

The South-east African Flora: Its Origin, Migrations, and Evolutionary Tendencies.

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INTRODUCTION.

FEW regions are more favourably situated than South-east Africa for the study of plant distribution and its bearing on questions of evolutionary history. It is being recognized that one of the main problems in connexion with the phylogeny of the Angiosperms is the relationship between the tropical, subtropical, and temperate floras as well as the origin of various ecological types. Now in South-east Africa within a comparatively small area there occur (1) a purely tropical flora, which is a southerly extension of the tropical flora of Central Africa on the coast-belt; (2) a derived subtropical flora, adapted to drier and cooler climates, which becomes increasingly prominent towards the south on the coast-belt and occupies most of the region of rising altitude (1,500 feet and upwards) away from the sea; and (3) a mountain or temperate flora, which occupies the higher altitudes (8,000 ft. and over it) on the Drakensberg and other mountain ranges, descends to sea-level in the south-western region of the Cape, and connects through the mountains of Central Africa with the temperate flora of the Northern Hemisphere. The relationship between the first two types is very close. The purely tropical species are in a very large number of cases closely allied to the frost-resisting or more xerophytic subtropical species, and the tropical-subtropical vegetation may be grouped together as one element of the South African flora. The various modifications of it in reaction to changed ecological conditions, e. g. succulence, spinescence, and other forms of xerophytism, herbaceous growth-forms with capsular fruits and many other types, afford abundant opportunity for one line of research. A comparison of the coast-belt species with their nearest allies in the mid-lands of Natal from the morphological and physiological standpoints is in progress, and the results already obtained are extremely interesting.

The temperate or mountain flora is a very distinct element. Of course it mixes to a certain extent with the tropical-subtropical element, but, in the

main, even the families represented are different. The relationship of this flora to the tropical is much the same as that of the great temperate flora of the Northern Hemisphere, and will be discussed more fully later.

Instead of beginning with general comparisons and attempting to work downwards to details, it would appear more promising and more in accord with the usual methods of science to begin at the other end and study the migrations of the flora in a smaller area, afterwards extending the observations to larger and larger areas. As far as South Africa is concerned, the present study of plant geography in the larger sense has gradually developed out of detailed ecological investigations. Movements of species were analysed in connexion with plant succession, various lines of migration were traced, at first somewhat hypothetically, but the hypotheses were tested by an appeal to the facts of distribution, and now the final attempt is being made to connect up the various lines of migration so as to obtain a complete picture. The accepted principles of evolution in floral morphology have been used to check the results, but, on the other hand, the history of general plant migrations may be used to throw some light on doubtful points in evolutionary history. The most logical arrangement would be to begin with the tropical flora, give the reasons why the sub-tropical should be considered derivate, and then trace as many of the changes as possible. I prefer, however, to follow the order in which this investigation was actually carried out, since it gradually developed out of other work.

RIVER VALLEY MIGRATION.

The rivers of South-east Africa flow in a general easterly direction from the Drakensberg to the sea. The deeply cut river valleys are dry with extremes of temperature, and the vegetation is xerophytic grassland, thorn veld, or succulent scrub, the most extreme types being on the south sides of the valleys which face the sun. Along the upper flanks, especially on the north side, mesophytic forest develops. There are also various types of rocky scrub and tree veld on the flanks of the valleys. In brief, the various trees and shrubs (including at least a thousand species) of South-east Africa, composing the woodland plant communities, are, on the whole, associated in their distribution with the river valleys and their slopes.

The first detailed study of plant succession was made in the thorn veld (1). It was afterwards seen that the other types of parkland tree veld were similar. The pioneers are trees. They migrate out from the river banks, and colonize the grassland areas, and are followed by other more mesophytic trees and shrubs.

This, however, is the last step in the process of migration. The bases of colonization are the various river-bank woodland communities which extend for long distances along the river. To carry the process a step

farther back, therefore, it appears clear that there is extensive migration along the rivers either up or down the valleys. The conditions, of course, are uniform, but it is worth noting that nearly all the African trees and shrubs have fruits and seeds that are distributed by animals, especially birds, and these also feed and migrate along the rivers. Succession in dense mesophytic forest differs in detail from that in tree veld, but it also follows the rivers and their tributary streams (for details see 3). The same applies to other subordinate types of scrub.

We thus reach a first generalization that for trees and shrubs (mostly distributed by animals) composing various types of woodland (thorn veld, mesophytic tree veld, succulent scrub, rocky hillside scrub, dense mesophytic scrub and forest) migration takes place most rapidly in a direction parallel to the river valleys. This, we shall see, applies chiefly to the midlands of Natal, where the river valleys are deeply cut, and many species seem to have difficulty in crossing the intervening ridge between one river valley and the next. This hypothesis has now to be tested by reference to the distribution of such trees and shrubs as have not spread all over the eastern side of South Africa. We find a large number of such relatively rare species confined to the coast-belt, and their lines of maximum dispersal and therefore presumably of their migration run parallel to the coast, but such species are for the most part purely tropical or slightly modified subtropical.

In the Midlands, on the other hand, almost without exception, the rarer species have a maximum distribution parallel to the river valleys and ridges and at right angles to the coast-line. As an example, the Tugela Valley and its tributaries may be chosen. The following species are confined to it, and have not, so far as we know, as yet been able to cross into the next main river valley of the Umgeni farther south: *Croton rivularis*, *C. menyharti*, *C. zambesicus*, *Vitex mooiensis*, *V. rehmanni*, *Heeria paniculosa*, *Euphorbia tugelensis*, *Ipomaea albivenia*, *I. oblongata*, *Convolvulus ulosepalus*, *Ceropegia barklyi*, var. *tugelensis*, *Fockea tugelensis*, *Raphionacme flanaganii*, *Viscum pulchellum*, *V. subserratum*, *Pouzolzia* sp., *Boerhaavia bracteata*, *B. repens*, *Clematis glaucescens*, *Capparis calvescens*, *Acacia robusta*, *Rhus excisa*, *Pavonia urens*, *Royena simii*, *R. scabrida*, *Mimusops oleifolia*, *Olea enervis*, *Strychnos dyssochyla*, *Lippia scaberrima*, *Lycium pendulinum*, *Pavetta gerrardi*, *Melothria maderaspatana*, and others. Many of these are true endemics, others occur farther north, e. g. in the Transvaal but not elsewhere in Natal. In high forest, along the flanks of the ridges, the component species are usually more widespread, but there are examples of new endemic and more mesophytic species which spread most rapidly in a direction at right angles to the coast, e. g. *Podocarpus henkelii*. The river valleys and intervening ridges, while serving as lines of migration, also serve as barriers to migration across them.

The vegetation of the Tugela and its tributary, the Lower Mooi River, though, as the above list shows, it is rather distinct from that of the rest of Natal, has certain fairly close connexions with that of the dry kopjes in the northern Transvaal, e. g. *Heeria*, *Vitex*, *Croton*, *Pappea*, *Ficus*. For a time this appeared somewhat of a distributional puzzle. The two areas are separated by a great stretch of high veld grassland, many hundreds of miles wide, where these species do not occur. The explanation is suggested when we observe that the Northern Transvaal bears the same relationship to the great valley of the Limpopo as the Lower Mooi River area does to the Tugela. The species in question spread along both of these main river valleys. It is clear that this river migration must be connected up with the general coast-belt invasion of tropical and subtropical species from the North.

COAST-BELT MIGRATION.

As we have already pointed out, the maximum distribution of the coast-belt species is in a line parallel to the coast. The whole flora has close tropical affinities, but the actual tropical species diminish in numbers towards the south.

At the outset it is necessary to distinguish clearly between seashore migration and that of the rest of the coast-belt. Strand plants and seashore sand-dune species, as well as mangroves and other plants of the mud lagoons, whose seeds are capable of withstanding submergence in sea water, are rapidly and widely distributed, as Guppy has fully demonstrated (5). In South Africa the southern limit of the mangroves and other tropical forms in Tembuland is probably determined by the increasing influence of the cold shoreward current from the south, which flows northwards as a counter-current to the warm Mozambique current from the north. The latter is, of course, so much larger that it warms the whole eastern side of South Africa and raises the average temperatures much above those of corresponding latitudes on the western side. The cold counter-current varies in strength at different times and in a way not thoroughly understood. Occasionally its influence is very marked, as when it kills the fish of the tropical waters with which it mixes, and these float ashore in shoals. It is just such extreme and exceptional occurrences that are of the greatest importance in their effect on the vegetation.

While the actual coast-line is a uniform easy pathway leading to rapid migration for its own characteristic flora, farther inland on the coast-belt migration is slower, and rather pronounced changes in topography and soil conditions have tended to impose a check on the invasion of many species. Reference to any physical map of Africa will show that the 1,000 foot coast-belt, which is several hundreds of miles broad in Portuguese East Africa, becomes narrowed like the neck of a bottle at Port Durnford in Zululand.

Northward from that point it is a broad, flat, sandy belt usually only 100 feet or so above sea-level, but in Natal it becomes confined to a strip a mile or two broad along the coast-line. A considerable number of tropical species have not penetrated farther south than Zululand, and this is due probably rather to the altered topography than to any general lowering of temperature, though the cold current already referred to makes its influence felt as far as Port Durnford, where the outward bend in the coast-line turns it round. The coast-belt flora is purely tropical to the north of Zululand, but in Natal and in the eastern coast-belt of the Cape it has produced large numbers of derived endemic species. Mr. R. D. Aitken is carrying out a statistical analysis of these on the lines adopted by Willis. Such coast-belt endemic species as remain confined to the frost-free localities differ but slightly from the tropical 'wides'. Other subtropical species are more modified and penetrate farther into the colder and drier areas.

Along the frost-free localities on the flanks of the river valleys the tropical flora of the coast-belt has tended to migrate often far inland. *Dichrostachys nutans*, for instance, a characteristic and often dominant tropical tree veld species, has penetrated as far as the Lower Mooi River area. Recently, while exploring the Umgeni Valley, I was much interested to find, at altitudes of 3,000 feet, such typical coast-belt species as the um Doni (*Eugenia cordata*, which is the dominant species in hygrophilous coast-belt bush), *E. gerrardi*, *Chaetacme aristata*, *Dracaena hookeriana*, and *Iboza riparia*.

Comparatively few, however, of the actual tropical and coast-belt species thus migrate inland. The flora of the Midlands and the Cape eastern coast-belt, in response to lower temperatures and drier conditions, has been modified and consists of species often closely allied to but usually not identical with those occurring in the tropics, or if they do occur farther north it is at higher and higher altitudes the nearer to the Equator. We can now complete a portion of the main picture.

Purely tropical vegetation consisting largely of mesophytic trees and shrubs with usually simple leaves has invaded South-east Africa along the coast-belt and, with diminishing numbers, has penetrated even into the Cape Colony south of Natal. Some of the species have migrated far inland along the flanks of the river valleys. From this purely tropical vegetation an allied modified subtropical vegetation has been derived, which has penetrated south as far as the limit of the area of summer rainfall (beyond Port Elizabeth) and has migrated inland at right angles to the coast-line along the river valleys and intervening system of ridges. The subtropical flora is adapted, on the one hand, to lower temperatures and, on the other hand, to drier conditions. This has led to a considerable diversity of growth form. A succulent habit is a very common result. Thorn development in response to dry conditions is very marked. Evidence is accumulating to show that

compound or divided leaves are far more common in derived subtropical species than in the purely tropical. The herbaceous habit is often derivative.

MIGRATION AND EVOLUTION: COMPARISON OF TROPICAL AND SUBTROPICAL FORMS.

The accepted principles of phylogeny on the whole support the view adopted, viz. that the subtropical flora has been derived from the tropical, but, as we shall see later when the temperate element is also compared, floral evolution has not always run parallel to that of the vegetative morphology. An examination of practically all the families has been made, but considerations of space prevent our dealing with more than a few comparisons here. The following families are chosen at random:

Flacourtiaceae. The tribe Erythrospermeae with the perianth leaves spirally arranged is the older and widespread in the tropics, having one genus, *Rawsonia*, which reaches Natal. The other nine South African genera are subtropical and more advanced in flower structure, having perianth leaves whorled and usually petals present as well as sepals.

Violaceae. The tropical-subtropical Rinoreae (shrubs and trees with nearly regular flowers) are to be contrasted with the subtropical and temperate *Violeae*, herbs with irregular flowers.

Loranthaceae. *Loranthus* has an hermaphrodite and less reduced, and therefore being parasitic probably an older, type of flower than *Viscum*. *Loranthus* is distinctly more tropical than *Viscum*.

Thymelaeaceae. *Octolepis* is the most primitive type, with a flat receptacle, and is purely tropical (seven species in West Africa). *Peddiea* is an East African tropical-subtropical genus with a two-celled ovary and fruit a drupe, not so primitive as *Octolepis*, but more so than all the other South African genera of shrubs, undershrubs, and herbs which have the ovary one-celled. There are certain pairs of families which might be compared and contrasted to illustrate the same thing, e. g. Apocynaceae, more tropical and relatively more primitive, and Asclepiadaceae, distinctly more subtropical or even temperate and relatively more advanced in floral morphology. Araliaceae and Umbelliferae, Myrsinaceae and Primulaceae are similar pairs.

Euphorbiaceae. This family is clearly tropical in origin, and the most recent and highly developed derivative types like *Euphorbia* have penetrated farthest into the colder and drier regions, while the tropical types, though they have broken up into great numbers of distinct genera, have retained more of the primitive floral characters. The genus *Euphorbia* with about 1,000 species has a remarkably uniform floral structure, and very extreme vegetative variation from tiny annual herbs up to large trees over sixty feet high. Variations in floral structure are confined to the involucre

glands, which, however, grade into one another completely, and sometimes vary in the same species or on the same individual. The systematic works say little or nothing regarding the probable evolutionary history of the genus, but if we follow it step by step along the lines of its invasion into South Africa we can give the following outline of its evolution. The more mesophytic tropical species of shrubs with erect, leafy, woody, spineless stems probably come nearest to the ancestral form. Some of them have invaded Eastern South Africa, e.g. *E. epicyparissias*. The purely herbaceous type has been derived, but has not diverged very far. Of the herbaceous forms the small annuals are most recent, and of these *E. inaequilatera* is one of the commonest and has spread all over Africa. Many are weeds of cultivation, e.g. *E. peplus* and *E. helioscopia*. A section of the perennial herbaceous types has developed tuberous root-stocks. The shrubby types have in another direction developed spines which, according to N. E. Brown (4), are of three types in the South African species: (1) where the apex of a branch becomes spiny, as in *E. lignosa* and *E. spinea*, two dwarf shrublets from Namaqualand (one or two transitional forms have tapering branches not acutely spine-tipped); (2) where the peduncle becomes transformed into a spine; and (3) the so-called 'stipular spines', which are in pairs but are probably not stipular in origin.

Spine development, as we have noted, is one of the general reactions to drier conditions. The main evolutionary tendency in the genus, however, has been towards succulence. It is seen in the large variety of low-growing forms that have probably developed from the perennial herbaceous forms and in the large succulent tree Euphorbias which come nearer to the primitive shrubby forms. The succulent, 'leafless', and often spiny Euphorbias have developed from the tropical types partly in the dry areas of the western side and partly in the dry river valleys of the eastern side where the species are usually distinct. The Karroo species are also distinct.

In support of the view that the numerous succulent South African species are recent and derivative we have not only the general origin of the subtropical South African flora, but the further fact that when cultivated under moist conditions succulent species show a tendency to revert to a shrubby type and develop slender leafy branches with no trace of succulence. This has been noted particularly by N. E. Brown in connexion with *E. gorgonis* as cultivated at Kew (see 4, and *Gardeners' Chronicle*, 1914, lvi. 230, fig. 91, p. 312).

Though succulence, thorn development, and other xerophytic characters are common features of derivative subtropical forms, it must not be assumed that evolution in the South African flora has always been in this direction. There are numerous extra-tropical mesophytic forest situations where recent endemic forms have been produced. Some genera show development in both directions.

Gymnosporia (Celastraceae). The oldest type of this genus, according to inflorescence and fruit characters, has no spines, and is represented in South Africa by such a type as *G. acuminata*, a small tree which occurs usually outside but sometimes inside forest. *G. peduncularis* is a closely allied large, mesophytic, forest tree. *G. cordata*, also near the ancestral type, is a coast forest species. A more recent type, with the inflorescence in clustered cymose panicles, is represented by *G. buxifolia*, a somewhat variable and widespread species all over South Africa. It is very spiny in the drier situations and illustrates the development, on the one hand, towards xerophytism. On the other hand, the rare endemic, *G. amapondensis*, is a recent type with the fruit one-celled instead of three-celled. It is known only from the Egossa forest in East Pondoland and illustrates the development towards mesophytism.

Any other large genus which is tropical and subtropical can be dealt with in exactly the same way as in the case of *Euphorbia* and *Gymnosporia*.

SUBTROPICAL GRASSLANDS.

The flora of the great subtropical grassland areas consists of species which, unlike the trees and shrubs, are mostly wind-distributed, and the origin and migrations of the type as a whole are not so easily traced. The origin of the grasses themselves is also somewhat obscure. In the Bamboos the grass flower approaches nearest to the ordinary monocotyledonous type, and possibly they are the most primitive. The twenty-three genera of Bambuseae are mainly tropical with a tendency to extend largely into the mountains of the tropics, but they are not grassland types. The tropical and subtropical grasslands are dominated mainly by genera belonging to the tribes Andropogoneae and Paniceae, where the spikelets are much reduced and highly specialized, phylogenetically an advanced type.

Aristida (Stipeae) is a large important genus adapted to drier subtropical and desert conditions.

Temperate grasses, on the other hand, belong mainly to the tribes Aveneae, Festuceae, and Hordeae, with spikelets less specialized and containing usually numerous florets. This would seem to suggest that, with the exception of the Bamboos, the temperate grasses have retained more of the primitive floral characters than the tropical, but there is little agreement on the course of evolution in the grass flower, and the subject must for the present remain obscure.

In South-east Africa the most distinctly tropical type of grassland is that of the coast-belt, where there is an admixture of species such as *Pollinia villosa*, *Perotis latifolia*, and species of *Panicum*, but the dominant species belong to the Andropogoneae, as in the high veld and low veld areas all over the eastern side. Species of *Aristida*, *Eragrostis*, and *Sporobolus* show adaptation to drier conditions and open formations. At

higher altitudes there is an admixture of temperate species of *Poa*, *Festuca*, &c., but all the eastern grassveld remains on the whole subtropical.

Mixed with the grasses throughout there are enormous numbers of herbaceous or shrubby species. The 'autumnal aspect societies', which tend to replace the grasses, are again tropical in their affinities. On the other hand, the great mass of 'vernal aspect societies', which are bulbous or geophytic as a rule in their growth forms, belong to such families as the Compositae, Papilionaceae, Geraniaceae, Asclepiadaceae, Liliaceae, Amaryllidaceae, Iridaceae, and, while constituting a special type of their own, the species being largely endemic, they have closer affinities with the temperate flora than with the tropical. They or allied species may occur on the mountains and elevated grassy plateaux of the tropics, but they are not characteristic of the tropical forest regions.

It is interesting to note that these vernal aspect societies are characteristic of early stages of the plant succession, being gradually suppressed as succession advances. I have pointed out elsewhere that in a subtropical region, as succession advances, the vegetation tends to become more and more tropical, e. g. on the Natal coast-belt (3).

THE TEMPERATE OR MOUNTAIN FLORA: MIGRATION ALONG MOUNTAIN RANGES.

Reference once more to a physical map of Africa will show that the whole eastern side is a region of elevation. Some of the river valleys, e. g. the Zambesi and Limpopo, have cut rather far back through the mountain escarpment of the inland plateau, but otherwise highly elevated land is continuous from Abyssinia to the Drakensberg and westward across the southern end of South Africa to the Cape Peninsula. The south-western region of the Cape with its winter rainfall and dry summers has a 'Mediterranean flora' of warm temperate rather than tropical affinities. This temperate flora at increasingly high altitudes is continued eastward through the Drakensberg in Natal and the Transvaal and northward through Central Africa to Abyssinia. It is not only distinct ecologically but also floristically from that of the tropics and subtropical eastern side.

The Compositae, Ericaceae, Proteaceae, Rosaceae (*Cliffortia*), Geraniaceae (*Pelargonium*), bulbous Monocotyledons, and many distinctive sections or genera in other families are most prominent in this mountain flora. The absence or rarity of such families as Acanthaceae, Capparidaceae, Anonaceae, Menispermaceae, the majority of the Euphorbiaceae, large sections of the Leguminosae, the Sapindaceae, Melianthaceae, Sapotaceae, Cucurbitaceae, and many others so prominent on the coast-belt is equally striking. The majority of the species of the temperate or mountain flora are either herbaceous or low-growing shrubs often gnarled and twisted. Mountain regions are regions of unstable topography and variable climatic conditions. Some

situations are very moist, others very dry; some are shady, others fully exposed to the intense light of high altitudes; some are free from frosts owing to the rapid cold air drainage, others near at hand are not, and all these varied types of habitat are usually thoroughly mixed up in any small area.

Judging from the number of endemic species characteristic of mountain ranges, such variable and unstable conditions are favourable for the production of new species. These may be very rare, but in other cases mountain species extend for immense distances along the ranges without descending to lower altitudes. Mountain ranges are, therefore, looked upon as great highways of migration for their own characteristic flora, and further, like the river valleys, they act as barriers to migration across them.

There is considerable difference of opinion regarding the origin of the temperate African flora. It is richest in numbers in the south-west of the Cape Colony, a region climatically most suited to it, and there it occurs down to sea-level. Eastward, as soon as the region of summer rainfall is entered, it becomes entirely a mountain flora. It was first investigated at the Cape and is best known there. It is natural to speak of the occurrences of *Ericas*, *Proteas*, &c., on the Drakensberg as 'outliers' of the south-west flora, a term which, to a certain extent, assumes an origin for it in the south-west. It has connexions with the flora of Australia and South America, and it is therefore looked upon as the remnants of the flora of a former temperate Antarctic continent. It is not, on the whole, phylogenetically an old flora in spite of assumptions to the contrary, and it is extremely doubtful whether any Antarctic continent has existed since the rise of the Angiosperms.

Other authorities believe that the mountain and South-western African flora has come from the north. The original immigrants travelled south along the mountain ranges crossing the Equator, and when they reached the more temperate south-western areas developed enormously and produced the great numbers of new species which now occur there.

It is not, of course, necessary to assume single centres of origin for any of the widespread component elements of this flora (such as the *Ericaceae*). So long as we deal with the larger groups such as the families and large genera there are many reasons for believing 'multiple origins' or polygenesis as the most likely, and the recent developments of genetics show that the polygenesis of species is also extremely probable. Without, therefore, arguing further concerning the exact geographical origin of the temperate African flora, we may turn to the question of real interest, viz. its relationship to the tropical-subtropical flora, with which geographically it is so closely associated.

Sinnott and Bailey (6) have brought forward much evidence from palaeobotany, anatomy, and phylogeny to show that the tropical woody

type of plant is an older form than the temperate herbaceous type. In addition to the evidence from other branches of botany, their argument from the geographical standpoint is summed up as follows: 'There is great preponderance of herbs in temperate regions and of woody plants in the tropics. The latter climate probably approaches more nearly to that under which Angiosperms first appeared. Herbs have a short life cycle and are therefore able to survive periods of cold underground or in the form of seeds. Their great development in temperate regions has probably been in response to the progressive refrigeration of the climate during the course of the Tertiary.'

Though there are a great many herbs (especially bulbous Monocotyledons) in the temperate African flora, there is also a high proportion of small woody shrubs, and the number of endemics is exceptionally large. Now Sinnott and Bailey argue that the endemic plants in a flora are to be regarded usually as its most ancient element, a conclusion exactly the opposite of that reached by Willis (8). Sinnott and Bailey would have it that the herbaceous element of the temperate African flora is recent and derivative, while the woody element is ancient, a conclusion which receives no support from its present-day distribution, nor from the phylogeny of the families to which most of the woody types belong, Compositae, Ericaceae, Proteaceae, &c. The same areas are occupied by both elements, herbs and woody shrubs. Before discussing these views further we may investigate what is to be learned by comparing the temperate and tropical floras.

COMPARISON OF TEMPERATE AND TROPICAL FLORAS.

Certain families have already been compared as regards their tropical and subtropical representatives. The conclusions there reached, viz. that the tropical types were older than the subtropical, apply also in many cases when the former are compared with temperate types. This is the case in the Violaceae, Loranthaceae, Thymelaeaceae, Apocynaceae, and Asclepiadaceae taken together, and similarly the Myrsinaceae and Primulaceae and Araliaceae and Umbelliferae, each pair taken together. In other families the same thing is seen, the more primitive section in floral characters being tropical, the more recent temperate, e.g. Boraginaceae, Santalaceae, Ulmaceae, Liliaceae, Rubiaceae, Leguminosae, and others. It is noteworthy that the more primitive tropical types usually have fleshy indehiscent fruits, while the more recent temperate types have usually capsular fruits.

There are, however, a considerable number of families in which the temperate representatives have apparently retained more of the primitive ancestral characters in their floral morphology. In the Verbenaceae the subfamily Stilboideae has usually nearly regular corollas and endospermic seeds, and is more temperate than the Verbenoideae, which has irregular corollas and exendospermic seeds, or than the other subsections, the Viticoideae

and Avicennioidae. The same thing is seen in the Iridaceae, the temperate forms or at least the south-western Cape forms having more primitive floral characters than the eastern and subtropical. The Orchidaceae, with the exception of the Diandrae section, have also, on the whole, retained the less highly developed types of floral structure in the temperate representatives. The Gramineae have already been dealt with from the same standpoint.

Phylogeny, therefore, does not support so definitely the deriving of the temperate flora from the tropical as it did in the case of the more closely allied subtropical. The temperate and tropical floras have probably both diverged in different directions from the ancestral forms. At the same time it is probably true, as Sinnott and Bailey maintain, that the tropical climate approaches more nearly that in which Angiosperms first appeared. Consequently the tropical flora has remained more primitive on the whole in its growth forms, which are usually of a woody mesophytic type with simple bifacial leaves.

The herbaceous form is on the whole derivative, the shorter life cycle being better adapted to colder seasons and drier situations. The bulbous and tuberous type with underground storage has been multiplied in an enormous series of forms in response to grassland conditions. Capsular fruits and wide dispersal of seeds have tended to replace fleshy fruits and animal dispersal in many families.

Various kinds of xerophytism, epiphytism, parasitism, and the aquatic habit are generally derivative. Leaf division is probably, on the whole, also derivative and relatively recent in the Angiosperms.

Evolution in floral morphology, however, has not always been parallel to evolution in vegetative form. In some cases the tropical representatives of a group are the most primitive in flower characters, in other cases not. It should not be forgotten that genera, and, where possible, species also, are named by the systematist on floral characters. Under favourable moist, warm conditions the tropical flora, while retaining a fairly uniform type of growth form, has broken up into an immense number of new and probably often fairly recent floral forms, i.e. genera and species. Each of these is rather rigid in its requirements, and shows little plasticity, though germinally each type may be relatively unstable and ready to break up into further new forms. At any rate, tropical vegetation is, as is well known, exceedingly mixed and the numbers of species extraordinarily great. The temperate flora, on the other hand, has produced a much greater variety of growth form, but has a smaller total number of species. Each type is individually more plastic. A succulent, for instance, will grow quite well under moist conditions if competition with other plants is removed, but a moist tropical species can endure neither low temperatures nor dry conditions.

While it is not safe to assume that the tropical flora has produced the temperate or vice versa, while it is better to consider that both have diverged

from the ancestral forms, yet there are many examples in the larger genera of a tropical or subtropical genus, e. g. *Rhus*, which has produced temperate representatives, or of a temperate or mountain genus, e. g. *Pelargonium*, which has invaded the tropics. The whole family of the Compositae are, according to Small (7), probably montane and temperate in origin, yet they have invaded the tropics in considerable numbers. By following the probable migrations of a genus among the mountain forms, as was done in the case of *Euphorbia* and *Gymnosporia* among the tropical-subtropical forms, interesting light is thrown on its evolutionary history.

Pelargonium, unlike *Euphorbia*, has somewhat variable floral characters, the only really constant generic character being the uppermost segment of the calyx forming a 'nectariferous tube', adnate to the pedicel. The petals vary in number (5, 4, or 2) and size, and from being subequal to very unequal. In the androecium there are ten filaments, but only from seven to two are fertile. Harvey has broken up the genus into fifteen sections, a division which other systematists have adopted, e. g. Knuth in 'Das Pflanzenreich', p. 53, 1912. The section *Hoarea*, consisting of stemless tuberous-rooted species, are placed at the beginning as section 1, but though the section is a large one, and all typically south-western, it is doubtful whether it should be considered the most primitive. The fact that it has a relatively narrow range of distribution would tell against its primitiveness, according to Willis's Age and Area law (8). The section *Eumorpha* has a wider distribution from Abyssinia to South Africa. Allied to it is the section *Peristera*, in which the petals are minute, scarcely longer than the calyx; the calyx tube is sometimes nearly obsolete, e. g. in *P. fumarioides*, which is almost an *Erodium*; the habit is herbaceous like that of a *Geranium*. This section is the most widely distributed of all, extending all over Africa and having one species in India and two in Australia. The central species in South Africa is *P. grossularioides*, which is found all over the Cape and is a mountain species in the Drakensberg. Other species of the section occur in Namaqualand and the north-west. Considering carefully these facts of distribution it would appear probable that the ancestral form was a slightly woody or suffrutescent type which probably arose somewhere in the extra-tropical mountain ranges. The woody habit was emphasized in many south-western forms, especially in the section *Pelargium* to which the well-known *P. cucullatum* belongs. Succulence either of stems or leaves is another common feature as an adaptation to drier conditions. The stemless tuberous-rooted sections *Hoarea* and *Seymouria* are all south-western.

The point of chief interest regarding *Pelargonium* is the way in which, though extra-tropical in its origin, it has produced many species which find a place in tropical or subtropical areas. I have listed seventeen species of *Pelargonium* in my 'Flora of Natal and Zululand' (3). Two are marked

'doubtful', five are purely mountain, but the others are found either in the Midlands or even on the coast-belt. *P. aconitifolium* is the commonest. It is, like the others, adapted to grassland conditions, and forms one of the commonest of the 'vernal aspect societies' in subtropical grassveld. This illustrates again the temperate affinities of those vernal aspect societies.

In the above account the South-east African flora as a whole has been dealt with in a general way, and the details mentioned have been used as examples. More detailed investigations on the above lines, in which our modern knowledge of morphology, physiology, and physiological anatomy is being utilized, are in progress at this centre, and the results appear likely to be very interesting.

SUMMARY.

1. South-east Africa has a flora composed of two distinct elements: (a) a tropical-subtropical element, and (b) a temperate or mountain element. The study of various lines of migration throws light on the origin of these elements and also on many questions of evolutionary history.

2. The various trees and shrubs composing the woodland plant communities are distributed mainly by birds and other animals, and they tend to migrate most rapidly along the main river valleys at right angles to the coast. This river valley migration, however, is the final step in a general migration from the north along the coast-belt.

3. The tropical flora has invaded South-east Africa and remains distinctly tropical on the coast-belt. The numbers of tropical species diminish southwards, being gradually replaced by allied subtropical species. A few of the tropical species have migrated for considerable distances inland along the valleys, but in general with rising altitude, lower temperatures, and drier conditions the flora becomes subtropical.

4. A comparison of the floral morphology in allied tropical and subtropical forms shows that the former is older and the latter derivative. Succulence, spinescence, and other forms of xerophytism in response to drier conditions are characteristic of the subtropical flora, as is illustrated by the evolution of the genus *Euphorbia*. Sometimes derived and recent species may be, on the one hand, more xerophytic and, on the other hand, more mesophytic, as in the genus *Gymnosporia*.

5. The species composing the South-east African grasslands are mostly wind-distributed and lines of migration are not so easily determined. The grasses are tropical or subtropical and also the autumnal aspect societies. Vernal aspect societies, however, while largely endemic, and of a type by themselves, have on the whole more affinity with the temperate element of the flora.

6. Great mountain ranges run parallel to the eastern coast of the African continent across the tropics and connect with the south-western

Cape region of winter rainfall. These form a great line of migration for the temperate or mountain element of the flora, which bears a relationship to the tropical flora much the same as that of the northern temperate regions. Mountains are regions of unstable topography and great climatic variations, conditions which appear to favour the production of new species.

7. A comparison of the floral morphology in allied tropical and temperate forms shows that in many families the tropical element is the older, but in others the reverse is the case, the temperate representatives having retained more of the primitive ancestral floral characters. It is suggested that the tropical flora has remained more primitive on the whole in its growth forms, which are of a rather uniform, woody, mesophytic type with simple bifacial leaves. Herbaceous forms, bulbous and tuberous forms, capsular fruits, plants with divided leaves, xerophytes, &c., are in general derivate and more characteristic of the temperate flora. Floral evolution and vegetative evolution have not always run parallel.

8. While it is considered advisable not to attempt to derive the temperate flora as a whole from the tropical or vice versa, yet examples are given of tropical genera producing species which have invaded temperate regions, e.g. *Rhus*, and of temperate genera which have invaded the tropics, e.g. *Pelargonium*.

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