Hons Seminar

EVOLUTION AND DIVERSIFICATION IN THE CAPE FLORA

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AUGUST, 1978

1.0 INTRODUCTION : A BACKGROUND TO CAPENSIS

Capensis comprises the distinctive temperate floral area of the south western and southern Cape Province with outliers in the Afromontane region (53, Fig. 1). As a phytogeographical unit Capensis, the home of the Cape Flora, is generally recognised as a floral kingdom of its own (16). The comparatively small size of the region and its tremendous floristic richness and complex affinities make it an interesting, if difficult, phytogeographical study. This present work is an attempt to review some of the information on phytogeographical and evolutionary aspects of the flora of Capensis.

Fig. 1 Phytochorological subdivision of southern Africa (names of some centres are included in the map).

- A. Guineo–Congolian Region
  - A1. Congolian Domain
  - A2. Nigerian–Cameroonian Domain (including Littoral South Atlantic Domain)
  - A3. Amboim Section of A2
- B. Indian Ocean Coastal Belt
  - B1. Tongaland–Pondoland Regional Mosaic
  - B2. Zanzibar–Inhambane Regional Mosaic
- C. Sudano–Zambezian Region (Zambezian Domain)
  - C1. Oriental Domain
- D. Afromontane Region
- E. Afro-alpine Region (Austral Domain)
- F. Karoo–Namib Region
  - F1. Namib Domain
  - F2. Namaqualand Domain
  - F3. Southern Kalahari Subdomain
  - F4. Western Cape Domain
  - F5. Karoo Domain
- G. Capensis

1.1 Floristic Characteristics

The Cape Flora is noted for its richness in species (an estimated 6 000) most of which are concentrated in the predominantly winter rainfall (mediterranean-type climate) region of the south western Cape (55). A comparison of the floristic richness of the Cape Flora with other mediterranean-type floras reveals that the Cape is the richest followed by south western Australia (34) with an estimated 4 400 species (16). The Californian Chaparral has 900 species of vascular plants (33). Comparative floristic studies of selected areas have revealed that the Chilean Mattoral is only marginally richer in species than the Californian Chaparral (35).

A further feature of the Cape Flora is the high number of taxa endemic to Capensis. Of the 462 taxa analysed by Weimarck (55), 406 or 87% are endemic; of the 546 taxa analysed for this seminar, 523 are restricted to Capensis. Weimarck (55) found that of 282 typical Cape genera, 212 (75, 18%) are confined to Capensis. This figure may be the highest rate of generic endemism in the world (16).

1.2 Vegetation

The typical vegetation of Capensis is the Cape sclerophyll or fynbos, a name which implies the fine leaved form of many of the shrubs (53). Plants that contribute to this vegetation are chiefly low shrubs, restiods, and geophytes. Trees are rare. Leaves of the woody plants are small, leathery, and often ericoid in type. They provide a marked contrast with most taxa of the mediterranean regions of California and Chile (9), but could have an equivalent in some mediterranean communities in Australia (25, 58).

1.3 Edaphic Peculiarity

Throughout the distribution of Capensis there is a tendency for fynbos communities to be restricted to soils derived from the sandstones and quartzites of the Cape fold mountaines (20, 58). These soils tend to be highly acidic and notoriously nutrient poor, especially with respect to nitrogen and phosphor us levels (11).

The soils of the intervening valleys and coastal plains are formed predominantly from Bokkeveld and Malmesbury shales, and are nutritionally and structually superior to the sandy mountain soils (11). A transition from sandstone to shale derived complexes is usually accompanied by a dramatic change in vegetation; on the coastal plain fynbos is replaced by Coastal Rhenosterbosveld (1) while karooid veld types occur on shale in the drier valleys and inland margins of the mountains.

Coastal Rhenosterbosveld, in its climax state, is probably a mosaic of dense bushveld of tropical affinities, and a fire-maintained grassland interspersed with ericoid (fynbos) shrubs. The latter become more important in regions of predominantly winter rainfall (1). Today much of the veld type has been ploughed up and most of the relic stands are severely down-graded and almost exclusively dominated by Rhenosterbos, Elytropappus rhinocerotis. Although fynbos taxa are fairly well represented in the Rhenosterbosveld, very few endemic species are recorded in this vegetation type (23,42,54).

The karoo vegetation is part of the rich and distinctive flora of the Karoo-Namib phytogeographical region (56, Fig. 1). The origin and evolution of the karoo flora will not be discussed here. However, it is interesting to note that the speciation of some karoo taxa has occurred in a manner which appears to resemble the massive speciation of some fynbos taxa in the Cape.

The Afromontane fynbos appear to be associated with nutrient poor edaphic conditions such as highly leached, immature mountain soils, bogs and quartzite outcrops (1,13,37,42,54,59). The nutrient status of soils derived from the Chimanimani quartzites in the Rhodesian highlands are comparable to that of fynbos soils (37). Furthermore, the Cape Flora is better represented, both in terms of total species and local endemics

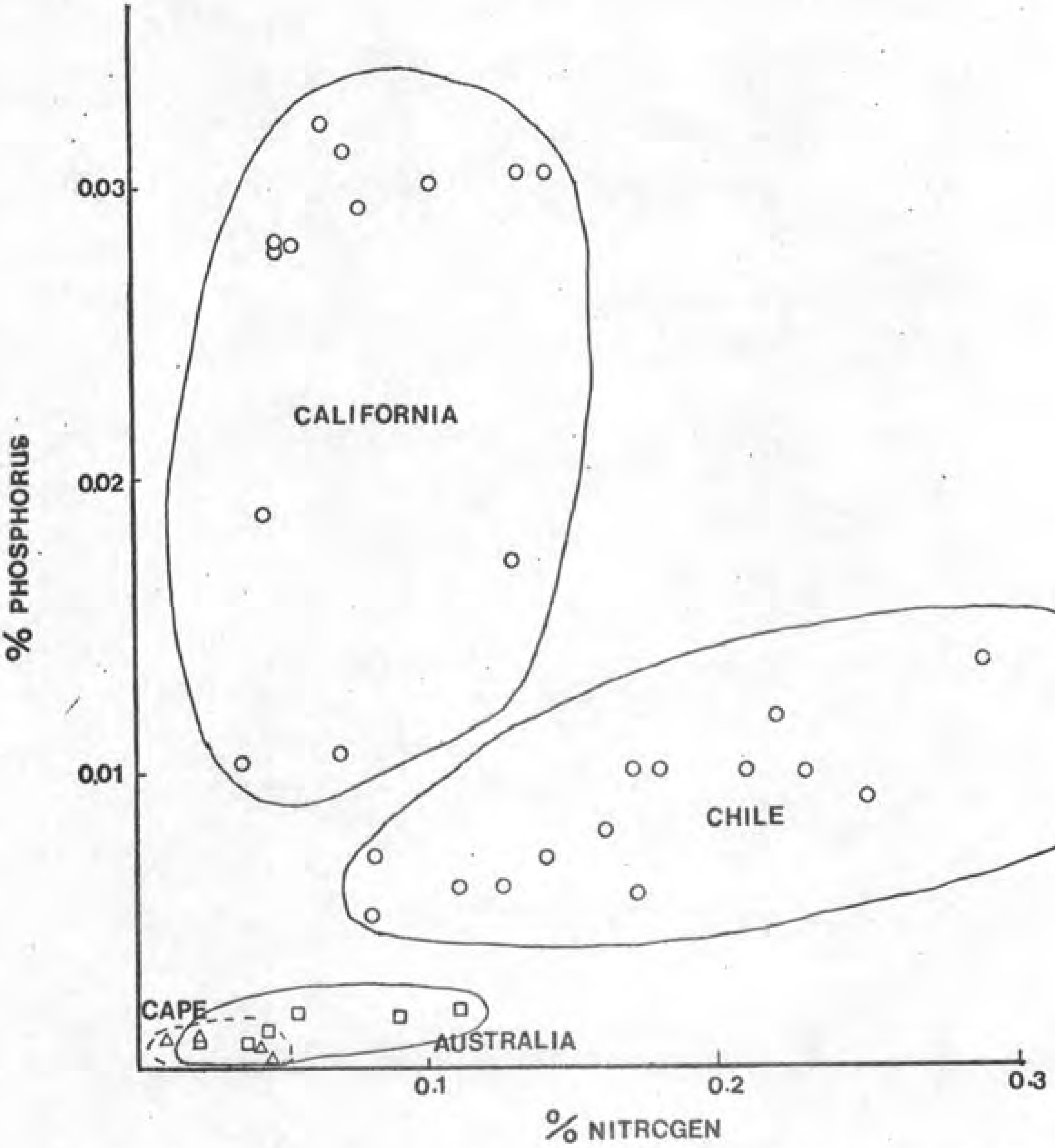


FIGURE 2. Percentage Nitrogen and Percentage Phosphorus in soils of Mediterranean Regions in California, Australia, Chile and the Cape. Data for California and Chile from Rundell (43); Australian data from Specht (46) and Stace <u>et al</u> (48); Cape data from Low (pers comm.).

on these quartzite derived soils than surrounding soils derived from granite and shale (59). This appears to be true for sandstone formations in Natal and the Drakensberg (42).

There are certain similarities between the Cape fynbos and the mediterranean vegetation of Australia in terms of their distributional patterns and edaphic requirements. In southern and south western Australia the sclerophyilous mediterranean vegetation is restricted to soils which have a nutritional status comparable to the fynbos soils (Fig. 2). Moreover, although the maximum expression of the Australian mediterranean-type flora is in western Australia, outliers of the vegetation occur in tropical, predominatly summer rainfall areas of Queensland, Borneo and Malaysia on isolated but extensive patches of infertile soils (47).

Specht (47) has suggested that the Australian mediterranean flora has been partially derived from the floristically and structually similar tropical sclerophyll vegetation. Fig. 2 shows the total nitrogen and total phosphor us levels for soils of mediterranean communities in California, Chile, S. Australia and the Cape. It can be seen that the soils of California and Chile are much more fertile than the poor and highly comparable soils of the Cape and Australia.

2.0 AFFINITIES AND ORIGINS OF CAPENSIS

2.1 Affinities

Although the vast majority of the Cape taxa are endemic to Capensis (55) certain affinities to other floristic regions are evident. These are listed below:-

The karoo element: Mesembryanthemum, Stapelia
Sub tropical-tropical element: Rhus, Euclea
Mediterranean element: Romulea
Antarctic (Austral) element: Acaena, Cunoniaceae, Podocarpus, Meterosideras
Cosmopolitan element: Polygala
Afromontane element: Erica, Protea, Stoebe, Aristea

The importance of these elements in the origin and evolution of the Cape Flora has been discussed extensively (e.g. 2,21,24,26,27). This discussion will be limited to the relationship between the floras of Capensis and the Afromontane region.

Afromontane forests exist in a series of island-like centres from the Cape Peninsula along the east African mountain chain, to the Ethiopian highlands with outliers in West Africa (Fig. 3, 57).

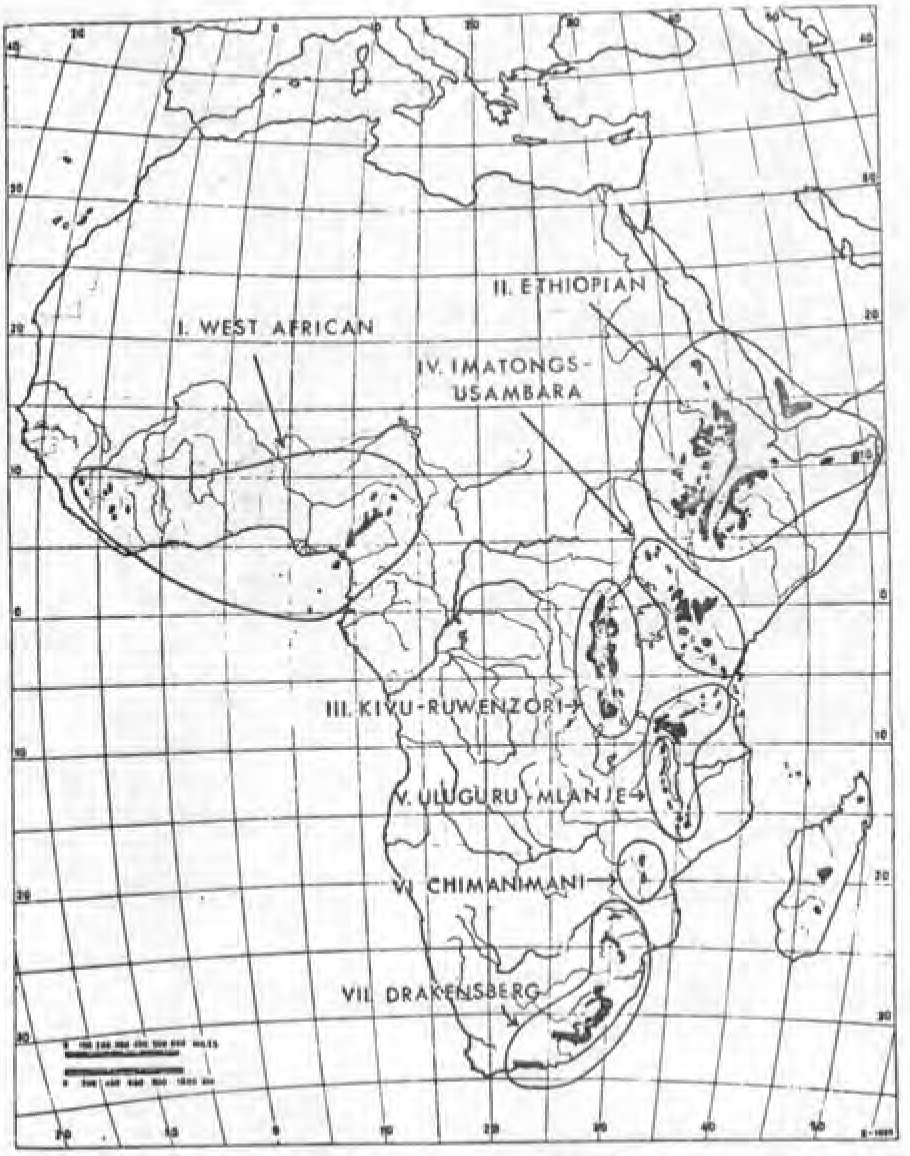


Fig. 3 Map. showing distribution of the islands of the Afromontane archipelago in the seven regional mountain systems. The distribution of montane vegetation in Madagascar is also shown.

These forest formations are characterised by taxa derived from the presumably once extensive but now depleted austral temperate forests (e.g. Podocarpus, Widdringtonia, Curtisia, Juniperus Cunoniaceae), and a distinctive array of species recruited from the adjacent tropical lowlands (Apodytes dimidiata, Olea spp, Nuxia spp, Rapanea melanophloes Xymalos monospora and others (57).

Throughout the range of Afromontane forests fynbos taxa form part of communities either seral to forest (1,12,13,18,30,31, 36,37,51,57), or grow on sites that are climatically or edaphically unsuitable for forest development (especially regions above the timberline often termed the Afro-alpine zone e.g. 17,18,40,54). The dynamic association of the Afromontane and Cape floras may provide interesting clues to the origin of present day fynbos.

2.2 Origin

It is probable that folding on the eastern part of the African continent which occurred during the Pliocene (19) could have resulted in the establishment, over a large continuous area, of a flora which consisted of elements comprising the evolutionary precursors of both the fynbos and the Afromontane forests. This Afromontane-Cape vegetation would have extended from the Cape to the highlands of north Africa. Boreal elements may have been incorporated into the flora via the ancient crystalline heights of the Sahara region (Haggar, Air, Tibetsi) during the early Tertiary (5). High ground would have provided an environment suitable for the northward migration of temperate austral taxa.

It is possible that the Proteacous flora of Capensis may have been derived from a montane forest flora (e.g. the presumably primitive genus Faurea) (7,24). Morphological investigation of African Proteas by Beard (7) has revealed that the more primitive members of the genus are concentrated in tropical Africa. In his study of Leucospermum Rourke (42) found a considerable amount of evidence to support Beard's theory. Levyns (23) in her study of Muraltia found that members of the more primitive subgenus Psiloclada are found in the Afromontane regions of tropical Africa. On the other hand, it is possible that the Restionaceae have migrated northwards in association with other austral taxa. A northwards migration is also possible of Leucadendron (60) although the time of migration in the latter was probably much later. In the Iridaceae both north and southwards migratory pathways are evident (14). In <u>Lapesrousia</u> (15) and <u>Lobostemon</u> (22) it appears that the migration route has been along the western side of the continent from S.W.A. and Namaqualand to the S.W. Cape.

Obviously the migration routes of Cape floral elements are both complex and bewildering. Furthermore, the evidence in defining the direction of migration routes is by no means beyond question. The use of assigning "primitive" and "advanced" characters (e.g. Beard (7), Levyns (23), Rourke (42)) and in this way deciding on the origin of a taxon is a highly contentious practice. Cytological examination (e.g. Goldblatt (14)) relies on the assumption that diploids are more primitive than polyploids and therefore represent the area of origin of a taxon. The idea of the Restionaceae having a southern origin ascribes to the age and area theory of Willis (61) which postulates that taxa have their origin in the area of maximum concentration. This theory has been rejected by Adamson (2) and Levyns (22) for many Cape taxa. It becomes evident that the individual source of the various groups is a difficult question and the place of origin of many taxa (e.g. Ericoideae) may never be known with certainty (5).

The idea of a more-or-less continuous distribution of Afromontane-Cape vegetation during the Tertiary could explain the widespread and disjunct distribution of some so-called primitive Cape taxa. Erosion of the highlands and the subsequent development of valleys with different climatic and edaphic characteristics would serve to isolate populations. The gradual drying of the climate during the Tertiary (4) would restrict the Afromontane-Cape flora to isolated mountain peaks where conditions remained favourable for its continued existence.

The concentration of Cape floral taxa in the south western Cape indicates that conditions were suitable for a massive speciation of the flora in this region probably as recently as the Pleistocene. Before discussing speciation in the Cape Flora it is necessary to have some idea of the phytogeographic distribution of its components.

3.0 PHYTOGEOGRAPHICAL CENTRES IN THE CAPE FLORA

In 1941 Weimarck published his paper entitled "Phytogeographical groups, centres and intervals within the Cape Flora". He recognised seven centres of endemism, some of which are subdivided into subcentres (Fig. 4). The centres are:-

(i) The Northwestern Centre comprising the area north of the Breede River-Great Berg River valleys and west of the line running from Cogmans Kloof near Montagu to Karoo Poort near Matjiesfontein (it is interesting that Acocks uses this same line to delimitate Macchia and False Macchia). The Olifants River and the Doorn River valleys constitute, as a rule, the northern and north eastern limits. Outlying areas occur in the Kamiesberg and the Hantam Roggeveld Mountains.

(ii) The Southwestern Centre comprises the area that is south and west of the Breede River valley.

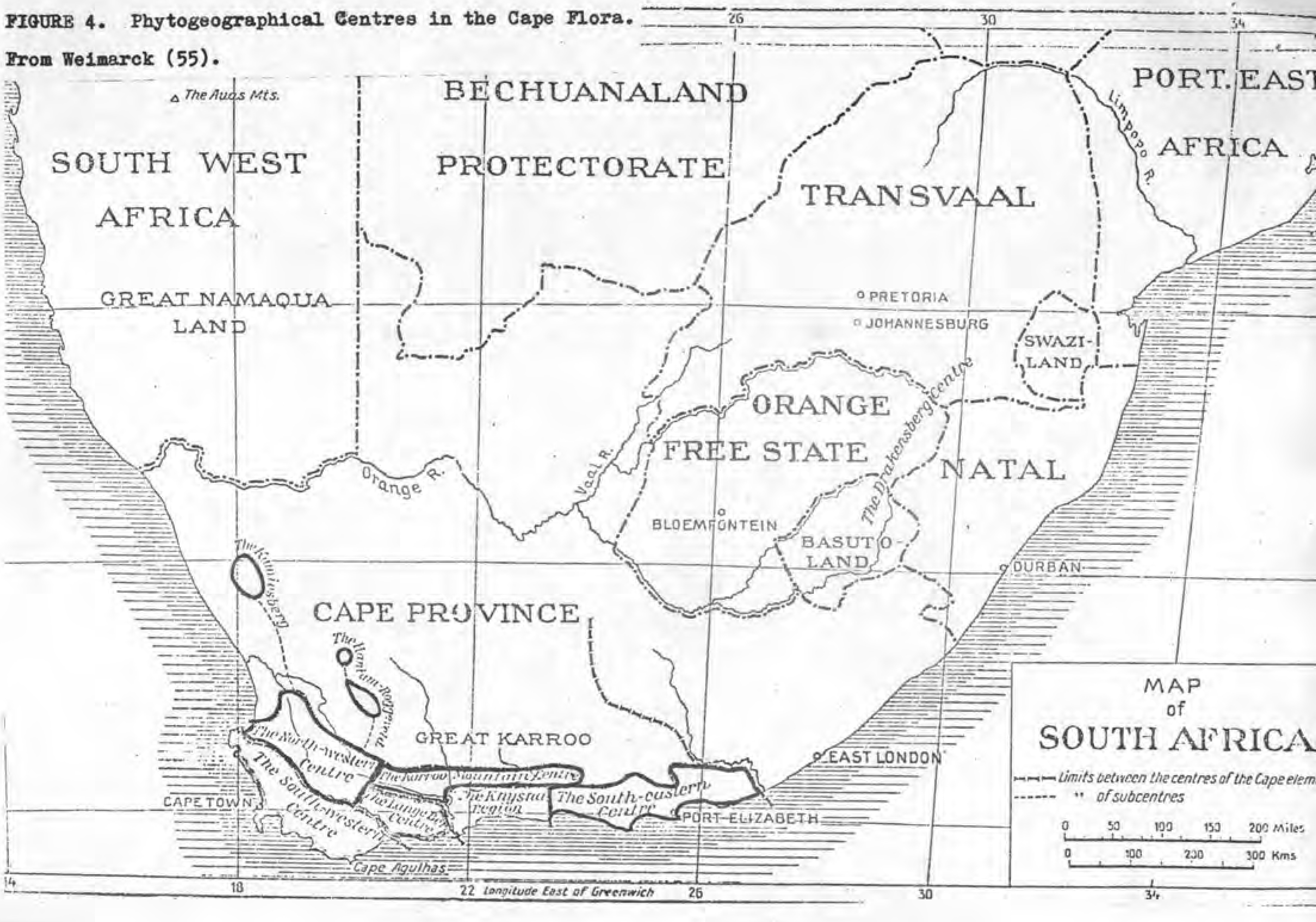
(iii) The Langeberg Centre is bounded in the north by Karoo vegetation at the inland margin of the Langeberg Mountains, to the northwest by Cogmans Kloof, to the west by the Breede River valley and to the east by the Gouritz River valley.

(iv) The Karoo Mountain Centre comprises several areas situated on the higher mountains within the Karoo from the Witteberg and Anysberg in the west to the mountains of the Willowmore district in the east. The Cape Flora occurs in areas separated from each other by lowlands occupied by the Karoo element.

(v) The Southeastern Centre comprises a narrow strip from about the border between the Humansdorp and Knysna districts to the mountains of the Alexandria and Albany districts. It is separated from the Langeberg Centre by the Knysna Interval. Weimarck believes that this interval exists as a result of the

FIGURE 4. Phytogeographical Centres in the Cape Flora.

From Weimarck (55).



Cape Flora coming under severe competition from the Afromontane type forests during the Pleistocene pluvials.

(vi) The Drakensberg Centre (and the Tropical African Mountain Centre) occur outside the geographical range of Capensis. Nevertheless, numerous elements of the Cape Flora exist here but rarely form an independent vegetation. The Drakensberg Centre comprises the Winterberg, Stormsberg, Drakensberg and parts of the Magaliesberg and Zoutpansberg ranges. Into this centre would be incorporated the Table Mountain Sandstone Outcrops of Transkei and Natal where some endemic species occur (e.g. 42).

The Drakensberg Centre is separated from Capensis by the Kaffraria Interval, and in particular the Great Fish River valley with its associated karroid vegetation.

(vii) The Tropical African Mountain Centre is composed of several mountains and highlands within tropical Africa north of the Limpopo (e.g. Chimanimani, Inyanga, Mljanje, Kivu, Usambara, Ethiopian Highlands, etc.). It is separated from the Drakensberg Centre by the Limpopo Interval which has acted as an effective barrier to transmigrations of the Cape Flora even during the Pleistocene pluvials (8).

Weimarck delimitated his phytogeographical centres as a result of the distribution patterns exhibited by 462 taxa, including genera of the Restionaceae, Cyperaceae, Compositae, Thymelaeaceae, Rosaceae (Cliffortia), Indaceae (Aristea) and others. In an attempt to critically evaluate his work a further 546 taxa from recent taxonomic revisions were analysed. The following genera were used:-

Muraltia - Levyns (23); Aspalathus - Dahlgren (10); Sorocephalus - Rourke (41); Spatalla - Rourke (41); Paranomus - Levyns (28); Leucospermum - Rourke (42); Leucadendron - Williams (60); Adenandria - Strid (52).

The results of both analyses are presented in Fig. 5.

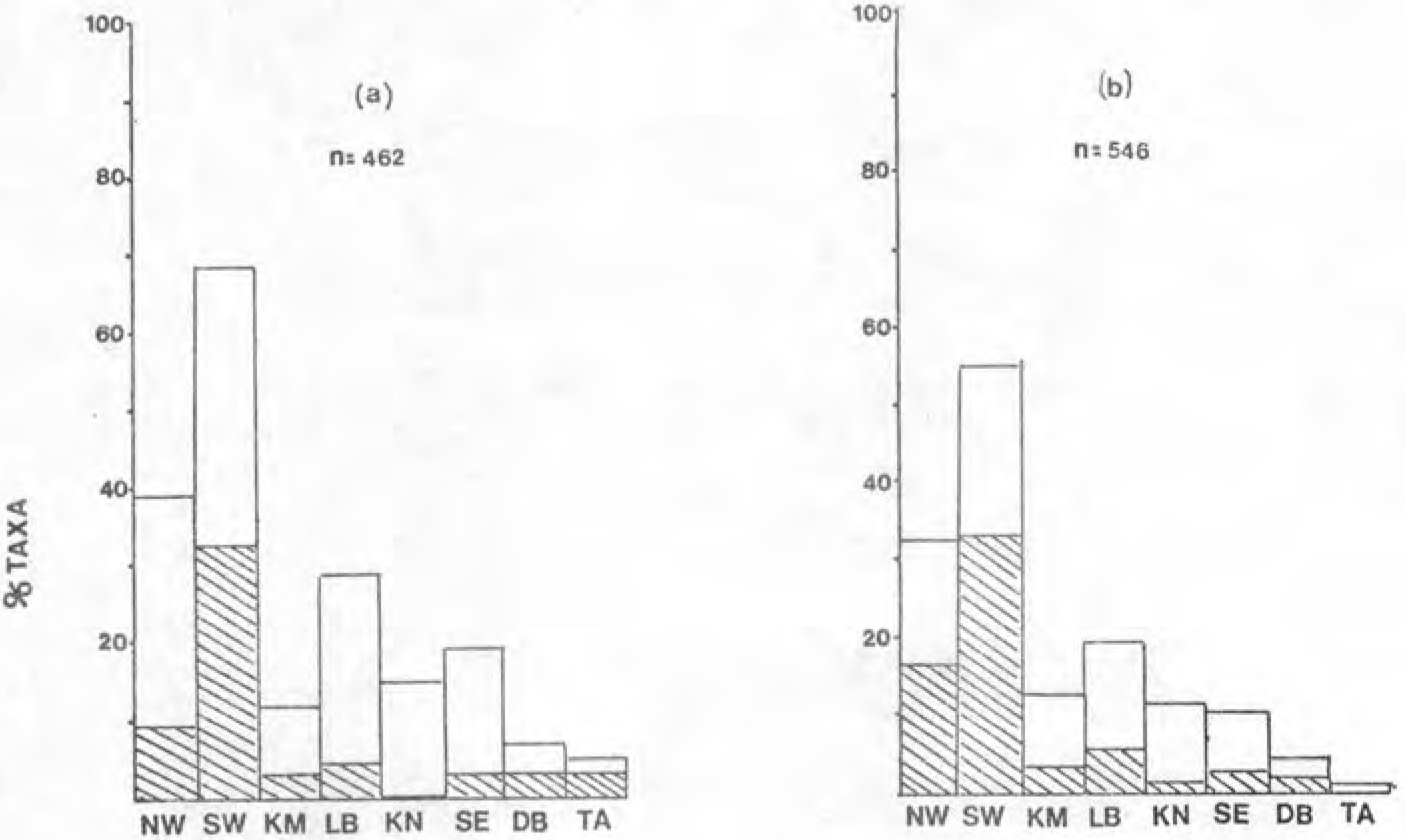


FIGURE 5. The distribution of taxa within the Endem Centres of the Cape Flora. Open columns represent the percentage of the total taxa (n) which are found in each Endem Centre while the hatched columns indicate the percentage of n which are endemic to each Centre. The results of Weimarck's (55) analysis are presented in (a) while those of the present analysis are given in (b).

It can be seen that they correspond very closely. The Southwestern Centre is the richest endem centre both in terms of total taxa and endemics. There is a progressive drop in relative floristic richness as one proceeds northwards and eastwards. The lowest number of taxa are found in the Drakensberg and Tropical African Mountain Centres where a large proportion of the taxa are endemic. (Of the total taxa treated by Weimarck (Fig. 5a) and the author (Fig. 5b) only 3,53 and 3,85% respectively are common to the Cape and extra-Cape centres).

Weimarck (55) and others (e.g. 23,42,60) have explained the high concentration of species in the Southwestern Centre as a result of the fact that it incorporates the junction area of the predominantly north and east running Cape fold mountain ranges, and therefore, the meeting place of two migration routes. Furthermore, the area is characterised by topographical diversity and a relatively high rainfall, concentrated mainly in the winter months. Apparently, fluctuations in the Pleistocene sea levels have resulted in tremendous speciation on the coastal flats and limestone hills in the Bredasdorp district (23,42,60).

The drop in floristic richness in the Northwestern Centre could be due to increased competition from the Karoo flora as a result of lower rainfall conditions. In the eastern centres a great proportion of the rain falls in summer resulting in climatic conditions which are most likely to enhance the competitive ability of tropical-subtropical floristic elements.

The only criticism I have of Weimarck's phytogeographical centres is an uncertainty with regard to the delimitation of the Knysna Interval. Of the taxa investigated in this work only 3 showed a Knysna Interval; many more showed a continuous distribution along the Outeniqua Mountains, sometimes linking the Langeberg and Southeastern Centres, while others have a distribution restricted to the coastal mountains between the Gouritz and Gamtoos River valleys.

A Knysna "interval" as such does not seem to exist. Instead, there is an area, comprising the Coastal Rhenosterbosveld between the Gouritz River and the vicinity of George, and the Knysna and Tsitsikamma forest areas as far east as the Storms River, where the Cape vegetation appears to be poorly represented, especially in terms of endemic species (exceptions do occur e.g. Muraltia Knysna-ensis (23) and others). It is suggested here that an Outeniqua Centre should be delimitated to include the higher peaks and northern slopes of the Outeniqua Mountains east of the Gouritz River, the Langkloof, Kamanassie and Kouga Mountains and the Tsitsikamma Mountains and lesser ranges in the Humansdorp district. The eastern limit of the centre would be the Gamtoos River Valley, thereby reducing Weimarck's Southeastern Centre to the Cockscomb and Suurberg Subcentres.

It must be stressed that these proposals are tentative; a great deal more scrutiny is required before they should be seriously considered.

Unfortunately, very few South African taxonomists make use of Weimarck's centres when discussing the geographical distribution of Cape taxa. In 1958 Levyns (24) stated: "Up to the present South Africa has not been divided into small phytogeographical units suitable for the plotting of the distribution of species".

We have seen that the maximum expression of the Cape Flora occurs in the Southwestern and Northwestern Centres. The climate of both these centres is a mediterranean type climate, characterised by predominantly winter rainfall. The establishment of a mediterranean type climate in the S.W. Cape appears to be a fairly recent phenomenon, having occurred probably after the first glacial in the Pleistocene (5). It appears that the tremendous outburst of speciation evident in the flora of Capensis can be associated with conditions during the Pleistocene, after this climatic type had become established (5,7,10,27,42, 55,60). It now follows to examine the evolution of flora under a mediterranean climate in the Cape and other regions in an attempt to unravel some of the mystery surrounding the tremendous floristic richness of Capensis.

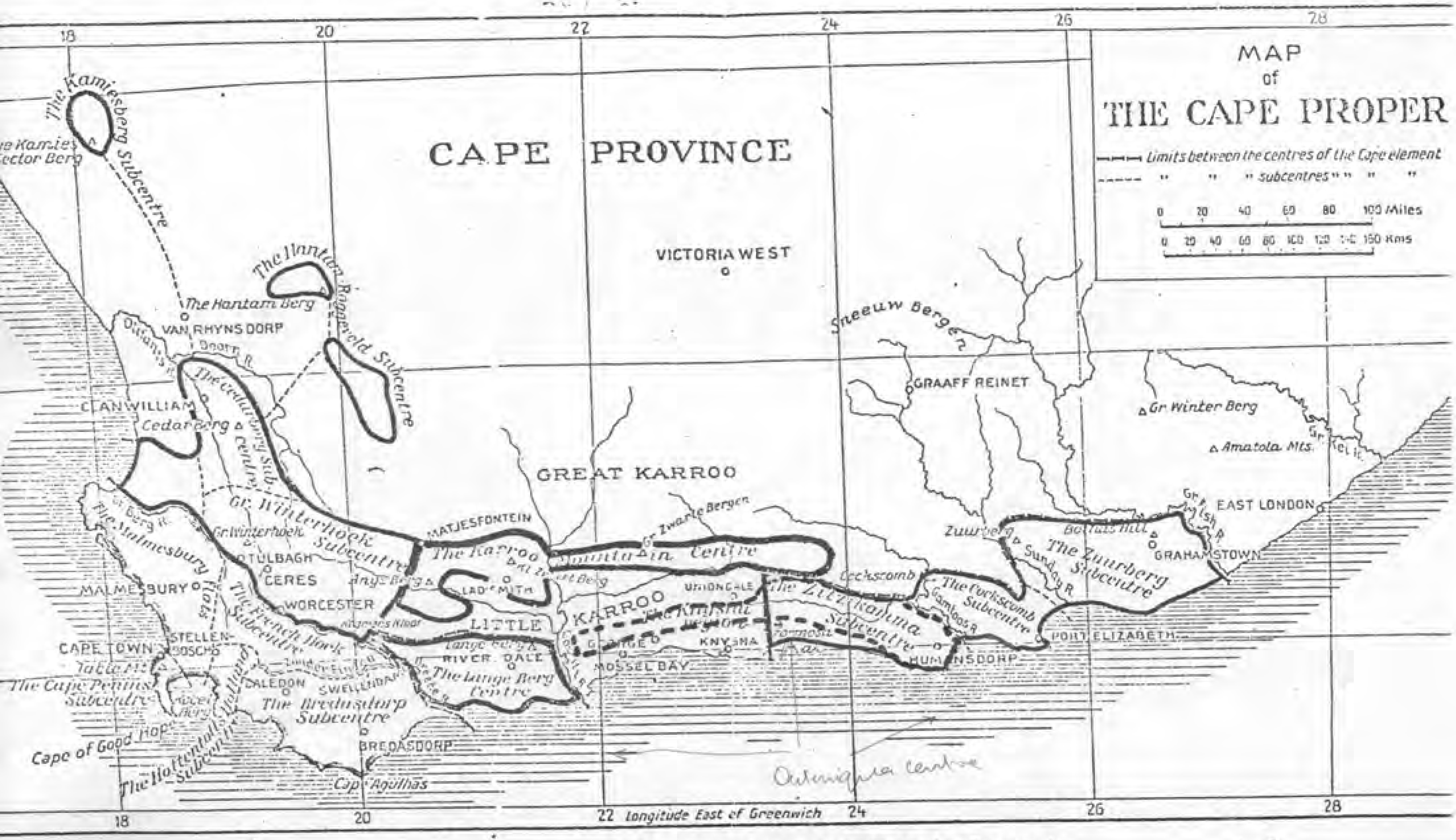


FIGURE 6. Phytogeographical Centres and Subcentres in Capensis. Dotted lines represent the delimitation of the proposed Outeniqua Centre (see text).

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4.0 SPECIATION IN THE CAPE FLORA

4.1 Evolution Under a Mediterranean Climate

The evolution of the Californian Chaparral is probably the best known of all mediterranean floras as a result of the accumulation and interpretation of much palynological data (3,50). From the early Miocene, California and bordering areas must be envisaged as having been occupied by diverse types of sclerophyll vegetation which probably evolved under conditions of summer drought (3). Communities of this type, floristically and structually related to the Chaparral, are found in the summer rainfall region from Arizona to Texas and south west Mexico (3).

The advent of the mediterranean climate at the beginning of the Pleistocene had a drastic effect on the Californian flora, the most significant result being the elimination of those species unable to withstand conditions of summer drought (3,39).

Subsequent speciation has occurred under the mediterranean climate. Intense mountain building on the west coast of north America during the Tertiary resulted in the exposure of a variety of parental rock formations which eventually lead to edaphic and topographic diversity. The intermittent nature of the mediterranean climate during the Pleistocene was an important factor in promoting speciation. Alternating cool-moist (pluvial) and hot-dry (interpluvial) climates led to large spatial shifts in populations, often resulting in their isolation and subsequent speciation (3). In California, most of the evolution under a mediterranean climate has been among the herbaceous plants, the woody genera Arctostaphylos and Ceanothus providing notable exceptions (50).

A similar mode of evolution appears to have occurred in the editerranean flora (Mattoral) of Chile (45) i.e. the elimination of taxa rather than massive speciation under a mediterranean climate.

The Cape, like California and Chile, is characterised by topographic diversity and evidence for pluvials and non-pluvials during the Pleistocene is fairly well established (54a). On the other hand, the mediterranean regions of Australia have a monotonous relief but share the high floristic richness and nutrient poor soils of the Cape. Is there any relation between these two last mentioned phenomena?

4.2 Evolution on a Nutritionally Poor Environment

What follows is an extremely hypothetical consideration:-

It has been demonstrated in the Australian sclerophyll vegetation, and elsewhere, that low soil fertility, particularly low levels of phosphor us, is positively correlated with xeromorphy (especially in terms of small leaf size) and sclerophylly (6,29,44). We have seen that in both Australia and Africa outliers of the present day mediterranean floras exist in the tropics in nutrient poor soils. It is suggested that many of these taxa were pre-eminently suitable to withstand conditions of summer drought since considerable pre-adaptation had occurred as a result of extreme xeromorphic characters developed on nutrient poor soils. Thus, unlike California and Chile, where the advent of the mediterranean climate led to the elimination of many taxa which could not withstand summer drought, the same conditions in Australia could have led to the evolutionary radiation of pre-adapted taxa. Examples of some large Cape genera are: Agathosma - 134 species; Aspalathus - 250; Cliffertia - 70; Erica - c.600; Muraltia - 106; Pelargonium - c.150; Phylica - c.140; Protea - 84; Restio - 94 (32).

At first, the high degree of speciation of some fynbos taxa on the limestone beds and calcium rich coastal sands of the Bredasdorp and Riversdale districts (23,42,60) appears contradictory to the above hypothesis. Unfortunately, there is no available data on the nutrient status of these soils, except that they are highly alkaline and thus differ from the essentially acidic sandstone derived soils (11). There is evidence that high calcium content in soils may cause phosphor us to become unavailable for plant assimilation (49). The success of fynbos taxa in edaphic environments of such extremes as limestone soils and acidic sands should make a fascinating study of nutrition, selection and evolution.

Finally, with regard to its application in the Cape, the abovementioned theory must be regarded with a great deal of caution. It suffers from a dearth of supportive evidence primarily in terms of palynological data relating to past plant communities and information on the composition, structure and edaphic environment of present day Afromontane-Cape fynbos communities.

5.0 SUMMARY AND CONCLUSIONS

The evolution of the Cape Flora, as described in this work, is summarised as follows:-

From the early Tertiary it is possible that the evolutionary precursor of the Cape Flora existed in association with primitive members of the Afromontane forests in more-or-less continuous belt from the Cape Peninsula along the eastern highlands of the African continent with outliers in West Africa. The original stock of the flora was derived from Austral, African and Boreal elements. During the Tertiary a drying of the climate and erosion of the landscape would serve to isolate Cape floral elements to an archipelago of mountain islands. In the southern part of Africa it is quite probable that the Cape Flora was more extensive due to the more temperate climate and extensive sandstone and quartzite mountain complexes (in tropical Africa it appears that the Cape vegetation is most prevalent on soils derived from quartzite and sandstone and under other ol otrophic conditions).

The advent of the mediterranean climate in the Pleistocene witnessed an outburst of speciation within the Cape Flora in the southwestern, and to a lesser degree, the southern Cape. It is hypothesised that the enormity of this speciation may be partially attributed to the fact that numerous Cape taxa were pre-adapted to withstand conditions of summer drought due to the acquisition of Xeromorphic characters resulting from an evolution in a nutritionally poor environment.

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