceae are a small family in South Africa, and to deal with other larger families in the same detail would be tedious. If many families are omitted altogether and others are dealt with very briefly, it is not because they do not provide equally good examples.

Cruciferae.

The genus *Heliophila* is endemic in South Africa. It is characterized by a peculiar embryo, the cotyledons being twice folded transversely. There is one species in Rhodesia, two in the Transvaal, four in Natal, and between fifty and sixty at the Cape. Excellent examples of our general principles may be found among the species concentrated at the Cape, showing that they apply to small areas as well as large. Thus *Heliophila diffusa* is marked by Bolus and Wolley-Dod as 'frequent' in the Cape Peninsula: *H. peltaria*, 'in similar situations but rarer', we find differs only in having shorter pods and two or three seeds instead of four to eight: *H. pilosa* is common all over the south-western region. Several other closely allied species, *H. graminea*, *H. linearis*, *H. stricta*, *H. divaricata*, are much rarer. Similar relationships are found among the shrubby species.

Bixaceae.

The genus *Kiggelaria* affords one of the best examples of a widespread xerophytic light-demanding pioneer shrubby type giving rise to a mesophytic forest tree type or possibly vice versa. Harvey, in the 'Flora Capensis', allows three species to stand—*K. africana* and *K. ferruginea*, both xerophytic; and *K. dregeana*, the forest type. Sim, in his 'Forest Flora' (31), sinks them all in one, *K. africana*, but admits that the forms are distinct. Such differences of opinion regarding specific rank are, of course, always bound to arise. The distribution of the forest forms is widely discontinuous, like the forests themselves.

Polygalaceae.

Several species of the large genus *Polygala* illustrate at the present day in South Africa the process of breaking up. *Polygala oppositifolia* is common from the Cape to Natal and Delagoa Bay. It is a typical pioneer of scrub occurring around the margins of bush. It has given rise to many more mesophytic forms. Harvey recognized eight varieties, but most of these, as well as others, have been recognized as distinct species by various authors. *P. myrtifolia* is another widespread species, which is very variable in its floral characters and leaves. In this case, Harvey recognized four varieties, all elevated to the rank of species by other authors. The fact that gradations between the distinct varieties can be recognized does not of course necessarily force them to fall into one species, for in a type like this hybridizing is quite likely.

P. virgata is also widespread and has five varieties, according to Harvey, and in addition a number of allied species, with more restricted distribu-

tion. *P. bracteolata* at the Cape has, according to Bolus and Wolley-Dod, produced a variety *umbellata* adapted to higher elevations on the hillsides. The genus *Mundtia* has two species, one at the Cape, the other in Brazil. *M. spinosa* has three varieties. *Muraltia* is a South African genus with about fifty species in the south-western region, four in Natal, two in the Transvaal; cf. *Heliophila*. *Securidaca*, on the other hand, is a typical genus with no representatives farther south than Rhodesia and the Transvaal. One species, *S. longipedunculata*, is very widespread from Abyssinia to the Transvaal and is very variable. The genus is much better represented in tropical America.

Malvaceae.

This tropical or subtropical family has many representatives which have spread over South Africa as over other temperate regions in other parts of the world. Species of *Sida* and *Abutilon*, genera well represented in the tropics, spread as weeds mostly over the eastern side. *Pavonia* is chiefly American, but some of the tropical African species (e.g. *P. macrophylla*, *P. odorata*) are very widely distributed from Natal to Abyssinia, and even to India. On the other hand, there are several endemics with narrow ranges (e.g. *P. Dregei*, *P. Kraussiana*) around the margins of coast-belt bush. *Hibiscus* as a genus is distributed all over South Africa and several of the species are interesting. *H. tiliaceus* is a tropical or subtropical sea-shore species, very distinct and remaining so, widely distributed all round the tropics. *H. trionum* is a very common subtropical weed, which gives rise to numerous distinct varieties. *H. aethiopicus* occurs all over South Africa and, like many others, could be broken up into several distinct species. *Malvastrum* is a genus with some twenty species mostly concentrated in the south-west, only one, *M. capense*, reaching Natal. It also comprises many American species.

It will be seen that, in the course of our survey of the families, we meet with many examples of isolated species with no obvious connexions, whose distribution can only be explained by ordinary methods of migration, e.g. *Hibiscus tiliaceus*. It is not our immediate object to give examples of these, except incidentally, but they will be referred to as a class later.

Sterculiaceae.

The genus *Hermannia* (including *Mahernia*) is a very large one, distributed over all South Africa, and with over 100 species. Again it illustrates most of our points. We find variable and widespread species like *H. candicans*, *H. salvifolia*, *H. flammea*, in the process of breaking up into several distinct varieties or species; we find *H. cuneifolia*, which is common at the Cape, replaced on the dry plains around Graaff Reinet by the nearly related *H. desertorum*; we also find that at the Cape itself *H. cuneifolia* has given rise to two other closely allied but rarer species, *H. decumbens* and *H. alnifolia*. The eastern species, in most large

genera distributed over South Africa, tend to fall into a group by themselves, distinct from the south-western. The genus *Dombeya* is tropical in its affinities. The South African species all come close together. *D. natalensis* and *D. rotundifolia* are both common in the coast and mid-lands of Natal (the latter also in Rhodesia). *D. dregeana*, which extends from Natal to Uitenhage, only differs in the flower-buds, leaves, and involucre leaflets from *D. natalensis*. To the north, in the Transvaal, there are six other species, and the genus is still better represented in the tropics. We thus see, as in so many other cases, the various steps of invasion from the tropics into South Africa, with consequent modification.

While the genera *Hermannia* and *Dombeya* afford perfect examples of the working of our general principles, when we turn to the genus *Sterculia*, as represented in South Africa, we find a case of the most extraordinary isolation. The genus is most abundant in tropical Asia, but there are seven species in the 'Flora of Tropical Africa' and one, *S. murex*, in the Lydenburg district of the Transvaal. *S. Alexandri* (Harv.), however, occurs completely isolated near Uitenhage. Harvey says it is allied to *S. foetida*, but differs in various characters, and adds, 'No one seems to have met with it but Dr. Alexander Prior, who found but a solitary tree in a narrow kloof, somewhere among the Van Staadem Mts., a locality rich in interesting plants and probably still concealing other novelties.' Schönland (30) refers to its complete isolation, but he does not say whether it has been collected since.

Tiliaceae.

The genus *Grewia* is a great tropical African genus which has produced species capable of invading South Africa. *Grewia occidentalis* extends from Abyssinia to the Cape Peninsula. It is a typical pioneer in the xerosere, important in establishing scrub and forest. *G. caffra*, which is common in the Natal coast-belt bush, is probably derived from it though specifically distinct, and many of the other rare species might also be connected. No better example could be found of the first of our categories, but cases of discontinuous distribution would be discounted as examples of polygenesis, because of the edible drupes. The genus *Sparmannia* has *S. abyssinica* not known outside Abyssinia, but apparently intermediate between the two South African species *S. africana* and *S. palmata*.

Geraniaceae.

Pelargonium is a large and characteristic Cape genus with a few outliers in tropical Africa, western Asia, and Australasia. We find that *P. multibracteatum* from Abyssinia is closely allied to *P. alchemilloides* from the Transvaal, Natal, and the Cape, the latter being a variable species. *P. flabellifolium* is common in the upper districts of Natal and is also recorded for Angola and the Transvaal. There are seventeen species altogether in Natal and ten in the Transvaal, but the largest section of the genus, the section *Hoarea*, is altogether south-western. Many of the species

are closely allied and some single species are extremely variable, e.g. *P. myrrhifolium*, of which Harvey gives nine varieties that have been described as distinct species by various authors. Though the eastern species are, as a rule, distinct from the south-western, in some cases they are nearly related, e.g. *P. lobatum* and *P. pulverulentum*. Only one or two, e.g. *P. alchemilloides*, *P. capitatum*, are common to Natal and the Cape. *P. inquinans*, the parent of most of the 'scarlet geraniums', extends from Natal to Uitenhage. The general distribution of the genus, with its fairly numerous outlying species and greatest concentration at the Cape, is the chief point of interest, since it is paralleled in so many others and throws light on the question of the origin of the south-western flora.

Oxalidaceae.

The only genus is *Oxalis*, with more than a hundred species, again chiefly concentrated at the Cape, but with seven in Natal and seven in the Transvaal.

O. corniculata is a ruderal, common in subtropical regions. The Abyssinian species *O. obliquifolia* is very near the Cape *O. convexula*, and *O. caprina*, another Abyssinian species, is also found at the Cape. The genus illustrates generally the same features as *Pelargonium*.

Rutaceae.

Calodendron capense, the Cape Chestnut, is a monotypic species, a large forest-tree whose distribution is to be explained only by migration. It is found in all the eastern forests and has no near allies. *Xanthoxylon capense* (Fagara), on the other hand, illustrates exactly the same points as *Kiggelaria* (Bixaceae) described above. Sim (31) sinks all the forms in one species, but the xerophytic forms are widespread, the more mesophytic forms have restricted and discontinuous distribution. The genus is tropical. *Toddalia lanceolata* (eight stamens) is widespread from the Cape to Mozambique and Mauritius. *Toddalia natalensis*, four stamens, but otherwise very similar, is only found in the Eastern Province and Natal. *Clausena inaequalis* is a Natal and tropical species, allied to the Indian *C. Willdenovii*.

The Rutaceae of the south-western region are strongly scented xerophytic shrubs, very different in every way from the eastern forest species. There are nearly two hundred species in the south-west, belonging to nine genera, of which *Agathosma* includes about half. Only one species, *Barosma lanceolata*, reaches Natal. This marked contrast and differentiation between east and west in the family is very striking.

Celastrineae.

The genus *Celastrus* illustrates again our chief points. The tropical African species appear to be all endemic, with mostly narrow ranges, except *C. senegalensis*, which extends from Mozambique to the Mediterranean and eastward to India. The twenty odd South African species are all different.

C. buxifolius is a widespread rather variable pioneer species all over South Africa, and is of considerable importance in the establishing of thorn-veld and scrub, though some of its more mesophytic varieties occur in the forest. *C. peduncularis*, which is without spines, is a large forest-tree common in eastern forests. *C. acuminatus*, like *C. buxifolius*, is widespread, usually outside but sometimes inside forest, and several other species behave in the same way. Some of the species have become adapted to coast sand-dune conditions, e.g. *C. maritimus*, or coast forests, e.g. *C. cordatus*. According to Sim's information regarding distribution (31), *C. undatus* in forest and scrub would appear to take the place of the pioneer *C. albatius*, which is closely allied (31, p. 186) and occurs on exposed rocky krantzies.

The relationship between the species of *Elaeodendron* is exactly the same as in the case of *Celastrus* and other large genera of trees and shrubs. A number of species are light-demanding pioneers, low-growing and shrubby, while others, like *E. croceum* (Saffron Wood) or *E. sphaerophyllum*, are large mesophytic forest-trees.

Ampelideae.

The numerous species of *Vitis* (*Cissus*) are nearly all eastern, *V. capensis* being the only species which reaches the Cape Peninsula, though several others reach the eastern parts of the south-western region. The headquarters of the genus is, of course, in the tropics, and again various steps of invasion into South Africa can be studied, as can be done also with members of the family Sapindaceae; but a still better field is afforded by the next example.

Anacardiaceae.

The genus *Rhus* illustrates better our various principles than probably any other genus, and it deserves further study from this as well as other standpoints. Not only is the genus very well represented in South Africa, but it extends through tropical Africa, North Africa, the Mediterranean, Arabia, India, the Himalayas, China, North America, Mexico. Schönland (29) says about it, 'No less than eleven species occur on the Cape Peninsula alone, yet the close analysis to which the sect. *Gerontogaeae*, Engl., which includes our own species of *Rhus*, has been subjected by Diels, leads him, and I think rightly, to the conclusion that this section has branched from the type (*stamm*) of the genus, presumably during early Tertiary in the southern portion of the eastern part of the northern hemisphere. Originally it probably included forms the organization of which was adapted to moderately dry and sunny localities. When, in the course of the Neogene, the geological revolutions in western Asia and Europe caused migrations on a large scale, and at the same time more intimate relations were established between East Africa and the Indian region, *Rhus* took part in the general invasion of Eurasian types into Africa and there commenced in numerous regions a more diverse development than in its original home.'

When we look at the present-day distribution of the species of *Rhus* in South Africa, we find certain of them (e.g. *Rh. dentata*, *Rh. villosa*) very widespread, as pioneer species in the xerosere. Others (e.g. *Rhus obovata*) occur along the streams and are important in the hydrosere, or (e.g. *Rh. crenata*) occur on the coast sand-dunes in the psammosere. As succession advances, we find species of *Rhus* (*Rh. dregeana*, *Rh. erosa*) dominant in climax vegetation on the dry doleritic Karroo kopjes. These two species are closely allied and may have been derived one from the other or by the splitting of an ancestral type. In more mesophytic forest areas we find various steps in the adaptation to more favourable conditions in a large series of forms till we reach such large forest-trees as the Red Currant (*Rh. laevigata*), which grows fifty to eighty feet high, and two to four feet in stem diameter. *Rhus* also shows adaptation to purely grassland conditions in the species *Rh. discolor*, which takes its place with numerous other associated plants of the grassveld. There are few examples of adaptation to grass-land conditions from the genera of trees and shrubs, the evolution of species being, as far as South Africa is concerned, usually in the other direction, widespread xerophytic types producing more mesophytic forms.

Leguminosae.

It will be necessary now to pass over certain large and important families in the briefest possible way. The present-day development of the Leguminosae could be made the subject of a monograph by itself. If we take any two allied species or any group of allied species, again and again we find that species A with a wide distribution has apparently produced one or more, B, C, D, &c., each with restricted and in some cases with discontinuous distribution, or there has been an apparent breaking up. Examples are seen in the genera *Podalyria*, *Crotalaria*, *Rafnia*, *Lotononis*, *Argyrolobium*, *Lebeckia*, *Buchenroedera*, *Aspalathus*, *Psoralea*, *Indigofera*, *Tephrosia*, *Lessertia*, *Vigna*, *Dolichos*, *Eriosema*, and *Acacia*. At the same time examples of isolated species with no obvious connexions are to be found, e.g. *Sutherlandia frutescens*, but they are not numerous. The suborders should, of course, be studied separately. The Caesalpineae invade South Africa from the tropics only along the eastern side as far as Uitenhage, and in the case of *Schotia speciosa* as far as Mossel Bay. Several of these tropical outliers in South Africa are interesting, e.g. *Bauhinia tomentosa* extends from Mozambique to Natal and is recorded from Angola. In South Africa, *B. garipensis* in Namaqualand, *B. Bowkeri* 'along the Bashe River, Kaffraria', are both closely allied.

The Mimoseae has the great genus *Acacia*, which is all over Africa and is even more characteristic of Australia. *Acacia arabica* extends from India through the whole of Africa to Natal, though the Natal variety *Kraussiana* is now separated as a distinct but allied species, *A. Benthami*.

A. horrida (*A. Karroo*) is commonest and most widespread in South Africa, being the most important pioneer tree in dry areas. It is interesting to notice its adaptation to more mesophytic conditions on the Natal coast-belt. Some species of *Acacia*, e.g. *A. Kraussiana*, *A. pennata*, have adopted the climbing habit in the bush. *A. caffra* has become adapted to moister conditions near stream-banks. Like so many of our larger genera, *Acacia* gives excellent opportunities of observing adaptation to various ecological conditions, but the majority are extremely xerophytic thorn-veld species. The Papilionaceae fall into two fairly well-marked distributional groups, an eastern and a south-western with eastern outliers in the south-west, e.g. *Crotalaria* and *Vigna*, and south-western outliers in the east, e.g. *Podalyria*, *Lebeckia*, *Rafnia*, but several large genera are distributed all over. The subject is too big to discuss in detail here.

I must pass over, for the same reason, such large genera as *Crassula* and *Mesembrianthemum*, though specialists dealing with them could illustrate many interesting points with regard to their distribution.

Rubiaceae.

This is one of the largest families of flowering plants, and is chiefly tropical and subtropical in both the Old World and the New. It is particularly interesting to follow the steps of its invasion into S. Africa, where it has produced not only large numbers of endemic species, but even characteristic endemic genera, e.g. the three belonging to the tribe Anthospermeae, viz. *Galopina*, *Nenax* (*Ambraria*), and *Carpocoe*, with 2 to 4 species each, *Galopina*, from Natal to Swellendam, *Nenax*, East London to Capetown, and *Carpocoe*, Grahamstown to Capetown. The centre of distribution of these anthospermous Rubiaceae has been, of course, thought to be rather from the south-west than towards it (27, 29). Another endemic genus is *Burchellia* (*B. capensis*), which is common from Natal to the Cape, but is certainly eastern or tropical in its affinities and origin, belonging as it does to the tribe Gardenieae. The distinctly herbaceous genera, e.g. *Galium*, *Anthospermum*, *Oldenlandia* (*Hedyotis*), are generally distributed over S. Africa with others (*Pentania*, *Spermacoe*, *Hydrophylax*, a strand plant) not quite so far to the south-west. *Pentania variabilis*, as its name implies, is extremely variable, and would repay intensive study from the distributional standpoint.

The shrubs and trees are mostly eastern, being very common around the margins of the forest and in scrub in Natal, especially on the coast-belt (see 12). The herbaceous genera are very distinct in every way from the shrubs and trees. Among the latter, the differences one notices as one passes from the subtropical Natal coast to the Midlands are very striking. Thus *Randia dumetorum* is a species which extends all through the tropics from Hongkong and India to Durban. Another species, *R. rudis*, is very common in the midlands of Natal, but is not tropical. It extends as far as

Grahamstown, and is one of the first arrivals under the pioneer thorn-trees in the thorn-veld (9). *R. parvifolia* (listed by Medley Wood) is hardly distinct from *R. rudis*. Similar relationships may be observed between *Gardenia Thunbergia*, a very widespread tropical species, and other South African species of *Thunbergia* (cf. Stapf and Hutchinson, 34). The genera *Tricalysia*, *Plectronia*, *Vangueria*, and *Pavetta* also illustrate our general principles.

Pavetta caffra is chiefly a coast-belt species. *P. Cooperi* is a very closely allied species, and is only found in the midlands. The genus *Plectronia* extends from Natal to the Cape Peninsula, the species being light-demanding pioneers. All the species come very close together, and may have been derived from the breaking up of a single widespread ancestral type.

Compositae.

Though this great family is full of interest in its distributional aspects, as has been very fully demonstrated by the detailed work of Small (32), it must also be passed over with very brief reference. Schönland (30) finds several more or less well-defined groups of genera according to their distribution in South Africa, viz. over 40 genera with general distribution, about 20 genera radiating from the Transvaal and Natal along the southern coast, over 40 genera mainly in the south-west, a small group chiefly central, and a few genera with very restricted distribution. There are also a very large number of species with extremely restricted distribution, as is to be expected in the family since it is a feature which it exhibits all over the world. On the other hand, many species are generally distributed, and many more have a wide range over one or more of the distinct climatic areas. Examples of our general principles may be found in the genera *Vernonia*, *Nidorella*, *Brachylaena*, *Sphenogyne*, *Pentzia*, *Cotula*, *Athanasia*, *Helichrysum*, *Metalasia*, *Stoebe*, *Othonna*, *Senecio*, *Euryops*, *Dimorphotheca*, *Osteospermum*, *Berkheya*, and many others.

Migration of widespread ancestral types has very clearly, in a great many cases, perhaps in the majority, been along the mountain ranges.

Ericaceae.

Schönland remarks (29) that the distribution of the Ericaceae defies at present a satisfactory explanation. 'Their prevalence in South-West Africa and the prevalence of Epacridaceae in Australia cannot be used as evidence that these two orders originated in the southern hemisphere from common ancestors (compare Drude in Engler-Prantl, iv. 1, 1897, 29).' We shall return to this point later.

There are 17 genera of Ericaceae with 146 species all endemic in the south-western region of Macchia. The genus *Ericinella* has one species at Graaff Reinet, one at Queenstown, and 3 or 4 in tropical Africa or Madagascar. The genus *Phillipia* has 4 species at the Cape, a few in tropical Africa, and 20 to 30 in the Mascarene Islands. The great genus

Erica has over 500 species, of which 469 are endemic in South Africa, mostly in the south-west, but about 20 in Natal, most of them, but not all, in the Drakensberg. *E. caffra* occurs even on the subtropical coast-belt, and several are common in the midlands. *Erica arborea* connects through the mountains of Central Africa with South Europe, where there are about a dozen species, none of which are South African. Other sections of the family are, of course, American and Himalayan, &c. These facts are mentioned because they would seem to have an important bearing on the origin of the South African flora, and they certainly do not count in favour of the supposed land connexions with Australia and South America. The enormous number of Cape endemics belonging to the genus *Erica* provides an interesting field for investigation. Why, for instance, are so many of them concentrated at certain points, e. g. the Cape Peninsula or the Van Staden mountains?

While we are dealing with facts of this general nature, I shall quote what Schönland (29) has said concerning one or two other families.

'The Penaeaceae and allied orders (the Thymelaeales) also fail to give us in their distribution an indication of their origin. Penaeaceae nearly allied to Thymelaeaceae; only distinguished by 4-merous ovary with 2-4 ovules each. All in South-West Cape Colony. 21 species and 5 genera.

'Geissolomaceae, 1 monotypic genus, closely allied to Penaeaceae, with which the order has frequently been united. South-west Cape Colony.

'Oliniaceae, fruit a drupe, while in the two previous orders the fruit is a capsule. About 6 species: 4 in Cape Colony, 1 in Usambara, 1 in Abyssinia.

'Thymelaeaceae, with the exception of the polar regions, distributed over the whole globe, but many genera and groups very localized.

'*Peddiea*, 6 species. South-east and tropical Africa.

'*Gnidia*, 80-90 species. Tropical and South Africa, Madagascar, and East Indies.

'*Struthiola*, 24 species, mostly in South Africa, 3 in tropical Africa.

'*Cryptadenia*, 4-5 species. Cape.

'*Lachnaea*, 18 species. Cape.

'*Passerina*, 4 species, and *Chrymococca*, 1 species. Cape; 2 allied genera in central and northern Asia.

'*Dais*, 2 species; 1 in Natal, 1 in Madagascar.

'Eleagnaceae. Chiefly in the northern, temperate, and subtropical zone: none in the southern hemisphere.

'The Bruniaceae, 12 genera and over 40 species, which are restricted to South Africa and even almost entirely to South-west Cape Colony, are so isolated among Saxifragaceae that we can also only point to their antiquity. About their origin no guess can be hazarded. . . .

'There are a number of genera of large orders which must be placed

in the same category, e.g. *Cliffortia* (about 40 species, mostly south-western Cape Colony), allied to *Bencomia* (a genus with 2 species in Madeira and the Canary Islands).'

The distribution of the Thymelaeales and *Cliffortia*, &c., would surely favour a northern origin, and would therefore tell against Schönland's postulate of land connexions in the southern hemisphere.

We shall now deal with some of the families belonging to the Tubiflorae, since these illustrate present-day tendencies extremely well.

Acanthaceae.

Thunbergia atriplicifolia is a variable veld species widely distributed over the whole eastern side. Three other species (in addition to a whole series of varieties), viz. *T. aspera*, *T. xanthotricha*, *T. Bachmanni*, only differ slightly from *T. atriplicifolia*. *T. aspera* is distinctly more tropical, Natal coast-belt and northern Transvaal; *T. xanthotricha*, Transvaal, near Barberton only; *T. Bachmanni*, Transvaal, Orange Free State, and Pondoland. The discontinuous distribution of *T. aspera* between the coast-belt and the northern Transvaal is paralleled in many other cases in various families.

Good examples exactly similar to this may be found in the genera *Dyschoriste*, *Belfharis*, *Crabbea*, *Barleria*, *Justicia*. *Blepharis molluginifolia* extends from India through tropical Africa to Mossel Bay, being very common all over the eastern side of South Africa. *B. setosa*, which differs only in the scabrous leaves and setose bracteoles, is recorded only for the Natal coast-belt and tropical Transvaal. Similarly *B. boerhaaviaefolia*, which has the same distribution as *B. molluginifolia*, has given rise to several allied but apparently rare species in the tropics. *Crabbea nana* and *C. hirsuta* are very closely related and are both widely distributed grassveld species, an example of splitting or of A giving rise to B. *C. robusta* differs in being larger and having larger leaves and flowers. It is of a distinctly higher ecological type, and is more mesophytic; only recorded for Swaziland. *C. angustifolia* differs from *C. hirsuta* in minor characters. Distribution: Transvaal and Bechuanaland, endemic. *C. pedunculata* is nearly related to *C. nana*, and is endemic in Natal and rare. The whole family is very rich in examples like the above. The genus *Chaetacanthus* has four species, all endemic and all closely related. Two of them are widely distributed, two rare, an obvious example of the breaking up of an ancestral form. The Acanthaceae are a tropical family which have invaded South Africa, chiefly along the eastern side. They are peculiarly characteristic of the moist marginal belt in Natal coast-belt scrub and forest. The grassveld species and more xerophytic species generally are, however, more widespread in South Africa.

Since we have already sufficiently indicated how numerous the examples are in practically all families of the application of our general principles to species and varieties, we shall now make use of some members of the

Tubiflorae cohort to illustrate their application to higher groups. Guppy, as already mentioned, has indicated how they apply in the same way to the Geraniales, Geraniaceae, &c. The series now to be dealt with affords an even better example.

Scrophulariaceae.

First of all, the Scrophulariaceae are a distinctly cosmopolitan family, though, on the whole, most frequent in temperate regions. No fewer than twenty-one genera have a very wide distribution over South Africa. Most of the genera afford examples of widespread species giving rise to rare endemics, &c. And we also find examples of localized genera, 7 in the east, 3 in the south-west, 3 in the so-called Kalahari region, and 2 in the western. This in itself indicates how we may apply our principles of distribution to the genera as well as the species, but we can do still better if we follow the origin and distribution of a single well-defined tribe.

The tribe Selagineae of the Scrophulariaceae is sufficiently distinct to have been separated as a family by itself in the 'Flora Capensis', but it only differs in the characters of the ovary and fruit (the latter being two-celled or one-celled by abortion and indehiscent or separating into two one-seeded nutlets). Different authors are not quite agreed as to how much should be included in the tribe Selagineae, but if we take it in its widest sense then a polygenetic and polyphyletic origin from the Scrophulariaceae is extremely probable. It then consists of 10 genera and about 240 species, which are concentrated for the most part in South Africa. There are about 20 species in tropical Africa and one in Madagascar. There is an outlying genus (*Lagotis*) widely dispersed through the north temperate zone, another in the Mediterranean region (*Globularia*), and a single monotype in Socotra (*Cockburnia*) (3). The fact that *Lagotis* has been referred to the tribe Digitaleae by Wettstein (in Engler and Prantl) and *Globularia* retained in a distinct family (the Globulariaceae) shows that a polyphyletic origin for the tribe as formerly recognized has been made the grounds for breaking it up, but this attempt fails to give value to the marked peculiarities of the organs of fructification. It seems far better to recognize the Selagineae as a natural systematic group to which the Scrophulariaceae bears the same relationship as that between numerous widespread species and their derivatives as mentioned above. The widespread family A (the Scrophulariaceae) has given rise to a separate tribe (or another family) B, the Selagineae with a very restricted and at the same time discontinuous distribution.

We now select the two genera of the Selagineae, *Selago* and *Walafrida*. *Selago* has 112 species in South Africa, 2 of which extend into the tropics. There are also 17 endemic species in the latter region, mostly in the hills. In South Africa *Selago* is concentrated for the most part in the south-west (cf. *Heliophila*, *Oxalis*, *Pelargonium*, *Muraltia*, *Protea*, *Erica*, *Cliffortia*, and numerous other genera with a similar distribution). *Walafrida* is

quite closely related to *Selago* (the calyx has 3 lobes instead of 5 lobes). It has 31 species in South Africa, one of which extends into tropical Africa, 4 in tropical Africa, and 1 in Madagascar. It has a similar distribution in South Africa to *Selago*, but on the whole rather more eastern. The two genera, being so nearly related, obviously may be regarded as the result of divergence from a common ancestral type, like so many nearly related species already dealt with. The genus *Hebenstreitia* is more distinct. Of the thirty species, most of the annuals are central or western, i.e. in the drier parts, while the perennials are widespread or eastern. One species extends as far as Abyssinia. All the species of *Dischisma* (11), *Microcodon* (5), *Agathelpis* (3), and *Gosela* (1) are endemic in the west or south-west.

Lastly, as regards the species, a few examples will suffice. *Hebenstreitia fruticosa*, *H. dentata*, and *H. integrifolia*, all three of which are very variable and come close together, occur all over South Africa. *H. Watsoni*, on the other hand, is only recorded for East London, and only differs from *H. integrifolia* in its more lanceolate and acuminate bracts. *H. Rehmanni* (Transvaal high-veld only), again, differs in its small flowers and very spreading bracts. *Selago* supplies numerous examples of the same kind.

The process of differentiation from the Scrophulariaceae, which we have just followed through the Selagineae (or Selaginaceae), might also be followed through the Myoporaceae, which Baillon ('Hist. Pl.' ix. 420) again reduces to a tribe of the Scrophulariaceae. The genus *Oftia* has two species, both endemic in the western and south-western regions of South Africa. There are 6 genera in the family and about 80 species, mostly Australian, with a few Polynesian representatives; 1 in the Sandwich Islands, 1 in Mauritius, 2 in China and Japan, 1 in the West Indies, 1 somewhat doubtful in tropical Africa, and 2 in South Africa.

Interesting points might also be brought to light by a comparison of the Scrophulariaceae and Bignoniaceae; in fact, the whole of the Tubiflorae affords an excellent field for the study of differentiation and distribution.

Verbenaceae.

This family is chiefly tropical in both hemispheres. In South Africa the primitive tribe Stilbeae, which has endospermic seeds and in three of the five genera regular corollas, is entirely endemic in the south-west. In the tribe Verbeneae, on the other hand, which has exendospermic seeds and zygomorphic corollas, one genus, *Bouchea*, which extends through tropical Africa, America, and India, is widespread over South Africa, and the others are all eastern. The tribe Viticeae, which differs in having the ovule inserted laterally instead of being basal erect, has two genera, *Vitex* and *Clerodendron*, each with nine or ten species, mostly rare Natal and Transvaal endemics except *Clerodendron glabrum*, which extends from Grahamstown

into the tropics, and *C. myricoides* and *C. spinescens*, which are also tropical.

Laurineae.

The genus *Cryptocarya* has over forty species in the tropics (mostly Indo-Malayan). There are six species in South Africa. *C. Woodii* is widespread over the eastern side. The species *C. latifolia*, *C. myrtifolia*, *C. Sutherlandi*, and *C. Wyliei* are all allied to *C. Woodii*, and are all rare Natal or Zululand endemics. *C. Woodii* is replaced in the south-west by a more xerophytic, more distinct, shrubby species with narrow leaves, *C. angustifolia*.

Proteaceae.

This family, as is well known, is concentrated mostly in the south-west, but, as a family, its distribution is similar to many genera already dealt with; it has certain eastern extensions. *Protea hirta* is fairly common all over Natal, extending down even to Durban on the subtropical coast-belt. There are about nine or ten other species, mostly on the Drakensberg, where they are dominant in the extensively developed Protea-veld (4). The genus extends along the mountains of tropical Africa to north of the Equator. The genus *Faurea* is typically eastern and tropical, with one species in Madagascar. Incidentally it again illustrates our general principles in that *Faurea saligna* is very widespread and sometimes dominant in tree-veld, while several other species, e.g. *F. natalensis*, *F. Macnaughtoni*, are very rare. The last-mentioned also shows discontinuous distribution. The northern and eastern extensions of the Proteaceae are emphasized because this family is typical of those which are used to demonstrate the connexions between South-West Africa and Australia. The 960 species are distributed as follows: 591 in Australia, 25 in tropical East Africa, a few in Angola, 2 in New Zealand, 7 in Chili, 36 in tropical South America, 262 in South-West Cape Colony, 2 in Madagascar, about 5 on the mountains of tropical Africa.

The Monocotyledons.

Here we find the same principles illustrated as among the Dicotyledonous families. The bulbous Monocotyledons may be looked upon as a type peculiarly suited to the variable veld conditions in South Africa in all the climatic areas, where they have multiplied enormously, but though there are a great many endemic South African genera, especially among the Iridaceae, they are by no means poorly represented in other parts of the world. The great southern genus *Moraea*, which is spread over South Africa, tropical Africa, Madagascar, and Australia, is hardly different from the northern genus *Iris*. *Romulea* extends to the Mediterranean, *Gladiolus* to Europe, &c. There are connexions with South America and Australia on which considerable stress has been laid by various writers. For details see Schönland (30). But the connexions with the north appear equally

notable. The divergence is always considerable in the case of the Australian and South African and South American connexions. The species and even the genera are usually distinct. In general the distribution of the bulbous Monocotyledons can be explained equally well by divergent invasion from the northern hemisphere as by land connexions in the southern.

As regards the South African species and their present-day distribution, practically all the large genera show relatively wide-ranging species around which relatively rare endemics may be grouped; or allied species in neighbouring areas or under different ecological conditions; or variable species in the process of breaking up. Being of a rather uniform ecological type, however, the examples are not quite so striking as when a xerophytic, widespread, shrubby species among the Dicotyledons is connected with a mesophytic forest species. The bulbous Monocotyledons nearly all belong to early stages of the plant succession.

Among the Liliaceae, the genus *Asparagus* is more varied in its ecological behaviour, and widespread species may be paired with rare endemics in a very striking way, e.g. *A. declinatus* and *A. Macowani*; *A. stipulaceus* and *A. Burchellii*; *A. striatus* and *A. erectus*; *A. sarmentosus* and *A. oxyacanthus*; *A. falcatus* and *A. Sprengeri*; *A. aethiopicus* and *A. myrioclados*; *A. medioloides* and *A. Krausii* and *A. volubilis*. The large genus *Aloe* similarly supplies numerous examples of the working of our general principles.

Orchidaceae.

There are eighteen endemic genera, of which one, *Huttonaea*, is eastern and the rest mainly or entirely south-western. Another twenty-eight genera are also found in tropical Africa, and these have invaded South Africa to a greater or less extent from north and east towards the south-west. For details concerning the distribution of the genera and other Monocotyledonous families, Schönland should be consulted (30).

Restionaceae.

As is well known, this is another of the typically south-western families, only two species (one each of *Restio* and *Leptocarpus*) being found in Natal. The family may, however, probably be connected with the Eriocaulaceae, which are much more widely distributed in the tropics of both hemispheres.

Gramineae.

The 500 odd species of grasses in South Africa fall naturally into two distributional groups, the south-western being distinctly separated from the rest. The south-western grasses are temperate in their affinities, the eastern, northern, and western are tropical. Eighty or ninety of the south-western species are endemic. The chief genera are *Danthonia*, *Pentaschistis*, *Pentameris*, *Achneria*, *Avenastrum*, *Brizopyrum*, *Lasiochloa*, *Ehrharta*. Though the temperate tribes are thus mostly concentrated in the south-

west, yet along the central and eastern mountain-ranges we have many representatives (there are twenty or so on the Drakensberg), and some even compete with subtropical species in the eastern grass-veld, e.g. *Danthonia purpurea* around Molteno and *Pentaschistis natalensis* in Natal. As Stapf (33) has pointed out, temperate species of *Avenastrum*, *Agrostis*, *Melica*, *Poa*, *Festuca*, *Bromus*, *Brachypodium*, form, as it were, a bridge across the mountains of the tropics connecting with the northern centres of distribution. The south-western section of the Gramineae, then, like most of the other characteristic south-western families and large genera, are not without representatives eastward and northward.

The Gramineae of the great eastern grass-veld region and of the central and western regions have much more obviously invaded South Africa from the tropics. The genus *Aristida* has produced species, many of them rather closely connected, e.g. *A. congesta* and *A. barbicollis*, the former very common and widespread, the latter much rarer, which are of supreme importance in the early stages of the establishing of grassland. Other similar pairs are *A. angustata* and *A. junciformis*, *A. bipartita* and *A. Burkei*.

Aristida has also a very distinct section (*Stipagrostis*), the species of which are adapted to desert and semi-desert conditions of the dry central and western areas. No better example of differentiation could be found anywhere than that of *Aristida* in South Africa.

Eragrostis is another great pioneer genus in grass-veld, with about fifty species. Many of the rare Transvaal and Free State endemics (*Eragrostis barbinodis*, *E. pallens*, *E. Wilmsii*, *E. sporoboloides*, *E. Atherstonei*, *E. echinochloidea*, *E. margaritacea*, *E. dura*) may very well have been derived from the widely distributed species, *E. curvula*, which is so widespread and abundant everywhere. Except for the shorter valves, the differences are in no case very great. Numerous similar examples could be given from the Andropogoneae, which are characteristic rather of climax grassland. *Andropogon hirtus*, for instance, has probably produced *A. auctus*; *A. nardus* is in the process of breaking up into several distinct species, and has already given rise to *A. plurinodis*. The variations of the dominant grass, *Anthistiria imberbis* (*Themeda Forskålii*), should be studied from the same standpoint. The numerous mesophytic species of *Panicum* and other Paniceae which are characteristic chiefly of the moist marginal belt surrounding forest and scrub are of interest, since some of them show discontinuous distribution, particularly between the Natal coast-belt and the northern Transvaal. Many of them, however, extend into the tropics and have simply invaded South Africa at different points. I regret that space does not permit of a fuller discussion of the Gramineae from the standpoint of the present paper. In fieldwork, I have recently found that the presence of many species in certain grassland areas can be explained only on these lines, i.e. by taking into account their probable origin from other widespread

species. Otherwise none of the ordinary ecological methods could account for their presence in one place, their absence in another.

Coniferae.

The genus *Podocarpus* is of great interest, not only because it has been found in the fossil Tertiary deposits of northern Europe and America, though it is now confined to Japan and the Southern Hemisphere and reaches such widely separated points as New Zealand, South Africa, and southern Chili, but also because species are so often dominant in the chief South African forests.

The two species *Podocarpus latifolia* (*P. Thunbergii*) and *P. elongata* are quite distinct and have, more or less, the same range. They are both old species; *Podocarpus falcata* is closely allied to *P. latifolia*, and it is probably identical with, or at any rate extremely close to, *P. melanjanus*. *P. falcata* is completely dominant in forests of a narrow belt along the southern end of the Drakensberg, but is apparently as completely absent from exactly similar habitats north of the Mont aux Sources. If it is the same species as *P. melanjanus* it begins again in Rhodesia and East Africa, and we have a striking example of discontinuous distribution in a dominant forest species. If it is not the same species as *P. melanjanus*, we have a case of two derivatives from the same species differing slightly in two distinct areas.

ISOLATED TYPES.

The above survey of families, genera, and species has now been made of sufficient length to show that the flora of South Africa affords abundant evidence of the origin of new species, according to the principles summarized to begin with. If I had cared to utilize all the notes that have been prepared the survey could have been extended to at least three times the length. While in the larger genera it is often very easy to see the nearest relationships and probable origin of rare endemics or the splitting up of variable species, &c., there are, on the other hand, many isolated species or genera, or even families (e.g. *Bruniaceae*), to which at the present stage of our knowledge it is impossible to apply those methods. Many examples are to be found among our forest-trees and shrubs, e.g. *Ocotea bullata*, *Pygeum africanum*, *Cunonia capensis*, *Clausena inaequalis*, *Calodendron capense*, *Ilex mitis*, *Noltea africana*, *Hippobromus alata*, *Curtisea faginea*, *Heteromorpha arborescens*, *Leucosidea sericea*, *Cunonia capensis*, *Platylophus trifoliatus*, *Choristylis rhamnoides*, *Xymalos monospora*, *Gerrardiana foliosa*, &c., which have no obvious connexions in South Africa, though several of them do have such in the tropics. In the latter case, their distribution in South Africa must be explained by the ordinary methods of migration. They must be assumed to have migrated into South Africa by themselves. They are not the descendants of immigrants. In the case

of endemic monotypes with no obvious close relationships the difficulty of reaching a satisfactory explanation is greater.

Fortunately there are not many such, and several which were once thought to be of this type have since had relations discovered in the tropics. If all other explanations fail, they must be considered relicts, whose immediate ancestors have disappeared. Guppy would class most of them as specialized types, the oddities of plant forms which have been produced not by differentiation from a more generalized type but by increased specialization. The Rosaceous *Pygeum africanum* or *Leucosidea sericea* are as good examples as any, but *Noltea africana*, *Hippobromus alata*, *Curtisea faginea*, are also monotypes.

Other isolated types have been referred to in the general survey of the families. It may be noted incidentally that monotypes and genera containing few species have generally more restricted distribution than others. (Cf. de Candolle, 'Origin of Cultivated Plants', 2nd edit., 1909, p. 395, in connexion with the origin of *Zea Mays*.)

GENERAL APPLICATIONS.

My object in bringing forward these facts and arguments has been mainly to afford illustrations of what I have begun more and more to realize in connexion with field ecological work, namely, the necessity for new view-points. The ordinary ecological methods of investigation are extremely useful up to a certain point. We find that certain plants occupy certain habitats, each with a certain range of the measurable factors, which vary to a considerable extent independently. As Clements has pointed out, and as can be seen by any one who has studied plant-life in the field, very fine measurement of each factor may be largely wasted effort, since (with the possible exception of some soil factors) it requires a relatively large difference in any single factor to cause any morphological adjustment. Nevertheless, since the factors vary independently, there are a fair number of permutations permissible. Thus as regards the moisture factor, habitats may be divided into aquatic, semi-aquatic, moist, mesophytic, dry and very dry, and any of these may be combined with habitats having full sunlight, diffuse light, and dense shade, and then with clay soils, sandy soils, and so on. In spite of their seeming complexity the essential inorganic differences between habitats are not so very difficult to recognize. Biological factors, however, are more complex, and ecologists are giving more and more attention to them. In its widest sense, this aspect of ecology includes the vegetation itself as a factor and embraces, therefore, the whole question of plant succession.

We are by no means near the end to be reached by the use of these ecological methods, and how very useful they are has already been shown by the results, but if we do not take into account the historical or geo-

graphical or evolutionary factor, whatever we care to call it, we are neglecting another very useful method of attack, and we fail to explain phenomena as fully as we might. The dominance of *Podocarpus falcata* in certain Drakensberg forests cannot be explained by considering habitats alone, for it is absent from apparently identical habitats in other parts of the range. The reason becomes clear when we consider its origin from the widespread *P. latifolia*. The presence of a mesophytic species of *Rhus* in a patch of moist scrub is not due simply to the fact of the more mesophytic conditions alone. We must connect its presence there with that of a widespread parent species over drier areas. In a word, it is not the present species alone that we must study, but wherever possible we must go back a step or two and consider allied or parent species and their behaviour and distribution.

The whole of our argument is based on the hypothesis that a species in the course of its migrations, when it comes into contact with conditions different from those which produced it, is, in many cases at least, capable of differentiation or of giving rise to new species suited to the new conditions. In a larger sense, and over a longer period of time, the same applies to larger groups, the genera, tribes, and families. While, in this paper, effort has been directed chiefly to bringing forward evidence of as varied a nature as possible to show that this takes place, there are many other interesting points which have not been dealt with. What conditions, for instance, are most effective in producing new species? Is the passage from tropical to temperate conditions more important than from dry to moist (or vice versa in each case)?

The examples of tropical species being replaced in South Africa by nearly related more temperate species are very numerous, but this is to be expected from the size of the areas involved. On the other hand, the examples of xerophytic shrubby species being closely allied to mesophytic forest species are also very numerous. The transition from siliceous to calcareous soil conditions has been closely investigated in Europe from this standpoint, but few observations have been made in South Africa on the effect of differences in soil conditions.

While the ecological aspects of this study are what have been kept most in view the methods of studying present-day tendencies obviously have a bearing on the question of the origin of the South African flora as a whole and its connexions with outside areas. From what was said in the introduction, it is clear that there are only two general views to be considered.

One lays emphasis on the South African connexions with the floras of Australia (particularly South-West Australia) and of South America and postulates land connexions to explain them, across what are now deep ocean basins. The difficulty with hypothetical changes of sea and land on a vast scale is always, as Wallace has expressed it again in his last work

(1911, 36), that they create more serious difficulties than they are supposed to explain. After a half-century of thought and work on this and allied subjects, Wallace had lost none of his vigour in denouncing theories of continental extensions. He concludes by saying, 'I believe it can now be truly said that no stratigraphical geologist accepts the theory of frequent interchanges of continental and oceanic areas, which are so hastily claimed by palaeontologists and biologists to be necessary in order to overcome each apparent difficulty in the distribution of living or extinct organisms, and this notwithstanding the number of such difficulties which later discoveries have shown to be non-existent'.

The other view of the origin of the southern floras is that of Thiselton-Dyer and Guppy, which has already been fully explained. A northern origin for many important elements of the South African flora has of course always been admitted. With regard to the south-western flora, a sufficient number of families and tribes, e.g. Proteaceae, Ericaceae, Rutaceae, Verbenaceae, Restionaceae, Gramineae, Selagineae, and large genera, e.g. *Heliophila*, *Muraltia*, *Pelargonium*, *Oxalis*, *Erica*, *Cliffortia*, *Selago*, *Danthonia*, *Pentastichis*, and many others, have been dealt with in our general survey to show that in practically every case, while the greatest concentration is in the south-west, and within that region in such 'cul-de-sacs' as the Cape Peninsula, yet there are eastern and northern outliers or relatives which in many cases extend right through the tropics to Europe and Asia.

It must of course be admitted that these are very meagre when compared with the rich development of species in the south-west, but, at the same time, there are no real grounds for the common assumption that the area where a family or genus is now best represented is necessarily the centre where it has originated. If the primitive ancestors of the south-western flora came from the north, there is no need to assume that the original immigrants were very numerous. They have left few descendants along the track of their invasion because conditions there are not generally suited to them, but when they reached more temperate areas in South Africa they multiplied exceedingly and produced many divergent types in the course of their differentiation.

One reason, perhaps the chief reason, why the second view appears the more acceptable is that it represents conclusions which can be reached by applying the principles which we can study at the present day within South Africa with regard to the origin of species. If we simply extend the time and the area, we can apply the same principles to the genera, tribes, and families, and the example of the origin of the Selagineae, at present mostly South African, and in South Africa mostly south-western, from the widespread Scrophulariaceae clearly throws light upon what has happened during the past.

The view-point adopted in this paper is also a useful one in connexion

with the general study of the phylogeny and inter-relationships of the Angiosperms, as has been demonstrated by Small in connexion with the Compositae (32). Morphologists and systematists are far from agreed on which characters in the flower are to be considered really primitive. If widespread species or genera or families have given rise to types with more restricted distribution and this is found to hold generally, the deductions are obvious. The hypothesis of course requires much testing, but it may serve to throw light on the question of how evolution has progressed and whether it has been mainly from the simple to the complex or vice versa. A comparison of some of the examples quoted in the general survey above, from this standpoint, would yield interesting results. Take, for instance, the genus *Eragrostis* among the grasses. *Eragrostis curvula* differs from the numerous endemic species which can be grouped round it chiefly in having longer valves. A shortening of the valves would appear, therefore, to be one of the evolutionary tendencies in this genus. Again, if we take the Gramineae as a whole, it is remarkable that the south-western genera—the older types—belong mostly to tribes (e. g. Aveneae, Festuceae) which have numerous florets in the spikelet, often much exserted from the glumes, while the presumably more recent invasion of grasses into South Africa, as represented by the eastern grass-veld genera, consists of types which, as a rule, have only one perfect floret in the spikelet (e. g. Andropogoneae, Paniceae). Similar facts have been briefly touched upon in respect to other families, but further work is necessary from this standpoint, as from the others. From all standpoints, the South African flora affords excellent materials and opportunities for the study of plant distribution.

SUMMARY.

1. Of those who have dealt with plant distribution, Darwin and Wallace objected to invoking geographical change as a solution of every difficulty, while Hooker was more inclined to postulate continental extensions to explain the connexions between the floras of the southern hemisphere. Schönland, after carefully considering the facts, finds a land connexion between South Africa and Australia and between West Africa and America to afford the simplest explanation. Thiselton-Dyer and Guppy agree on a theory of southward migration from the northern hemisphere. Guppy also elaborates a theory of differentiation, which he applies to families, tribes, genera, and sections of genera. These each tend to fall into two groups, primitive and derivative, the first widespread, the second restricted in area. Willis has developed the 'age and area' theory based on the fact that endemic species in any area tend to have a narrow range, non-endemic species a wider. The older a species is, the wider its range. Engler, Drude, and Clements agree that 'multiple origins' are possible, the former admitting the possibility chiefly in the case of larger groups, but Clements applying it also to species. The writer in

this paper considers present-day tendencies in plant distribution in South Africa, directing attention chiefly to the origin and distribution of species, but extending the observations also to larger groups.

2. The present-day conditions in South Africa are summarized and the climatic areas are arranged in increasing order of mesophytism: (a) Western region, (b) Central Karroo region, (c) Cape or South-western region, (d) Sandveld region of the Kalahari, (e) Thornveld areas of the eastern side, (f) Highveld and mountain areas of the eastern side, (g) Coast-belt of the eastern side.

3. Traversing all these areas are certain primitive habitats which are occupied by widespread species: (a) Cultivated land, waste places, &c.; (b) lakes, streams, marshes; (c) sea-shore habitats, mostly sandy; (d) mountain ranges; (e) drier areas of various kinds. To the north a fairly uniform tropical zone crosses the continent and allows tropical species to invade South Africa at different points.

4. A widespread species in the course of its migrations, when it comes into contact with conditions different from those which produced it, is often capable of giving rise to a new species suited to the new conditions. In South Africa, at the present time, such derived species are usually more mesophytic than the parent species, but they may be more xerophytic. In many cases, tropical species give rise to temperate species. One widespread species may give rise to several derived species or may itself break up into several, and, in many cases, the same derived species may have widely discontinuous distribution while its parent form is common all over the same area, a fact which suggests the possibility of 'multiple origins' or polygenesis.

5. Certain objections to the evidence for this are discussed and then a large number of examples are recorded. These are drawn from as many different families as possible, and but for consideration of space could have been largely increased. The cohort Tubiflorae is used to demonstrate that the same principles may be applied to larger groups, the widespread family the Scrophulariaceae having produced the Selagineae chiefly confined to South Africa but with outliers elsewhere, and similarly the Myoporaceae in Australia, &c. Also attention is directed to the distribution of characteristic south-western genera and families and their eastern outliers or connexions as throwing light upon the question of the origin of the South African flora.

6. In conclusion, general applications are discussed with special reference to (1) plant ecology, (2) the origin of the angiospermous flora of South Africa, (3) general phylogeny of the Angiosperms.

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