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THE TAXONOMIC AND ECOLOGICAL BASIS OF CHOROLOGY

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Taxonomy, ecology and chorology are interdependent and should always be studied together. If the subject of this paper had been "The ecological and chorological basis of taxonomy" its contents might not have been very different.

I shall first state and discuss three general principles or aphorisms which I think are basic. These will be followed by two chorological aphorisms, which apply particularly to the situation in Africa. I shall illustrate these aphorisms with examples from my own recent work. The latter will only be briefly discussed, since they have been, or will be, more fully treated in a series of publications on the Ebenaceae (White 1957, 1962, 1969) or in a recently completed work on *The evergreen forests of Malawi* (Chapman & White 1970).

The family Ebenaceae has certain advantages in general studies of this kind, since most species are habitually dioecious. This means that complications due to inbreeding or apomixis are, respectively, impossible or unlikely to occur.

Some of the ideas put forward in this paper have arisen from attempts to relate the results of my own detailed studies to the patterns shown by the vegetation types on the new AETFAT/UNESCO Vegetation map of Africa (White [ed.] in press). During the compilation of this I have had the unique advantage of friendly collaboration with a wide range of specialists, most of whom belong to our Association. Their collective experience covers the whole of Africa. Here I should like to express my warmest appreciation for their assistance.

I am sure that some of you already accept these aphorisms as selfevident truths. Since, however, only casual contact with recent literature is sufficient to show that their acceptance is far from universal, I hope you will forgive me if I sometimes appear to be stating the obvious.

Biogeography has two main aspects — *descriptive,* or static, which is based on accurate knowledge of present-day plant distributions, and *historic,* or dynamic, which attempts to explain present-day distributions in terms of historic events — chiefly climatic, geological, migrational and evolutionary.

In his masterly account of the history of the British flora, Godwin (1956) has shown that, for the British Isles at least, more than a century ago, distributional data were sufficiently completely known for brilliant hypotheses to be expounded (FORBES 1846) to account for the discontinuous distribution of certain species, such as those of the Arctic-alpine element.

Since then the essential character of evidence from distributional data has not greatly altered, but "what has altered very greatly has been our knowledge of the whole background of climatic and geological changes through the Pleistocene period ... Biogeographic hypotheses have multiplied to keep pace with our knowledge of this climatic-geological history of the last one million years: warmth-demanding species are explained as having immigrated in the Post-glacial climatic optimum. [Examples of other hypotheses are also given] ... There is nothing inherently improbable about this kind of explanation, and indeed it may very well be along such lines that our final theory will shape itself; what is lacking is any positive evidence, as opposed to the purely circumstantial evidence, that a given hypothesis does apply to a given species, and that a given species was indeed present in these islands at the periods demanded by the hypothetical explanation." The greater part of GODWIN's book is devoted to providing such evidence.

For Africa the situation is much more complex than that described by GODWIN for the British Isles. Not only is the flora infinitely richer, but our knowledge of present-day distributions and past climatic and geological events is much more sketchy. Nevertheless there are indications that historical plant geography in Africa is about to enter a vigorous and fruitful phase.

Every careful taxonomic or chorological study of African species reveals variation or distribution patterns which demand historical explanations. We already know sufficient of Pleistocene (and earlier) climatic and geological changes to realize that their repercussions on plant distributions and taxonomic relationships must have been considerable. It is not yet possible, however, to explain contemporary variation or chorological patterns in terms of specific historic events, but recent palaeobotanical studies (e. g. HEDBERG 1954; COETZEE 1967; LIVINGSTONE 1967; MORRISON 1968; MULLER 1970) indicate that this may not always be so.

In the meantime we must proceed inductively. Hypotheses should be used as an aid to the interpretation of observed facts and as an incentive to further investigation, not as starting points. Patterns of plant distribution, taxonomic relationships and ecological requirements, when detected, should show palaeobotanists what to look for, and help them to interpret their discoveries.

It may be that the history of the African flora has been too complex and the preserved historic evidence may be too incomplete to permit interpretations comparable to those which have been achieved for the North temperate flora. Even if that were so, and it is by no means certain, I am convinced that if the interdependence of chorology, taxonomy and ecology is recognized, much of outstanding interest will be discovered.

GENERAL APHORISMS

1. *Taxonomy, chorology and ecology are interdependent. Each, in isolation, is a sterile pursuit. Unless their reciprocal relationships are exploited, significant patterns remain undetected.*

The examples discussed below should demonstrate the truth of this aphorism.

2. *Detection of pattern requires rigorous objective analysis. What is compared must be truly comparable. Communication depends on effective display of the evidence.*

Taxonomists working with higher organisms, particularly in the early stages of their work, are able to do much pattern analysis 'by eye', because of the remarkable ability of the human brain, at least in some individuals, to remember and subconsciously compare large numbers of visual impressions.

Most taxonomy (and also much chorology and ecology) would be both prohibitively time-consuming and deadly dull if it were not possible to detect patterns, at least tentatively, by using what ADANSON and BURTT have called 'perception' (see BURTT 1965, p. 428). There is, however, a temptation for taxonomists to assume, without making adequate tests, that their powers of perception are sufficiently well-developed to deal with all variation patterns they encounter, however complex.

In my own experience the geographical patterns of variation shown by most widespread and variable species are too complicated to be understood or satisfactorily described without the use of special methods of analysis.

Since the publication of ANDERSON's book on Introgressive hybridization (ANDERSON 1949), several taxonomists working on the African flora (e. g. DUVIGNEAUD, MARLIER & DEWIT 1952; HEDBERG 1955, 1957; WHITE 1957, 1962) have realized that the methods ANDERSON devized primarily for analysing and displaying the variation patterns of *populations* could equally well be used for *analysing* and *depicting* the variation patterns and relationships of *species* using herbarium samples.

In the application of Andersonian techniques to herbarium taxonomy the first stage is the preparation of an ideograph for each specimen. On a separate card or slip of paper the features being investigated are recorded as simply as possible, by symbols or measurements, together with a record of locality and collector's name and number and any other information with which variation may be correlated. Any significant pattern which emerges from a study of the ideographs can be visually displayed using various methods, of which the pictorialized scatter diagram (fig. 2) and pictorialized distribution map (figs. 1, 3, 4) are the most useful. When this is done, the reader can see for himself the evidence on which taxonomic decisions and statements about patterns of variation have been based. If the ideographs are filed in the herbarium, they will provide a permanent record of the complete study and not just of those characters used in the published account.

It must be realized, however, that Andersonian methods can be seriously misapplied unless they are used intelligently, and special checks are taken to ensure accuracy and objectivity. The first requirement is that, what is being compared should be truly comparable. In scoring leaf-shape and size, for instance, useful comparisons can only be made if the material is at the same stage of development and comes from the same part of the plant; this usually means using only flowering and fruiting specimens, and not using the former if the flowers are produced before the leaves are fully developed. On a typical shoot, leaf-shape and size varies according to position of insertion on the branchlet, and comparisons must be made between leaves from comparable positions in the "'leaf spectrum' (see MELVILLE 1953). For practical purposes, however, I have found that in most cases satisfactory and repeatable (using comparable subsequent samples) results can often be obtained if the largest leaf on each specimen is scored. In *Podocarpus,* for instance, sufficiently similar results are obtained if the longest leaf, the mean of the 3 longest leaves and a leaf from a defined position in the leaf spectrum are used (WHITE & CAVENEY, unpublished). The above remarks may seem obvious, but methods which at first sight appear to be sound and objective are sometimes found to be seriously misleading.

Two species may be quite distinct in leaflet-shape when comparable leaflets (e. g. the ante-penultimate) are compared. If, however, the leaf spectra are compared there may be a very great overlap. In this case if, say, "three leaflets per specimen chosen at random' (I quote from a recent publication) are scored, the discontinuity in the variation pattern could be completely lost. This is only one of the many misapplications of statistics in biology.

A second requirement is that it should be possible for character states to be consistently scored in the same way by different workers, using the same material, or by the same worker on subsequent occasions. Fig. 3 is based on ideographs for which Mrs. CAVENEY and I recorded one of three character states for four characters of *Diospyros whyteana.* The same material was subsequently scored by a research student who has worked with Asiatic

Fig. 1. Pictorialized distribution map of *Diospyros monbuttensis* and *D. senensis,* showing main similarities and differences, and maximum, minimum and mean calyx-, acumen- and leaf-lengths based on all material studied. *D. monbuttensis:* A, leaf (VIGNE 1897); B, leaf (LEBRUN 3183); C, indumentum of lower leaf-surface (LEBRUN 3183); D, flower-bud (JOHNSTON 87/32); E, peduncle and pedicels of ♂ inflorescence (LEBRUN 3183); F, fruit (LYON 2640). *D. senensis:* G, leaf (WHITE 2963); H, leaves (LOVEMORE 182); I, leaf (BANDA 39); J, indumentum of lower leaf-survace (TORRE 6081); K, flower-bud (LOVEMORE 230); L, peduncle and pedicels of ♂ inflorescence (TORRE 6081); M, fruit (BANDA 31). T. 1. Type locality of *D. monbuttensis;* T. 2. Type locality of *D. senensis.*

(Leaves × 0.4, flowers × 2.4, peduncles etc. × 2, indumentum × 8, fruits × 0.8).

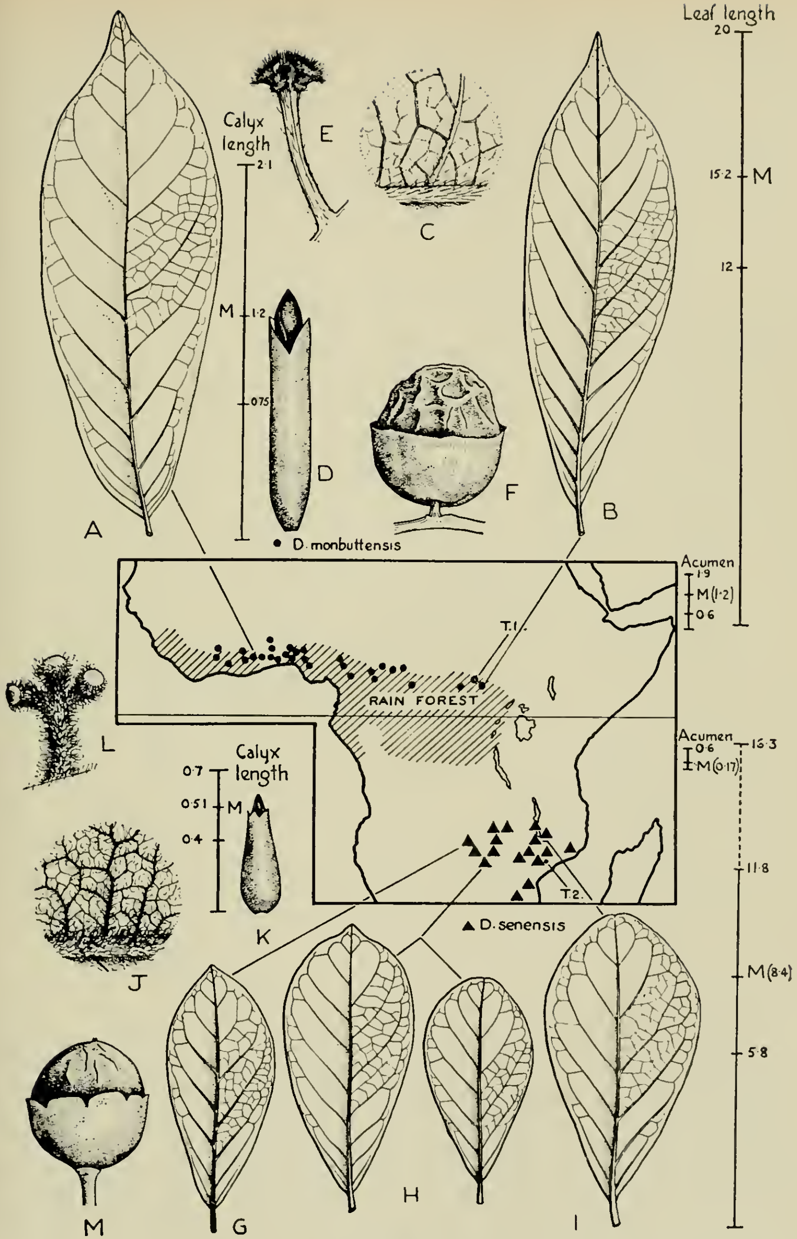

Leaf length
20
15·2
M
12
Calyx length
2·1
M
1·2
0·75
E
C
D
F
A
B
● D. monbuttensis
Acumen
1·9
M(1·2)
0·6
T.1.
RAIN FOREST
L
Acumen
0·6
M(0·17)
15·3
Calyx length
0·7
0·51
M
0·4
K
J
11·8
M(8·4)
5·8
▲ D. senensis
T.2.
M
G
H
I

FIG. 3

Ebenaceae but does not know the African species, and a technician with no previous experience of botany. The research student's results were 94% concordant with the first results and the technician's results were 91% concordant. The only discrepancies between the three sets of results concerned certain intermediate and essentially border-line character states where discordance can be most expected, and were so slight as not to affect any conclusions which could be drawn from the study.

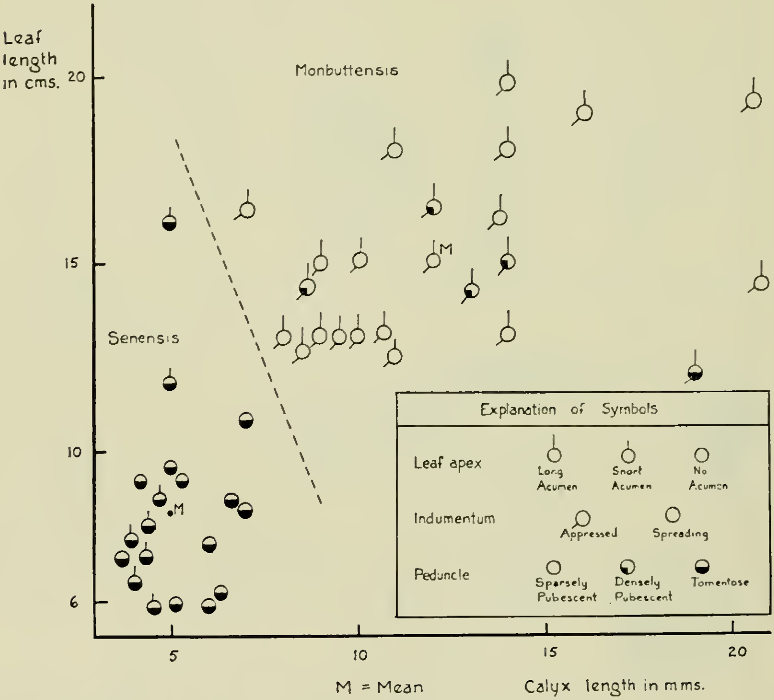


Fig. 2. *Diospyros monbuttensis* and *D. senensis*. Pictorialized scatter diagram showing correlation between maximum leaf-length (vertical axis), maximum length of calyx (horizontal axis), maximum length of leaf acumen, quality of indumentum on leaves, and density of indumentum on peduncle. The symbols are explained concisely by the key in the bottom right-hand corner and more fully by WHITE (1957, pp. 524—9). All specimens from north of the Equator lie to the right of the broken line, and those from South Tropical Africa to the left. The uppermost symbol for *D. senensis* may be abnormal (see WHITE 1957). M and M indicate the combined mean values of maximum leaf-length and maximum calyx-length for *D. senensis* and *D. monbuttensis* respectively.

Accurate scoring of qualitative character states is only possible if the specimen being scored is compared with a "standard" which covers the whole range of each character state. In fig. 4 drawings H and I define the range covered by the character state "slightly pubescent"; in a similar way K and L illustrate "densely pubescent"; the intermediate state falls between I and K and is not illustrated.

Andersonian techniques depict complicated variation patterns with economy and clarity. Pictorialized distribution maps published before a study is complete may effectively communicate existing knowledge to those who can assist in its completion. If, however, it is claimed that a pictorialized distribution map accurately represents the situation 'on the ground', steps must be taken to show that this is indeed so. Our work in Oxford (still largely unpublished) shows that for many woody species which are not too difficult to collect, there is more than enough herbarium material to establish the major features of both distribution and variation patterns. Here I can only refer to one published example. In 1962 I published two illustrations (reproduced here as figs. 1 and 2), which show the distributions of and summarize the main differences between the two closely related species *Diospyros monbuttensis* and *D. senensis*. The 1962 illustrations were based on 43 *élite* specimens of *D. monbuttensis* and 30 of *D. senensis*. By 1969, a further 38 specimens of *D. monbuttensis* and 37 specimens of *D. senensis* had become available. All come from localities within or immediately adjacent to the distributions previously established, and, apart from one or two trifling measurements, the ranges of variation for all characters selected fell within those of the first samples; the mean values are almost identical (see White 1969). The situation discussed above is relatively simple, but we have evidence that the same is true for much more complicated patterns such as that illustrated by fig. 4 for *Euclea natalensis* and by fig. 3 for *Diospyros whyteana*. Similarly for many other species of *Euclea* (White and Caveney, unpublished) and *Diospyros* sectio *Royena* (Caveney, unpublished). For these species hundreds of specimens are involved.

What I have said for taxonomy is equally true of chorology though the methods are different.

According to Léonard (1965) the delimitation of phytogeographical territories should be based on several criteria — principally the *aspect* of the terrain, which itself depends on the ecological conditions and the physiognomy of the vegetation as well as on floristics, that is on considerations based on geographical distribution of species. In emphasizing *aspect* Léonard is underlining the fact that, in the early stages of chorology, *perception* plays as important a part as it does in the early stage of taxonomy. In both cases the tentative conclusions based largely on visual comparison and memory are valuable, but further progress is dependent on more rigorous methods.

Progress in chorology depends on an accurate knowledge of the distribution of species *combined with* a knowledge of their taxonomic relationships and ecology. In chorology we may either study the flora of a chorological territory in order to define its boundaries more precisely, or, by analysing its genetic elements we may shed light on its history, or we may analyse the flora of a restricted area in order to discover to which chorological territory it belongs. But whatever we do, it is more useful to base one's analyses, in the first instance, on the dominant species of the most characteristic vegetation types and subsequently to study other well-defined ecological elements separately, rather than to attempt a single composite analysis of the whole flora. If the latter is done the distinctive pattern shown by the different ecological elements will be lost in a mass of statistics. MOREAU (1966) reached a similar conclusion for the birds of Africa — 'much is lost if a bird fauna is dealt with *en bloc*'. He shows that if a bird fauna is divided into groups which are broadly ecological as well as taxonomic, the comparisons revealed are enlightening in point after point, and that in the various analyses significant differences are obtained.

My own preliminary analysis of the Sudano-Zambezian Region (WHITE 1965) was confined to 426 tree species more than 5 m tall. The first stage of my analysis of the Afro-montane Region (CHAPMAN & WHITE 1970) is based on the 196 species that normally or frequently exceed 8 m in height and grow in the evergreen forests of Malawi. In dealing with such a small number of species it is possible to learn sufficient of their chorology, taxonomy and ecology to detect significant inter-relationships. These could not emerge from an, of necessity, superficial study of an entire flora.

3. *Taxonomic, chorological and ecological patterns are usually irregular. Nevertheless they are historically significant.*

If, in the evolution of organisms, change had always been divergent, and if in all lineages all characters had evolved at the same rate, taxonomy would be easy. There could only be a single unequivocal natural classification. It would also be a perfect mirror image of the evolutionary tree. Evolution, however, has been more complex than this and taxonomy and the evolutionary interpretation of taxonomic systems are often difficult.

Similarly for the distribution of plants. If the world's climate had remained unchanged, or had changed only slowly and in a regular manner, since, for instance, the origin of the Angiosperms, and if migration and speciation had taken place in a correspondingly regular manner, then it would be a relatively simple matter to use the facts of present-day distributions to interpret the course of past migrations. As we learn more of the dramatic and complex changes which have affected most, if not all, of the world's surface throughout the Pleistocene, it becomes increasingly difficult to believe that the relationship between the facts of plant distribution and historic events giving rise to them, can be other than complex.

If it is true that the evolutionary history and the Pleistocene migrational history of most plants have been complex, we should abandon assumptions and speculations which fail to take this complexity sufficiently into account. Similarly, our methodologies must be capable of accommodating, without undue distortion, the complex patterns of variation and distribution we may expect.

Much of our recent literature, however, reveals that certain widely held assumptions and frequently expressed hypotheses and certain widely practised methodologies are only consistent with the belief that evolution of species and past climatic and physiographic changes have been simpler and more regular than the known facts warrant.

Unwarranted assumptions

1) *The centre of variation is the centre of origin.*

There has been so much climatic and physiographic change since the origin of so many genera of flowering plants, that the phytochoria to which they belong would have been destroyed if they had not migrated, often for considerable distances. What is known of Pleistocene climatic change in Africa has been ably summarized by MOREAU (1966). Even if the situation described by MOREAU is only partly true, the great bands of vegetation of Africa must have changed their positions several times and undergone great changes of relative area.

To me it is inconceivable that the centre of origin of any taxon or of any genetic element can be deduced from contemporary patterns, whether taxonomic or chorological, if we define centre of origin *in a precise topographic sense*. If, however, we accept that the great phytochoria have undergone migration then the historico-geographical methods, developed in particular by WULFF (1943), may still be useful provided they are used intelligently.

To give some examples from the Ebenaceae. *Diospyros monbuttensis* (fig. 1) occupies a narrow belt of seasonal rain forest along the northern fringe of the great Guineo-Congolian rain forest region. *D. senensis* occurs on the other side of Africa in deciduous thicket or dry forest in the lowlying valley of the Zambezi and its tributaries towards the southern limit of the Sudano-Zambezian Region. Their ranges are separated by an interval of 2.200 km. Although the claims of these two taxa to specific rank are well substantiated, they are so closely related that they have been confused by competent taxonomists in the past. The hypothesis which best explains their close relationship is that at some time in the past (possibly in the Pleistocene) an ancestral species had a range which included the interval which separates the daughter species today.

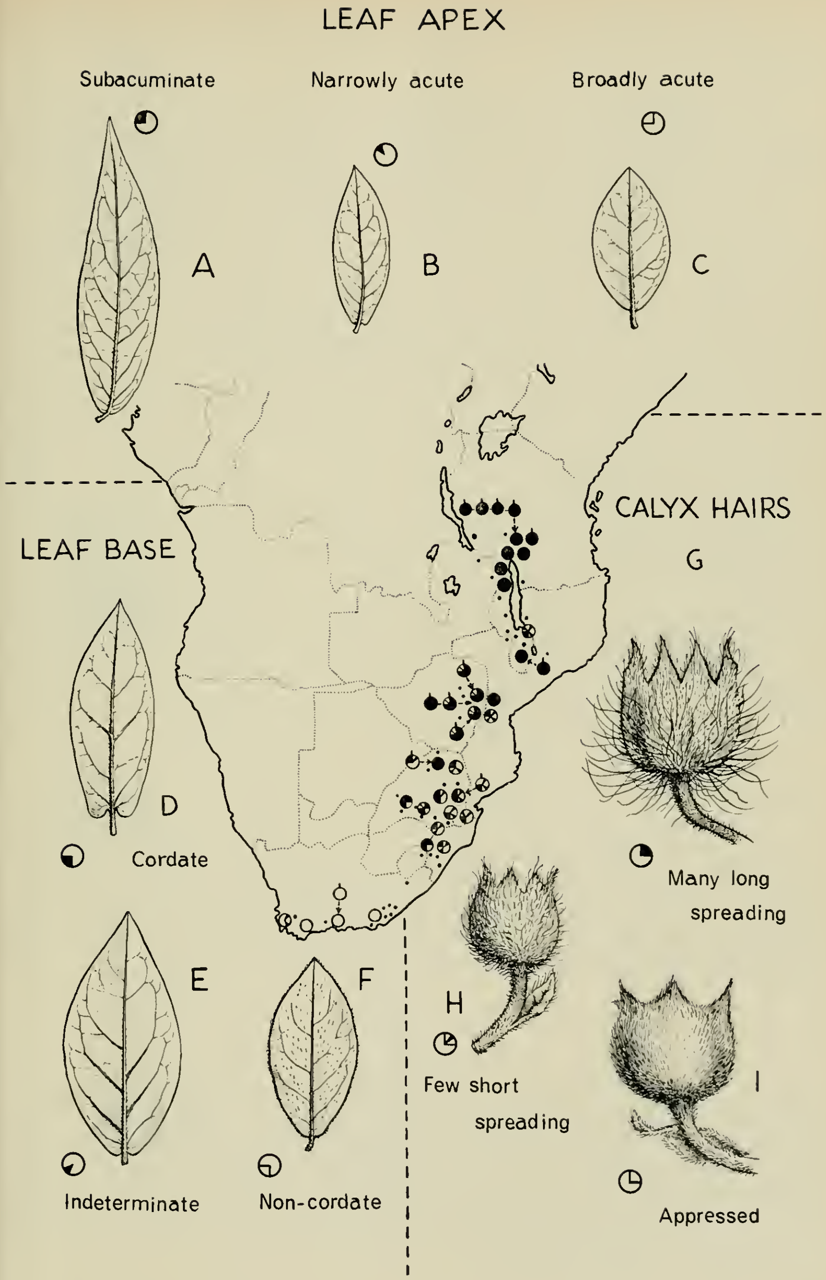
The overwhelming majority of African species of *Diospyros* are confined to the Guineo-Congolian forests (WHITE 1962) and many of these have no close relatives in the other phytochoria. On the other hand, most species occurring outside the Guineo-Congolian Region have close relatives within it. This suggests that the ancestors of species like *D. senensis* belonged to a phytochorion similar to that which includes *D. monbuttensis* today, rather than the converse, but it does not mean that the ancestral species were situated in that part of Africa occupied by Guineo-Congolian forest *today* at the point in time (if there was a definable point in time) when *D. senensis* first originated as a species.

Similarly it is shown further on that one of the Afro-montane genetic elements consists of species which are very closely related to lowland species of the Guineo-Congolian Region. It is in no way implied that this element has achieved its present-day distribution by a single simple migration accompanied by specific differentiation from that part of Africa occupied by the Guineo-Congolian Region today.

One must also interpret taxonomic patterns with care. It is sometimes claimed that the centre of origin corresponds to the centre of maximum variation — either where a species is most polymorphic or the genus has most species (TURRILL 1939, 1964). Fig. 3 shows the geographical pattern of four characters *D. whyteana*. The total range comprises a northern and a southern area of uniformity and a central area of extreme diversity, in which, however, most individuals are intermediate (for the four characters considered) between the northern and southern forms. This might suggest the recent contact of two previously isolated taxa, but in view of the large size of the area of diversity and its great complexity, simple deductive reasoning in our present state of knowledge, would be most unwise. When more species with similar distributions to *D. whyteana* have been studied in the same way, we might be on firmer ground. When Andersonian methods of presentation are used, geographical patterns of variation which demand historical explanations forcibly present themselves. If similar patterns occur in different taxonomic groups it is more likely that the same extrinsic historical factors are responsible.

Let us now consider the genus *Euclea*. The Ebenaceae consists of two genera — the pan-tropical *Diospyros* with about 400 species, most of which occur in lowland rain forest, and *Euclea* with 13 species confined to East and Southern Africa. Of these 13 species, 5 are widespread and 8 have very restricted distributions. Of the widespread species, 3, *E. divinorum*, *E. schimperi* and *E. natalensis* (fig. 4) occur extensively in East and South tropical Africa and to varying degrees extend into extra-tropical South Africa. The remaining widespread species, *E. crispa* and *E. undulata* are widespread in South Africa but also occur in South tropical Africa.

Fig. 3. *Diospyros whyteana*. Pictorialized distribution map showing variation in 1) leaf-apex, 2) leaf-base, 3) indumentum of calyx and 4) degree of lobing of the calyx. The three character states of characters 1—3 are illustrated. The bottom right-hand corner of the circle refers to character 4; if it is left white the ratio of calyx lobes to calyx length is less than 0.25; half black = 0.25—0.4; completely black = > 0.4.


LEAF APEX
Subacuminate
Narrowly acute
Broadly acute
A
B
C
LEAF BASE
D
Cordate
E
Indeterminate
F
Non-cordate
CALYX HAIRS
G
Many long spreading
H
Few short spreading
I
Appressed

The 8 geographically restricted species are confined to small parts of South Africa, or in two cases also have outlying stations north of the Tropic of Capricorn.

Taking the genus as a whole the greatest concentration of species is in a narrow peripheral band of South Africa extending from the Cunene River to Natal. Within this area *every* species occurs, and it might be assumed that the genus originated there, but on other grounds this is most unlikely.

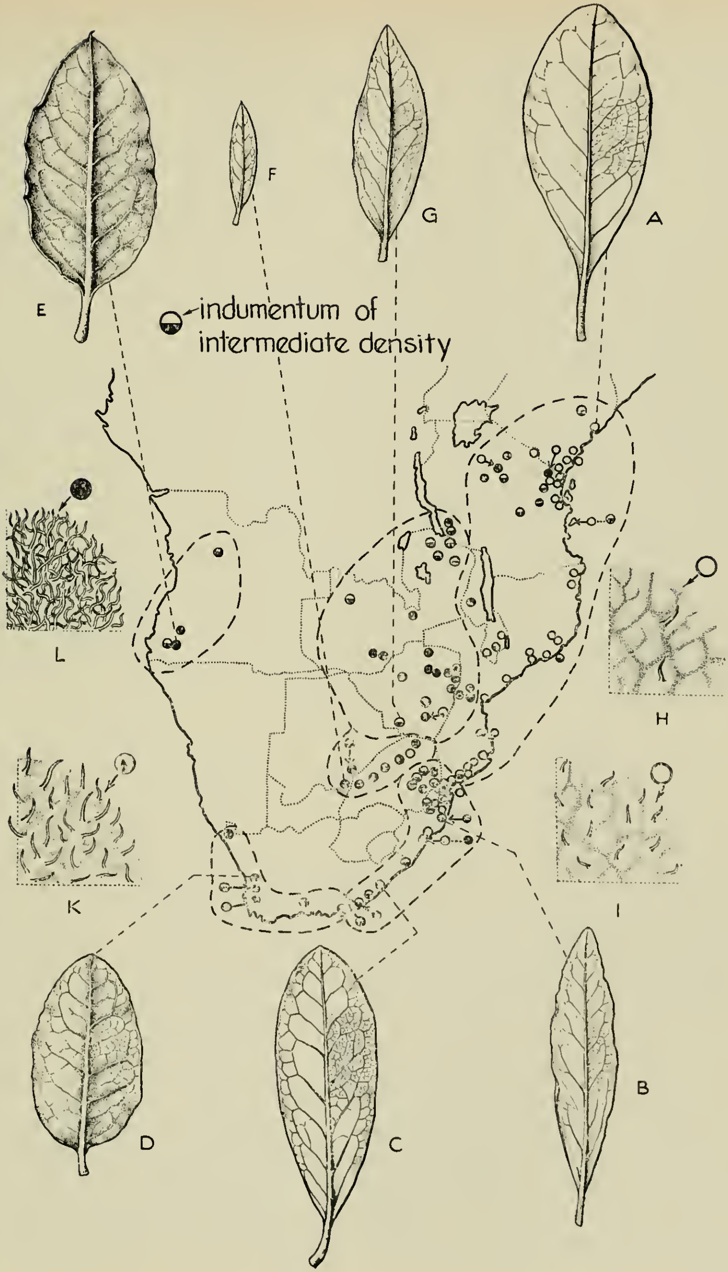
First, the 5 widespread species are essentially intruders into this coastal band, and have the greater part of their ranges further inland and further north. Each of the widespread species is very variable. Some features of the variation of one widespread species, *E. natalensis,* are shown in fig. 4 *E. natalensis* is more variable than some older and more conservative taxonomists would normally allow, but if we apply HEDBERG's axiom (1955) — "for specific distinction we demand correlated discontinuous variation in more than one character" — *E. natalensis* at the species level, is indivisible. The variation pattern of *E. natalensis* is such that only a relatively small amount of extinction could convert it into a "super-species" of 6 closely related allopatric species, each as distinct as any of the 8 species of restricted distribution. The northern tropical part of the range of *Euclea* must be infinitely richer in biotypes than the peripheral South African coastal part, though this is not reflected in the number of species. The fact that the northern species are widespread and variable and the southern endemics are so geographically restricted and invariable is of great chorological interest but its significance is lost if facile deductions about centres of origin are made. A northern rather than a southern origin for *Euclea* is also concordant with other evidence, but this cannot be discussed here.

2) *Mountains on the continents are as geographically isolated as oceanic islands.*

This assumption is rarely made explicit, but it must have provided the motive for much botanical exploration in the past, and the, perhaps barely conscious, justification for the description of many 'endemic' species. Isolated mountains might be expected to have endemic floras comparable to those of oceanic islands, if the geographical position of the great phytochoria had

Fig. 4. *Euclea natalensis.* Pictorialized distribution map showing variation in leaf-shape and size, and indumentum of the lower leaf-surface. A. ELLIOT 875 from Kenya. B. WARD 1413 from Natal. C. MEEUSE 9762 from the Eastern Cape. D. ACOCKS 14169 from the Western Cape. E. GOSSWEILER 12677 from Angola. F. YALALA 178 from Botswana. G. GREENHOW 49/51 from Rhodesia. H. SEMSEI 2251 from Tanzania. I. TORRE 3932 from Moçambique. K. CODD 2898 from the Transvaal. L. GOSSWEILER 12703 from Angola.

Leaves × 1. Indumentum × 35.



E
F
G
A
indumentum of intermediate density
L
H
K
I
D
C
B

been stable and if the mountains themselves were ancient. But most of the African mountains are not very old, and those Pleistocene climatic changes which can be inferred to have taken place are generally regarded as being sufficiently large to have broken down their isolation in many cases, at least for large parts of the Afro-montane flora (see HEDBERG 1969). This is not the place to discuss the origin and history of the Afro-montane flora. The subject is complex and many problems remain. The latter will only be solved by a cautious, inductive approach in which the different genetical and ecological elements are studied separately. If the results of these separate studies point in the same direction, confidence in their interpretation will be increased. Discordant results will raise new problems, the interpretation of which should be equally significant.

For the Afro-alpine flora, endemism on the African mountains has been discussed by HEDBERG (1969) based on his own fine series of earlier taxonomic and ecological studies. The Afro-montane flora which is much richer and diversified than the Afro-alpine, and so presents a more formidable problem, has not yet been studied as thoroughly. There are some indications that, among herbs and small woody plants, especially at higher altitudes, a moderate degree of endemism and vicariism may exist (WILD (1964). My own work on tree species occurring in the Afro-montane forests of Malawi, suggests that both endemism and vicariism in this element is very slight. In Malawi 60 species (68⁰/₀) of the larger trees occurring in the submontane and montane forests are endemic to the Afro-montane Region. But of these, apart from the doubtful case of *Dasylepis burtt-davyi,* none is endemic to a single mountain, nor indeed endemic to Malawi.

Unwarranted methodologies

1) *The hierarchical subdivision of species.*

As is implied in the discussion above, if evolution had always been regular and divergent, we could expect geographical variation patterns to be sufficiently well-defined to provide the basis for the objective delimitation of infra-specific taxa. There is *no evidence* that this regularity occurs in widespread and variable species, and hence no justification for the elaboration of complicated hierarchical systems such as that proposed for *Dichrostachys cinerea* by BRENAN & BRUMMITT (1965). If the characters vary independently, even though the variation of each character taken separately may show significant geographical trends, it is impossible to establish a single objective system which best accommodates the facts. A large number of alternative systems are possible and the choice between them is purely arbitrary. This can easily be demonstrated for *Euclea natalensis* (fig. 4). The geographical pattern of variation is insufficiently precise to allow the recognition of more than one species, but variation in several characters follows definite geographic trends. Leafshape is very variable, but 6 main regional types occur. The leaves of about 90% of the specimens from any of the six areas shown on the map resemble the particular leaf illustrated as representative of that area more closely than they resemble any of the other leaves shown in fig. 4. Those leaves which do not conform in this way, usually resemble the leaf illustrated for a contiguous region. This particular pattern *could* justify the recognition of 6 more or less allopatric subspecies, but the precise location of the boundaries between them would be arbitrary, since intergradation occurs. Furthermore, it could be claimed that leaves A, B, and C, and D and E, and F and G are sufficiently similar to justify the creation of only 3 subspecies. The other characters are not sufficiently correlated with leaf-shape to help us decide. Although leaves D and E are somewhat similar, their associated inflorescences are very different and represent the extremes found in the species. Other considerations might suggest a different treatment. Of the 6 potential subspecies, that characterized by leaf A is the most constant, not only in leaf-shape but also in indumentum and inflorescence (not shown in fig. 4). It could be argued that this justifies the recognition of only 2 subspecies, one based on leafshape A, which is monotypic, and the other comprising the essentially hairy remainder. The latter could be subdivided into varieties based on leaf-shape. This bewildering array of possibilities would be greatly increased if other characters such as pedicel length and flower size were also taken into account.

I believe that the pattern of variation shown by *E. natalensis* is historically meaningful, and that some day it might be possible to explain it. In the meantime it is important in any chorological discussion involving *E. natalensis,* for the nature of its variability to be taken into account. I fail to see how the facts of variation presented in fig. 4 could be better expressed by the creation of infra-specific taxa. The creation of such taxa *before* the basic facts are displayed in this way, is both scientifically unjustified and, as a means of conveying information, quite inappropriate. The authors of the *Dichrostachys* paper claim that the infra-specific taxa they recognize are primarily geographical, but of the 14 subspecies and varieties which occur in Africa, 12 have ranges which are wholly or partly sympatric with the widespread variety *africana.* It is a pity that the complicated pattern on which this elaborate system is based was not displayed using Andersonian methods, so that it could be compared with the patterns of other species with similar distributions. Formal hierarchical classifications, because of their subjective nature hinder rather than facilitate such comparisons.

Since the units of hierarchical infra-specific classifications are so subjective, they should not be included in floras unless it can be shown that there is a definite need. To subdivide variable species in this way and, as is done in some floras, only give information concerning distribution and ecology under the infra-specific taxa, and not for the species as a whole, implies a negation of the biological nature of the species.

2) *The hierarchical subdivision of phytochoria.*

Ever since Humboldt (1807, 1816) discovered that areas occupied by plant species conform to more or less definite patterns, botanists have tried to use the facts of distribution to divide the face of the earth into mutually exclusive territories or phytochoria, based on their degrees of similarity and difference. For Africa several more or less static hierarchical systems have been proposed. In recent years the following categories have been most frequently used — region, domain, sector, subsector, district and subdistrict.

In my opinion the major phytochoria of Africa — the 9 chorological Regions, based on the work of Lebrun (1947), Monod (1957) and White

Fig. 5. Map of Africa showing phytogeographical Regions.

(1965), and shown on fig. 5, are sufficiently well-defined to provide a stable and useful frame of reference. Some of them can be profitably subdivided into Domains. Further subdivision, however, is mostly unwarranted, and can be rejected on theoretical and practical grounds. This is discussed in the section on chorological aphorisms.

Unwarranted speculations

This is not the place to discuss the part that can be played by speculation in the development of ideas. One cannot, however, fail to be struck by the frequency with which taxonomists, in their published accounts of difficult groups, produce speculative explanations of the situations they describe and sometimes invoke them as justifications for the particular taxonomic treatments offered. Again and again, it is suggested that hybridity, "ancient" hybridity, introgression, polyploidy, apomixis, polytopy or clinal variation is the cause of the particular variation pattern discussed. It seems to me that the reason why these facile and unsupported explanations are offered is because their authors believe that the evolutionary history of their taxa has been so simple that causal explanation can be deduced from casual visual inspection of variation patterns alone.

A more realistic and more theoretically sound approach would be based on analysis and display of results using Andersonian techniques. In this way precise hypotheses can be framed and procedures suggested for their confirmation. In the case of *Diospyros whyteana* (fig. 3) visual inspection at first suggested clinal variation. Only subsequently, after rigorous analysis, did it emerge that the central part of the range is one of great variability, and that the overall pattern of this species probably requires an extrinsic historical explanation of some complexity.

CHOROLOGICAL APHORISMS

1. *Chorological patterns are too complex to provide an objective basis for a formal hierarchical classification of phytochoria except at the highest levels.*

This aphorism can be derived from the third general aphorism. I have briefly discussed its implications elsewhere (White 1965 and in Chapman & White 1970) and will deal with it more fully on a future occasion. Here I shall merely list a few supporting reasons.

a) Adjacent phytochoria differ greatly in floristic richness and in the complexity of the patterns formed by their subordinate elements.

b) The replacement zones separating adjacent phytochoria vary greatly in their width and steepness.

c) The differences between adjacent phytochoria may be due, either to both of them having distinct endemic floras, or to one of them merely being an impoverished variant of the other.

d) Some phytochoria have compact, continuous distributions, whereas others, which taxonomically and ecologically are just as distinct, have disjunct or even archipelago-like distributions.

Hauman (1955), Monod (1957) and Hedberg (1965) have suggested that the Afro-alpine flora, despite its archipelago-like distributions, is sufficiently distinct to merit recognition as a Region. I have suggested (in Chapman & White 1970) that the Afro-montane flora should be treated in a similar way. One could argue endlessly as to whether these two floras are in fact sufficiently distinct to be regarded as comparable with, say, the much more extensive and floristically rich Guineo-Congolian Region. Their precise *status*, however, is not important, and, because of the complexity of the overall chorological situation, cannot be objectively established. It is important, however, to recognize them as being fundamentally distinct, both ecologically and taxonomically, from, and not merely facies of, the prevalent lowland phytochoria within which they occur.

e) Centres of endemism can be more profitably recognized then the lower ranking phytochoria of formal systems. Unlike the latter, centres of endemism need not have contiguous boundaries. If they had, that would amount to a contradiction in terms. They can, however, when the situation justifies it, have overlapping boundaries.

The recognition of chorological patterns and their analysis in terms of ecological and taxonomic relationship is much more important than the elaboration of complex static systems which are more likely to obscure than reveal significant correlations.

2. *The detection and understanding of genetic elements depends on careful ecological and taxonomic studies.*

Wulff (1943) states that genetic elements are grouped according to their region of origin, and Hedberg (1965) defines genetic elements "according to the *supposed* areas of origin of each species — that is, in practice, after the areas where they have the majority of their closest relatives". Hedberg, who was chiefly concerned with demonstrating the extremely diverse origin of the Afro-alpine flora, and not with a critical study of any particular element, nevertheless, with reference to *Myosotis keniensis*, stressed the importance of a knowledge of *degree* of taxonomic relationship. The following example from my analysis of the Malawi sample of the Afro-montane forest-tree flora (in Chapman & White 1970) is intended to confirm the importance of a knowledge of degree of relationship, but it also suggests that for species which are both chorologically and taxonomically somewhat isolated, there may not be any close relatives because of recent extinction. In such cases a knowledge of the ecology of the plants concerned may provide vital clues to past events and pointers to future research.

The Afro-montane forest-tree flora of Malawi includes 61 species which are confined to the Afro-montane Region and so belong to the Afro-montane geographical element.

Of these, 24 (39%) belong to genera which are totally absent from the lowland tropics, or almost so. They belong to the eu-Afro-montane genetical element, which can be further subdivided according to the diverse distributions of the genera and families to which they belong.

25 species (41 %) belong to genera, which in Africa, irrespective of their overall distribution, are confined to, or have their greatest concentration of species in, the lowland forests of the Guineo-Congolian Region. In a few cases, e. g. *Diospyros whyteana*, the specific relationship is not particularly close, though in Africa *Diospyros* is pre-eminently a Guineo-Congolian genus. The majority of species in this group, however, are very closely related to one or more Guineo-Congolian lowland forest species. In some cases, e. g. *Entandrophragma excelsum*, the species are perfectly distinct and their claim to specific rank has never been questioned, but in other cases the differences, though apparently constant, are slight, e. g. *Chrysophyllum gorungosanum*. Most of the species in this group are so closely related to their Guineo-Congolian relatives that it is reasonable to assume that they have relatively recently evolved from Guineo-Congolian ancestors. I have suggested that this close relationship could be expressed by referring to them as Guineo-Congolian 'nephews'. The genetic element to which they belong is the 'Afro-montane element of Guineo-Congolian nephews' or 'Afro-montane nephews' for short.

The remaining 12 species (20%) belong to genera or families which, although represented by many species at low and medium altitudes in the humid troics of the old or new worlds or both, are absent from the humid lowland tropics of Africa *today*.

Taxonomically, these species are more isolated. *Ficalhoa*, for instance, is monotypic and confined to Africa, and, elsewhere in the lowland tropics, is replaced by species of the closely related genus *Eurya*. *Cylicomorpha* has two species endemic to the African mountains; the rest of the family is confined to the American tropics. The other species belong to genera with only one (e. g. *Ilex*) or few species in Africa, but many to several hundreds in the lowland tropics elsewhere. In considering the relationships of these species two things should be borne in mind. First, they are unlikely to owe their present distribution in Africa to long distance dispersal. *Ocotea*, for instance, is represented by hundreds of species in America, but the African species are confined to the *eastern* side of the continent. Second, since the groups to which they belong are characteristically humid tropical lowland groups, it is possible that they formerly occurred in Africa but that their lowland representatives became extinct during the climatic vicissitudes of the Pleistocene, leaving a few remnants in the more mountainous parts of Africa, where there might have been better opportunities for survival during periods of rapid climatic change. If this hypothesis is correct then the precise geographic location of the most closely related *contemporary* relatives of members of this group of species is irrelevant, since their immediate ancestors, which occupied a different part of the earth's surface, have recently become extinct. If the members of this group have recently lost their closest relatives we may refer to them as "orphan" species. This concept is not quite as fanciful as may at first appear. It is useful to keep these species together in the same assemblage since most of them are similar in their ecology. If they are grouped according to their nearest (but not very close) *still extant* relatives, what is essentially a homogeneous group is fragmented into several meaningless entities. In this connection it is interesting to record that MOREAU (1966) has found it necessary to invoke widespread extinction to account for the present-day distribution of certain birds in Africa.

There is also some botanical evidence which supports the hypothesis of widespread extinction in the African lowlands. The genus *Ternstroemia* is widespread in the humid lowland tropics from South America to Queensland, but with only two species in Africa, *T. polypetala* on the East African mountains, and *T. africana* in the lowlands, *T. polypetala* is thus an Afro-montane 'nephew', but it differs from all others in this group in having only one Guineo-Congolian relative, and that has a very restricted geographical distribution in West Africa, where it is only known from one locality in Angola near the mouth of the River Congo and one locality in Nigeria (HEPPER, Kew Bull. 21: 429—431, 1968). No doubt it also occurs in some other places in the Guineo-Congolian Region, but, if it does, in view of the intensity of collecting in Africa in recent decades, it is likely to be both localized and rare. Here it appears that we have a pan-tropical genus which has only just managed to survive in lowland Africa. If extinction had proceeded a little further *Ternstroemia polypetala* would belong to the class of Afro-montane 'orphans'!

Palaeobotanical evidence for restriction of range of contemporary Angiosperms in Africa is still somewhat fragmentary. ERDTMAN (1962) shows that there is palynological evidence that the family Ctenolophonaceae was formerly much more widespread than it is at present. It is now represented by the single genus *Ctenolophon* with three species in tropical Asia and one in Africa. The area of the African species is very similar to that of *Ternstroemia africana* discussed above.

Ecological evidence is also compatible with the hypothesis that the 'orphans' are derived from Guineo-Congolian ancestors. It is not unreasonable to suppose that species with similar ecological requirements have, at least in the recent past, had similar evolutionary and migrational histories.

All 25 of the Afro-montane 'nephews' occur in what I have called 'submontane forest' and, in Malawi, all but one are either confined to it, or are much more characteristic of it than of other forest types. All 12 Afro-montane 'orphans' likewise occur in submontane forest and only 3 are equally characteristic of other forest types. Of the four emergent species of submontane forest, two *(Aningeria adolfi-friedericii,* and *Entandrophragma excelsum)* are 'nephews' and two *(Ficalhoa laurifolia* and *Ocotea usambarensis)* are 'orphans'.

It would, however, be a mistake to attach too much importance to this hypothesis. Like all hypotheses it must suggest future lines of enquiry. It should direct the attention of palaeobotanists to the possible occurrence of fossil remains of congeners of these species in deposits in the lowland parts of Africa.

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