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Phytogeography of fynbos

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ABSTRACT

Previous classifications of the vegetation of the Cape Floristic Region, or Capensis, are outlined. The distinctive features of the Cape flora such as species diversity, endemism and distribution patterns are discussed in an attempt to elucidate the origins and evolution of the principal vegetation type of the region, known today as fynbos. Evidence suggests that the present species-rich Cape flora has mainly evolved in and radiated from the southwestern part of Capensis, an area where a true mediterranean-type climate is found.

RÉSUMÉ

PHYTOGÉOGRAPHIE DU FYNBOS

On rappelle schématiquement des classifications antérieures de la région floristique du Cap, ou Capensis. Les caractères distinctifs de la flore du Cap, tels que la diversité des espèces, l'endémisme et les modèles de distribution sont discutés pour tenter d'élucider les origines et l'évolution du principal type de végétation de la région, connu aujourd'hui sous le nom de fynbos. Les indices disponibles suggèrent que la flore du Cap actuelle, avec sa richesse en espèces, a principalement évolué dans le sud-ouest de la province du Cap et a rayonné à partir de cette région qui possède un climat de vrai type méditerranéen.

INTRODUCTION

In recent works both Takhtajan (1969) and Good (1974) allocated the rank of Kingdom to the Cape flora despite its small area on a world scale, thus according it equivalent phytogeographical importance to such vast regions as the Holarctic Kingdom which encompasses the whole of the temperate and arctic northern hemisphere.

The Cape Floral Kingdom is concentrated in the region known today as Capensis, the Cape folded-mountain belt, that comprises the distinctive temperate floral area of the southwestern and southern Cape Province occurring between latitudes 31° and 35° south and longitudes between 18° and 27° east. The western part has a distinctly mediterranean-type climate with dry summers and wet winters but eastward the rainfall becomes increasingly non-seasonal. Over the area as a whole, rainfall varies from extremes of 300 to 3 000 mm.

Capensis is bounded to the west and south by the coast and to north and east principally by the Karoo-Namib Region (Werger, 1978a) together with some outliers of the Sudano-Zambezian (Werger & Coetzee, 1978) and Afromontane Regions (White, 1978). The Karoo-Namib flora penetrates into Capensis in the Little Karoo, an arid area between the coastal and inland mountains (Werger, 1978a). On mountains in the Knysna region Capensis intergrades with the Afromontane flora, and several Cape species such as *Berzelia intermedia, Diospyros glabra, Leucadendron eucalyptifolium* and *Protea cynaroides* become dominant as one ascends from foothill forest to Mountain Fynbos (White, 1978).

The vegetation of Capensis consists principally of fynbos, a broad category of diverse evergreen sclerophyllous shrublands comprising Acocks's (1975) veld types 47 (Coastal Macchia), 69 (Macchia) and 70 (False Macchia), but includes two transitional veld types, Coastal Renosterbosveld and Strandveld, that contain a mixture of Cape and other floristic elements.

The broad phytogeographic demarcation of Capensis began in the last century when botanical travellers included "the region of the Cape flora" in their descriptions of vegetation formations and floristic kingdoms. Among these pioneers were Schouw (1823), Drège & Meyer (1843), Grisebach (1872), Rehmann (1880), Engler (1882), Drude (1887, 1890) and Schimper (1898). Their vegetation descriptions and maps, based on scant information, were largely conjectural, and are of mere historical interest today.

From the turn of the century, resident botanists like Bolus (1886, 1905) and Marloth (1906, 1908) began to describe and map the vegetation of South Africa. Fynbos delineation was gradually refined by Bews (1916), Pole Evans (1936), Adamson (1938a) and others, until finally Acocks (1953) in his well-known map that is still in use today, recognized the three fynbos types mentioned above. In his discussion of these and later works, Werger (1978b) concludes that reasonable unity of opinion on the zoogeographical boundaries in Africa was reached much earlier than was the case with phytogeographical boundaries. The latter are, indeed, still being debated (e.g. Axelrod & Raven, 1978) and a clear picture will only emerge when the taxonomy and distribution of present floras, including lower plant groups, are known in detail.

CHARACTERISTICS AND AFFINITIES

The singular biogeographic features that led phytogeographers to give the Cape flora such a high status in their classifications include the great concentration of species, the high degree of endemism, the characteristic distribution patterns of typical elements despite a general lack of species dominance, and the predominance of certain families and genera. The Cape flora "is noted for its richness in species, both in small areas and over its whole range" (Taylor, 1978), and has been claimed as being one of the richest in the world for its size (Oliver, 1977). For diversity at the community level (alpha diversity), Taylor (1972) has recorded 121 species of flowering plants in a single 100 m² quadrat in a homogeneous stand of Mountain Fynbos. This figure, although probably not the final tally, considerably exceeds the average level of alpha diversity in equivalent shrubland communities of mediterranean-type ecosystems elsewhere (Kruger *et al.*: paper delivered at the Second International Symposium on African Wildlife Management and Research, Pretoria, July 1977). Plant species richness at the landscape level, such as a mountain

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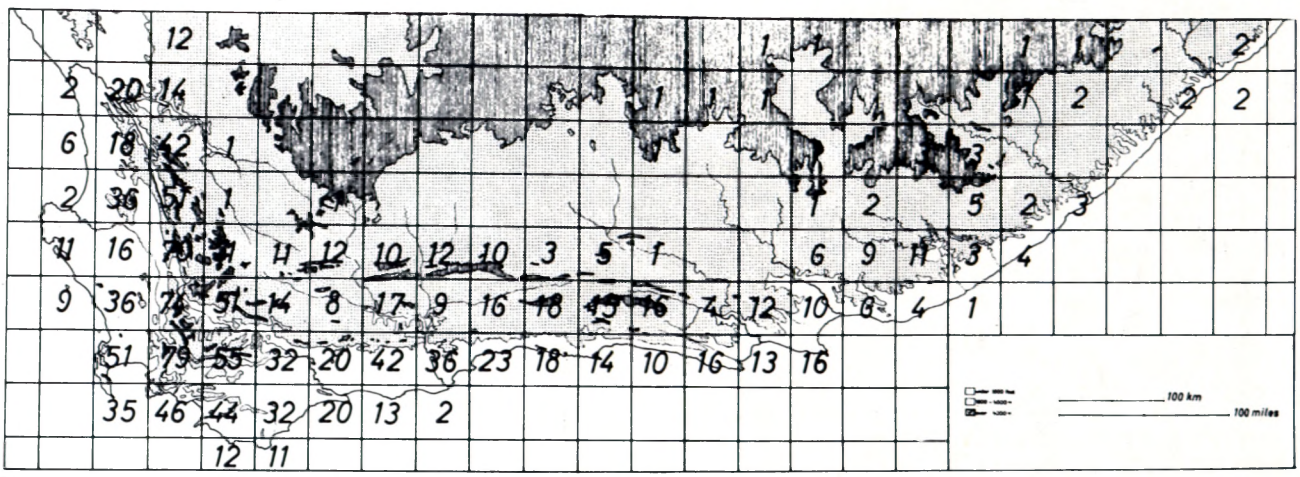
range (gamma diversity—Whittaker, 1972), is much greater than that of southwestern Australia, the richest floristic zone in that continent (Kruger, 1977); while at the level of a floristic kingdom or province, Goldblatt's (1978) figure of 8550 species of vascular plants in the Cape Floristic Region compares well with the figure of 7 000 given by McLarty (1952) for the whole of Western Australia, an area about twenty times that of Capensis.

Two of the three families that are characteristic of the Cape flora, Restionaceae and Proteaceae, have a pronounced austral distribution. Both of them occur on all three southern continents and have very few representatives north of the equator. The third Cape family, Ericaceae, has no connections with either of the other two southern continents. Its subfamily Ericoideae that occurs in the Cape has a strictly north-south distribution. All three families have strong concentrations of taxa in Capensis. Outliers occur on mountains not only in adjacent dry areas to the north, especially Namaqualand (Adamson, 1938b), but also intermittently along the eastern highlands of the continent as far north as central Africa (Oliver, 1977). Many other typical Cape taxa have similar distribution patterns. In fact there are so many in the Drakensberg that both Killick (1963, 1978) and Edwards (1967) have described a type of "fynbos" for that area, and Boughey (1957), Hedberg (1965) and Wild (1968) have recognized a "Cape element" on the mountains of Rhodesia and East Africa. But the floras of high mountains in southern and central Africa are incompletely known and intensive plant collecting is needed to provide data for a full phytogeographic study of these interesting migration routes.

Families that are richest in genera at the Cape but widely distributed in other parts of the world include Fabaceae, Iridaceae, Rosaceae and Thymelaeaceae. In contrast, many taxa of high rank are endemic to the Capensis region or nearly so. These include Bruniaceae, Penaeaceae, Stilbaceae, Grubbiaceae, Roridulaceae and Geissolomataceae, the tribe Diosmae of the Rutaceae and large genera such as *Aspalathus, Phylica, Muraltia* and *Cliffortia* (Oliver, 1977; Axelrod & Raven, 1978; Taylor, 1978). Weimarck (1941) found that of 282 genera with their centre of origin in Capensis, 212 were endemic, and he estimated that more than 3 500 species were endemic out of the total of 4 200 that he surveyed. In examining local endemism, Weimarck found that the two westernmost centres together contained 45,5 percent of the total number of endemics represented within the "Cape proper."

Taxonomic studies show that both palaeo-endemics, or relics, and neo-endemics, or recently evolved species that are still limited to a small area, occur in the Cape flora. These types have local or disjunct distributions or both. The Proteaceous species *Orothamnus zeyheri, Mimetes hottentoticus* and *Leucadendron argenteum* are, by virtue of their distribution and biology, considered to be palaeo-endemics. Rourke (1972) reports vicariad groups of neo-endemic *Leucospermum* species on coastal lowlands of the southern Cape and Levyns (1954) shows that several *Muraltia* species occupying the same coastal strip are also youthful endemics. From phylogenetic evidence, Oliver (1977) considers some species in the minor genera of the Ericaceae, and even some of the genera themselves, to be neo-endemic. Marloth (1929) and Goldblatt (1972), among others, have attributed this local endemism and disjunction partly to the diverse topography of the region, in which the concomitant diversity of soils and local climates, and the appearance of new land surfaces along the coast, gave opportunities for recent speciation, and partly to the great age of the flora, members of which may have been able to survive climatic changes by retreating into favourable localities.

Weimarck (1941), Levyns (1938, 1952), Dahlgren (1963), Williams (1972) and others have shown that typical families and genera of the Cape flora have a characteristic distribution pattern in which the highest numbers of species per area are concentrated in the western part of the region (see Fig. 1). Levyns (1952) went so far as to state it as a "rule that all genera of the Cape Flora show a concentration in the south-



Map 3. Concentration of *Aspalathus* species. The figures express the number of species represented in the area of each square. The map is based on dot maps of all the species. The distribution in Natal and the Khamiesberg area are excluded (cf. map 1). It is seen that the squares with the greatest concentration of species cover the mountain regions in the southwest. The number in the square covering most of the Cape Peninsula is surprisingly high considering the area occupied by the Cape Flats, which are poorer in species, and the sea. A high number of species is found in all the squares covering the western and southern mountain ranges. The great contrast between the relative richness in the Witteberg--Zwartberg mountains and the poverty of species in the Little Karroo deserts has only partly been possible to demonstrate.

FIG. 1.—Map 3 from Dahlgren (1963).

west. Any apparent constituent, which does not show this particular pattern of distribution, may be suspected of being an invader." The Restionaceae, Proteaceae and most of the Ericaceae show this pattern, as do the endemic families Bruniaceae and Penaeaceae and the larger genera *Cliffortia, Aspalathus, Phylica, Muraltia* and *Leucadendron.*

On the other hand, genera like *Babiana, Ferraria* and *Pteronia* that are fairly common in Capensis have their maximum concentration in Namaqualand. Among other "apparent constituents" that do not show the typical southwestern distribution are species of *Aloe, Erepsia, Carpobrotus, Crassula* and *Zygophyllum.* The presence of such species within the Cape flora and the presence of fynbos outliers on high mountains in Namaqualand as far north as Springbok suggest an intermingling of the Cape flora with those floras abutting it to the north.

In contrast, certain austral forest elements that also do not have the typical southwestern concentration occur within Capensis only as relic patches of forest vegetation in moist or sheltered habitats and not as constituents of fynbos. Such genera as *Podocarpus, Cunonia, Platylophus* and *Curtisia* are examples of these (Levyns, 1962). Though their presence suggests a previous wider distribution of forest, there is little evidence that they are becoming adapted to the typical rigorous habitats occupied by fynbos.

The Cape flora also contains elements that are found more commonly in more distant lands. The grass *Hyparrhenia hirta* has a wide but disjunct distribution in the coastal Mediterranean, in east Africa and in southern Africa, linked only by high mountain outliers in the Sahara (Quézel, 1978). Genera such as *Anemone, Rubus, Scabiosa, Geranium* and *Dianthus* have their main centres of concentration in the northern hemisphere. *Aloe, Euphorbia* and the Asclepiadaceae are prominent members of other African floras. *Gladiolus* is widespread elsewhere in Africa and beyond. *Rhus* and *Euclea* have many more species in subtropical forest, scrub and savanna than in fynbos (Taylor, 1978). Similarities at the generic level suggest comparatively recent migrations and intermingling. Similarities at a higher taxonomic level suggest older affinities. Adamson (1958) considered that pairs of taxa like *Selaginaceae* (Cape) and *Globulariaceae* (Mediterranean), *Dimorphotheca* and *Calendula, Lobostemon* and *Echium, Crassula* and *Sedum,* and *Widdringtonia* and *Tetraclinis* provided evidence of a once widespread flora that became fragmented as the climate changed and then evolved in isolation.

The affinity of the Cape flora with that of southwestern Australia is striking but more remote than its affinities with northern hemisphere floras. The Thymelaeaceae, Haemodoraceae and Droseraceae are common to both continents and the endemic Cape family Roridulaceae is closely paralleled by the Australian Biblidaceae. Diosmae (Rutaceae) of the Cape has its counterpart in the Australian tribe Boroniae (Bolus & Wolley-Dod, 1904) and the genera *Tetraria* and *Gahnia,* and *Phylica* and *Cryptandra* are closely related (Adamson, 1958).

A picture emerges from this account of a present flora with high alpha and gamma diversities, a flora uniquely characterized by three widespread families and some endemic ones, and by many endemic taxa of lower rank, some young, some old, some widespread within the region, some restricted or disjunct in distribution. The flora has a high concentration of species in the west, it shows some close taxonomic affinities with abutting floras and with the central African mountain flora, obvious but more distant affinities with the flora of southwestern Australia, and tenuous relationships with northern hemisphere floras. In all, the Cape flora is floristically and phytogeographically unique. Despite migrations and interminglings, it appears to have been isolated for a long time and to have suffered vicissitudes that have encouraged speciation, radiation and hybridization at a singularly high rate.

ORIGINS AND EVOLUTION OF FYNBOS

Such features suggest a long and varied history of geology and climate. On these grounds and because dominance by one or more species is a rare phenomenon in mature fynbos, the flora has hitherto been generally regarded as an ancient one (Marloth, 1915; Bews, 1925; Weimarck, 1941; Levyns, 1952; Adamson, 1958; Dyer, 1966). Yet despite general agreement on its age, there has been much controversy about the origin of the Cape flora. One school postulated an origin in the northern hemisphere, another in the southern, while yet a third contended that it originated somewhere in central Africa.

Until very recently the third theory has seemed most plausible, mainly as a result of the perceptive work of Levyns (1938, 1952, 1958, 1964), summarized by Van Vuuren (1973). She pointed out that very many members of the Cape flora, though they are concentrated in the Capensis region, show clear traces scattered throughout Africa, mainly on mountains as far north as Ethiopia. Proceeding southwards these "islands" become more frequent until, south of the Swartberg, all the scattered mountains of the Little Karoo have cappings of Cape plants while the flora of the lowlands is entirely different (Levyns, 1950). Levyns showed, too, that the more primitive members of Cape plants in many groups are to be found in mountain outliers within the tropics, whereas in the southwestern Cape many of the species are advanced and occupy restricted geographical ranges. These distribution patterns suggest that a flora of the Cape type was once widespread in central Africa, and that this flora retreated southward when the climate became unfavourable in the north, leaving traces on the northern mountains and speciating in the favourable temperate conditions found in the southwestern Cape.

This subject has been recently reviewed by Taylor (1978) who quoted further evidence suggesting that the presumed central African origin in fact represented a secondary centre of establishment for a flora that originated in austral lands. A review by Axelrod and Raven (1978), which appeared at the same time as Taylor's, presents evidence to support this theory. The evidence strongly suggests that the summer-dry climate is of recent origin in southern Africa and probably only appeared at the beginning of the Pleistocene some 2,5 million years ago. But already in the early Miocene, rapid speciation probably took place in South Africa with the broad warping and uplift of the continent. Further study of fossil floras like those of Coetzee (1978a, b) is needed to substantiate this. At about this time increasing glaciation in Antarctica brought the cold water of the Benguela Current to the west coast, accentuating the trend to increased summer drought on the western land surfaces. Then, when strengthening high pressure

systems brought this drier climate to the interior, sclerophyllous taxa that had lived earlier under summer and winter rain were adapting to increasingly dry summers. With dry summers spreading from the west, the taxa that required summer rain were gradually restricted eastward. This left the western environment open for the sclerophylls with tolerance to withstand summer drought, and many of those that survived in this new habitat had great opportunities for evolutionary radiation. This supports the findings of Levyns and others, mentioned earlier, that typical members of the Cape flora show a concentration of taxa and of endemics in the west.

But not all fynbos species originated in their present area. Axelrod & Raven (1978) postulate that even during the most recent climatic changes in the Pleistocene, fynbos in its present area may have been restricted by the expansion of forest and other vegetation, and could then have been displaced to the north, into the regions now occupied by desert and semi-desert. At the end of the Tertiary when the area of dry climate expanded, fynbos would have retreated to its present area and, during this retreat, interchange between fynbos and isolated pockets of relic sclerophyll vegetation may have contributed directly and through hybridization to the overall diversity of the flora. Thus, the rich flora of the present Capensis region "may represent but a remnant of a much richer sclerophyllous flora that ranged over the present desert and steppe areas into the Pleistocene" (*ibid.*, 1978).

Though Axelrod and Raven's hypothesis is attractive, the diversity and high rate of speciation in fynbos may not simply be the result of mass plant migrations following climatic change. As Levyns (1963) has pointed out, a vegetation category, like fynbos, is not "a flock of sheep" but an association of taxa that extend and diminish their ranges, not collectively but individually, in response to different factors to which the taxa are variously adapted. For example, the fact that fynbos is largely restricted to nutrient-poor soils would preclude its movement *en bloc* into the Karoo-Namaqualand area, even though individual taxa may adapt to the richer soils there.

The pulse of alternating cooler and warmer, and at times wetter, climates during the Quaternary would also have contributed to the high diversity in the Cape flora. At times of moister climate, some taxa of the sclerophyllous Cape flora could have spread widely over the present Karoo region and speciated there. "As drier climate returned, the flora shifted coastward into its present area, bringing new taxa with them and leaving relic stands in moist situations" (Axelrod & Raven, 1978, p.116). Thus, even during recent climatic changes in the Quaternary, the Cape flora may have been far more widespread (Levyns, 1938 in Axelrod & Raven, 1978), and has only been restricted to its present environment for a relatively short time.

An interesting feature in support of this view is that some Cape plants enter into a period of rapid vegetative growth towards the end of summer at a time when water supplies in the southwestern Cape are at their lowest. This strangely ill-adapted growth rhythm suggests that the ancestors of these plants "evolved in some place having a summer rainfall. The same phenomenon has been recorded for South Australia, where a similar change in climate is postulated to account for the same, apparently inexplicable, features of growth" (Levyns, 1964). This suggests that the mediterranean climate is not ancient, but is so youthful that the plants have not yet fully adapted to it. Further research on South African plants is needed to clarify this phenomenon.

As stated earlier, a true mediterranean climate is present only in the western part of Capensis. It is this western part that was first colonized by primitive sclerophylls, and in the southwestern corner which has the highest rainfall and most diverse topography, speciation has been most active, producing the greatest concentration of taxa and endemics. This rich southwestern centre can be regarded as the true home of the Cape flora from whence it has radiated. To the north its spread is limited beyond Vanrhynsdorp by an arid climate, but eastward along the well-watered south coast it extends into the regions of non-seasonal and summer rain as far as Grahamstown. The eastern extension, having relatively low diversity and few endemics, is presumably younger than the western part. Fynbos would probably only have started colonizing this eastern area when the coastal temperate forest was reduced by a drying climate (cf. Acocks, 1975, Maps 1 & 2), but it has expanded its range faster within historic times owing to the destruction of forest by man (Von Breitenbach, 1972), and veld mismanagement is now encouraging its spread further eastward into mountain grassland (Trollope & Booysen, 1971).

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UITTREKSEL

'n Oorsig word gegee van vorige klassifikasies van die plantegroei van die Kaapse Floristiese Gebied of Capensis. Die onderskeidende kenmerke van die Kaapse flora, soos verskeidenheid van spesies, endemisme en verspreidingspatrone word bespreek in 'n poging om lig te werp op die oorsprong en evolusie van die vernaamste plantegroei-tipe van hierdie gebied wat vandag as fynbos bekend staan. Daar bestaan bewyse dat die huidige ryk Kaapse flora ontwikkel het in die suidwestelike deel van Capensis, 'n gebied met 'n egte Mediterreense klimaat.

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