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Geographical distribution of present-day Cape taxa and their phytogeographical significance

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ABSTRACT

The Cape Flora, one of the six floral kingdoms recognized by phytogeographers, is remarkable for its species richness and high degree of endemism, but no overall statistics are as yet available. Several long-term projects have recently been started to enumerate all the species and to record their distribution patterns. The latter aspect has been completed for 1 936 species from the three most characteristic families, i.e. Restionaceae, Ericaceae and Proteaceae, the endemic families and some of the largest genera, i. e. *Aspalathus* and *Muraltia*. Computer analysis of the distribution patterns is being undertaken and the species concentrations and centres of endemism are being calculated. The concentration of species in the mountains of the south-western Cape is confirmed and the grid square 3418 BB is found to be the richest. For the groups dealt with, the degree of endemism was found to be as high as 98%. The phytogeographical centres so far outlined agree with those of Weimarck.

RÉSUMÉ

RÉPARTITION GÉOGRAPHIQUE DE TAXONS ACTUELS DU CAP ET LEUR SIGNIFICATION PHYTOGÉOGRAPHIQUE

La flore du Cap, un des six empires floristiques reconnus par les phytogéographes, est remarquable pour sa richesse en espèces et son haut degré d'endémisme, mais aucune statistique d'ensemble n'est encore disponible. Plusieurs projets à long terme ont été rédemment entrepris en vu d'énumérer toutes les espèces et de noter leurs modes de distribution. Ce dernier aspect a été réalisé pour 1936 espèces appartenant aux trois familles les plus caractéristiques, c'est à dire les Restionacées, les Ericacées et les Proteacées, aux familles endémiques et à certains des plus grands genres, comme Aspalathus *et* Muraltia. *Une analyse par ordinateur des modes de répartition est en cours de réalisation et les concentrations en espèces et centres d'endémisme sont actuellement calculés. La concentration en espèces dans les montagnes du sud-ouest du Cap est confirmée et le carré du quadrillage cartographique 3418 BB se révèle être le plus riche. Pour les groupès étudiés, le degré endémisme a pu s'élever jusqu'à 98%. Les centres phytogéographiqies définis jusqu'à présent s'accordent avec ceux de Weimarck.*

INTRODUCTION

The flora of the southernmost tip of Africa is one of great biogeographical interest because of its remarkable richness and high percentage of endemic species. This led Takhtajan (1969) and Good (1974) to recognize the Cape Floral Kingdom, one of the six floristic kingdoms of the world, equal to their Palaeotropical Kingdom which consists of the whole of the rest of Africa and south-east Asia.

Marloth (1908) put the number of species 'in the Cape' at about 6 000, but this figure is certainly low when one takes into account the more complete records and modern monographs of recent years. Goldblatt (1978) gives the figure of 8 550 species occurring in the Cape Region (sensu Goldblatt), a mere 89 000 km^2, and comprising 42% of the southern African flora. An analysis of the latter flora with an emphasis on the Cape Region is given by him.

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Much has been written about the phytogeography and evolution of this unique Cape Flora, the most comprehensive papers being Marloth (1908), Weimarck (1941), Levyns (1964) and some excellent recent reviews by Taylor (1978, 1980), Goldblatt (1978) and Axelrod & Raven (1978). The most significant one in regard to phytogeography is that of Weimarck entitled 'Phytogeographical Groups, Centres and Intervals in the Cape Flora' in which he analysed 462 species. In much of the work repetition of previous results has of necessity been prevalent except when authors have been able to interpret the results of their own revisions.

Since 1941 much more collecting has been done and this has extended the distribution ranges of many taxa and increased the size of the flora and here we must acknowledge the outstanding work done by Miss E. Esterhuysen. Critical revisionary work has resulted in the recognition of many synonyms. This made an objective re-appraisal of Weimarck's work of recognizing phytogeographic centres within the Cape Flora a necessity.

In addition to phytogeography, there has been much discussion on the possible origins and migrations of the Cape Flora (Levyns, 1938, 1964; Adamson, 1958; Axelrod & Raven 1978). The bulk of the Flora clearly shows a northern origin, whereas some elements may be remnants of an ancient Gondwanaland flora. During the Pleistocene extensive fluctuations in the area of the Flora were thought to have occurred (Levyns, 1964; Axelrod & Raven, 1978) with the Flora being displaced from its present habitat by extension of the temperate forest. A thorough analysis of the phytogeographical patterns in the present Cape Flora may cast some light on its history.

Two major issues had to be resolved at the outset first, what area had to be sampled and second, what taxa are typical of the Cape Flora.

The definition of the Cape Flora and the boundaries of its area have also been discussed by many authors. The southern and south-western Cape (Fig. 1) contain three main and distinct vegetation types (Levyns 1964; Taylor 1978):

1. Sclerophyll type which forms the Cape Fynbos vegetation that is the home of the distinctive Cape Flora (Levyns, 1964; Oliver, 1977; Taylor, 1978).
2. Temperate Evergreen Forest of the Knysna area.
3. Karroid Broken Veld of the Karoo-Namib Region.

In many areas tongues of vegetation of the above types occur deep within each other thus rendering exact and simple definition of their boundaries very difficult. This led Goldblatt (1978) to choose a broad geographic unit as the Cape Floral Region for the purposes of his survey. We have sampled the entire area of the main block of fynbos as delimited by Kruger (1979) (Fig. 2), but also included outliers south of 30°S (plus a few in Namaqualand and the Richtersveld) and west of 28°E.

The taxa constituting the Cape Flora are those forming fynbos vegetation and consequently can be defined as those that are most diversified within the area of the fynbos vegetation although outliers may be found in other vegetation types as far afield as North Africa and, in some cases, on other continents. Physiognomically, fynbos is characterized by three elements, namely restioid, ericoid and proteoid. The degree to which a taxon may be considered as a 'typical Cape Floral taxon' depends on the extent to which the taxon shares both distributional and physiognomic criteria.

A long-term project has been started and aims at recording by means of maps the distribution patterns of taxa occurring within the Cape Floral Region. This paper presents the preliminary results. Another long-term project to record the exact number of species within the Cape Floral Kingdom in the form of a checklist has been under way for the last few years (Goldblatt & Fairall, pers. comm.). These two projects should complement each other very well.

METHODS

The following taxa were selected as representing typical Cape Floral Region taxa. Recently published revisions were available for *Leucadendron* (Williams, 1972), *Leucospermum* (Rourke, 1972), *Sorocephalus* and *Spatalla* (Rourke, 1969), *Diastella* (Rourke, 1976) in the Proteaceae; *Aspalathus* (Dahlgren, 1960–1968) in the Fabaceae; Penaeaceae (Dahlgren, 1967–1971); *Adenandra* (Strid, 1972) in the Rutaceae; *Bobartia* (Strid, 1974) in the Iridaceae; *Muraltia* (Levyns, 1954) in the Polygalaceae; *Anaxeton* (Lundgren, 1972) in the Asteraceae. Where revisions are in progress information was provided by the monographers, i.e. Diosmeae-Rutaceae (Williams), remainder of the Proteaceae (Rourke), minor genera of the Ericaceae (Oliver), *Psoralea* (Stirton). For the remainder of the taxa, distributional data were derived from the numerous herbarium specimens housed in the following herbaria: *Erica* (PRE, BOL, NBG, SAM, STE, GRA, NH); Restionaceae (BOL, NBG, SAM, PRE) with checking by Linder and Esterhuysen; Bruniaceae (BOL; NBG; PRE) and

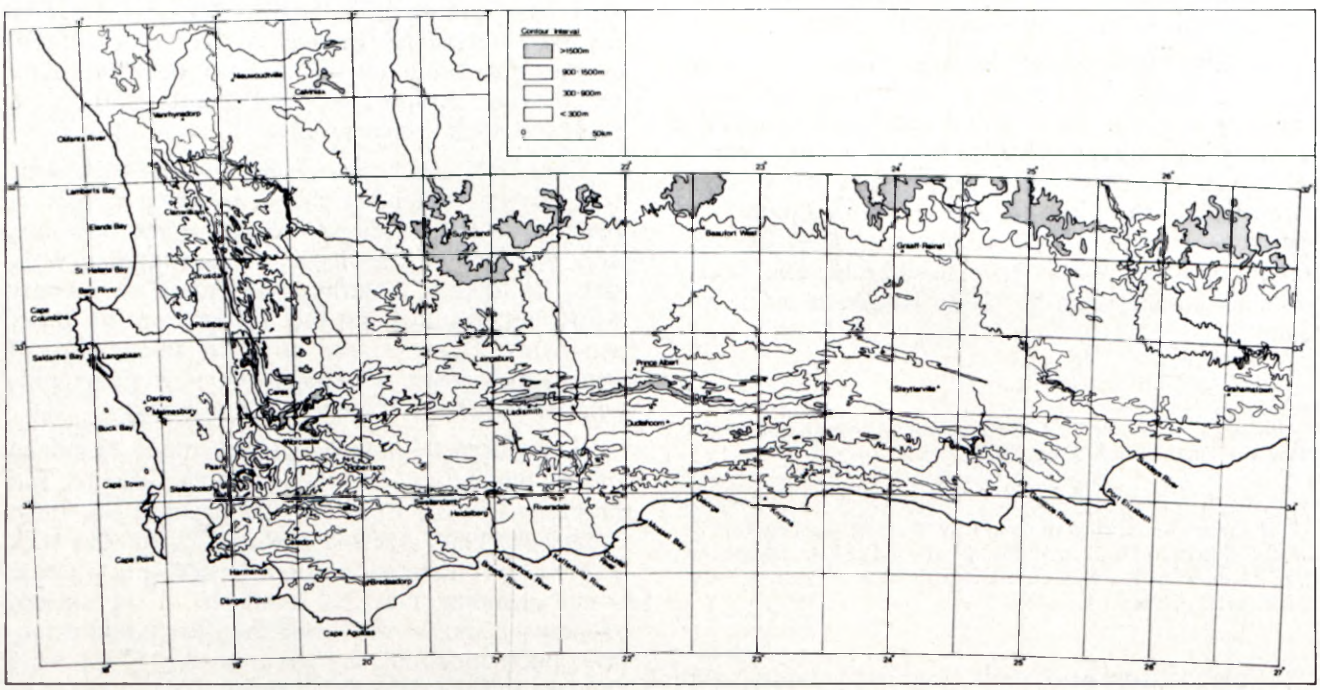

FIG. 1.—Main area covered in this survey.

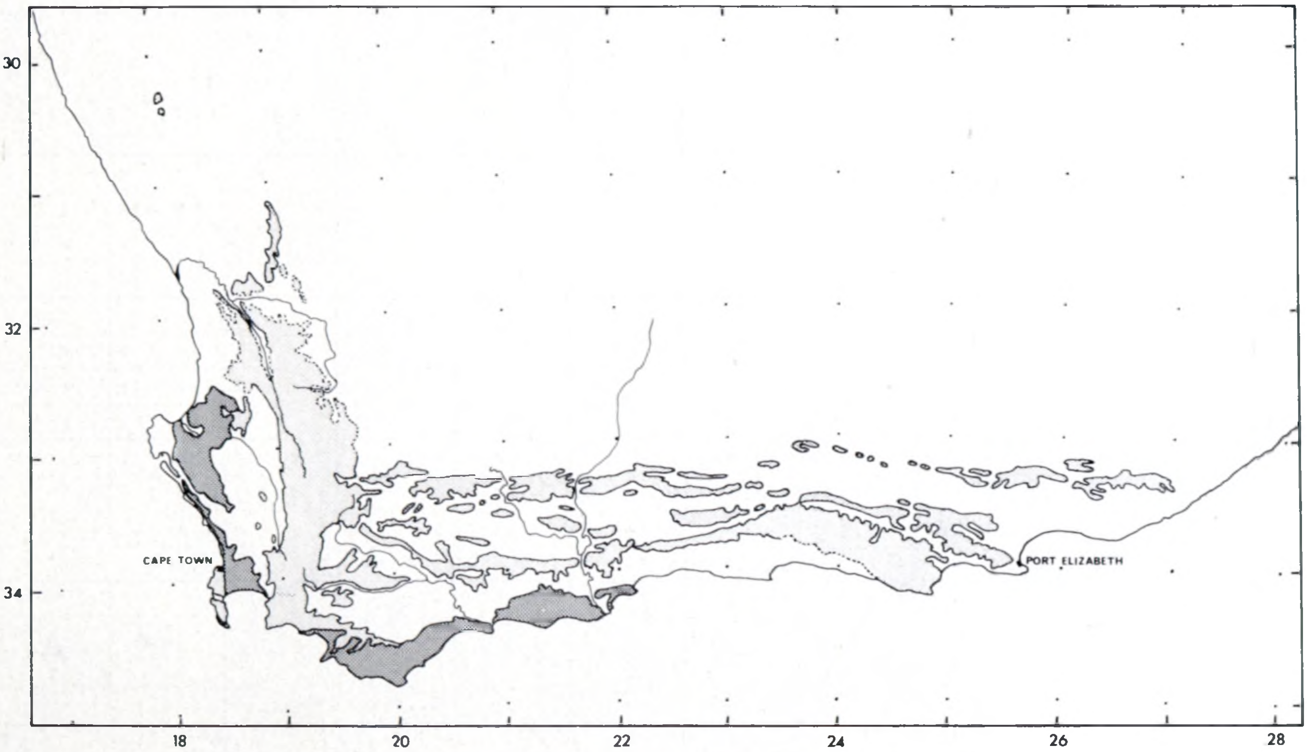

FIG. 2.—Distribution of fynbos. Heavy shading indicates coastal fynbos and light shading, mountain fynbos (after Kruger, 1979).

records additional to Levyns's revision of *Muraltia* (PRE). We had, of necessity, to accept the identifications on the specimens. In some cases these will be erroneous, but it was felt that the percentage of incorrect identifications would not affect the survey to any extent. The species were listed and numbered following the taxonomic order within each genus and family in the revisions and the herbaria. This selection of taxa gave a sample of 1 936 species with 1 810 occurring within the sample area.

For each species all specimens were recorded and coded according to the grid reference system of Edwards & Leistner (1971). This gives a quarter degree square unit with an area 23 × 23 km of ± 760 km^2 in the south-western Cape. The scale of this grid system and its positioning was found very suitable for covering the south-western Cape. Grids were only recorded for precisely locatable localities. The grids in the study area were numbered in a linear sequence from west to east from Nos 1, 2 and 3 near Cape Agulhas to No. 311 in the Richtersveld. Lists were compiled of the quarter degrees and maps compiled by hand for each species. The grids and species were then encoded solely on presence per grid with no weighting for frequency per grid. Weighting is not possible from herbarium records alone and can only be done after detailed field surveys.

The data were grouped using the PHYTOTAB program package (Westfall *et al.*, 1982) on an IBM 370/148 computer. This program package provides a preliminary grouping of species as well as grid squares based on Jaccard's community coefficient (Müller-Dombois & Ellenberg, 1974). PHYTOTAB 20 provided an objective clustering program to facilitate initial grouping of the data matrix. Final grouping was obtained by user sequencing of parameters according to the techniques used for Braun-Blanquet tablework (Westhoff & Van der Maarel, 1973; Werger, 1974). This program was developed for relevé/species analyses in vegetation surveys and seemed eminently suitable for the phytogeographic analyses of this project. The maximum matrix size of the program is 2 000 relevés by 2 000 species, hence the restriction on the number of species chosen for the preliminary survey.

In a recent survey of a very similar type, Denys (1980) produced a tentative phytogeographical division of tropical Africa based on mathematical analysis of published maps. His complicated analysis of 494 taxa used factor analysis.

RESULTS AND DISCUSSION

Patterns of species richness

The first print-out using PHYTOTAB 10 provided a basic matrix for checking input data, but also provided totals of the number of species per quarter degree square and of quarter degrees per species. This appeared on all subsequent print-outs as a cross-check.

The total number of species per quarter degree square is shown in Fig. 3, but as a percentage of the total sample. Values are to the nearest whole number. Maps for each family and/or genus were produced by visual inspection of the print-out (Figs 4–12). Isoflor maps were produced for the three major families to show the nodes of species richness (Figs 3B, 4B, 5B & 7B).

Levyns (1938) was the first to show with a few small genera that the Caledon District is the centre

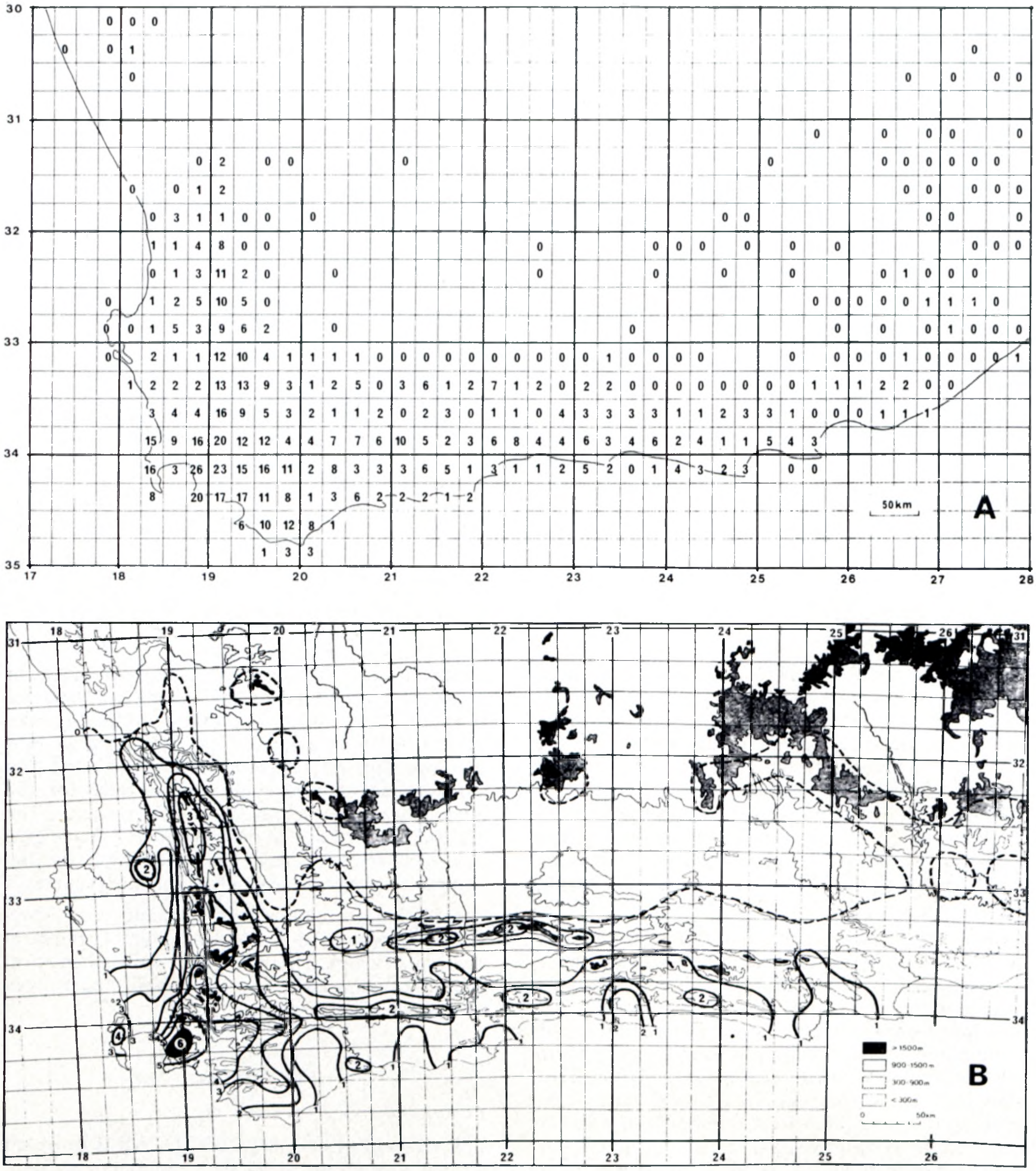

FIG. 3.—Distribution of the total number of species dealt with in this survey. A, expressed as a percentage to the nearest whole number per grid square (0 represents <1%); B, as isoflors (0–1 = 0–2%; 1–2 = 3–4%; 2–3 = 5–9%; 3–4 = 10–14%; 4–5 = 15–19%; 5–6 = 20–24%; 6 = 26%).

of species richness with a reduction in numbers to the north and east. She suggested that this pattern may be used to define true Cape genera. All our maps confirm this view. The more detailed analysis here indicates that the quarter degree, 3418 BB centred on Sir Lowry's Pass and the Hottentots-Holland Mountains is the richest area in the Cape Floral Region with 26% (476 species) of the sample. This includes 207 species of Ericaceae (with 175 species in the genus *Erica*), 74 species of Restionaceae and 70 species of Proteaceae.

This is a remarkable concentration of species and is made more so when one realizes that approximately 25% of the grid is sea and another 25% inhospitable flats. The remainder consists of mountain range rising from sea-level to 1 268 m within only three kilometres and an upland plateau at ± 450 m. In this grid square, all three geological formations of the Cape System occur, i.e. Table Mountain Sandstone, Bokkeveld Shale and Cape Granite. The average annual rainfall gradient is extreme from 700 mm on the flats to 3 600 mm at the

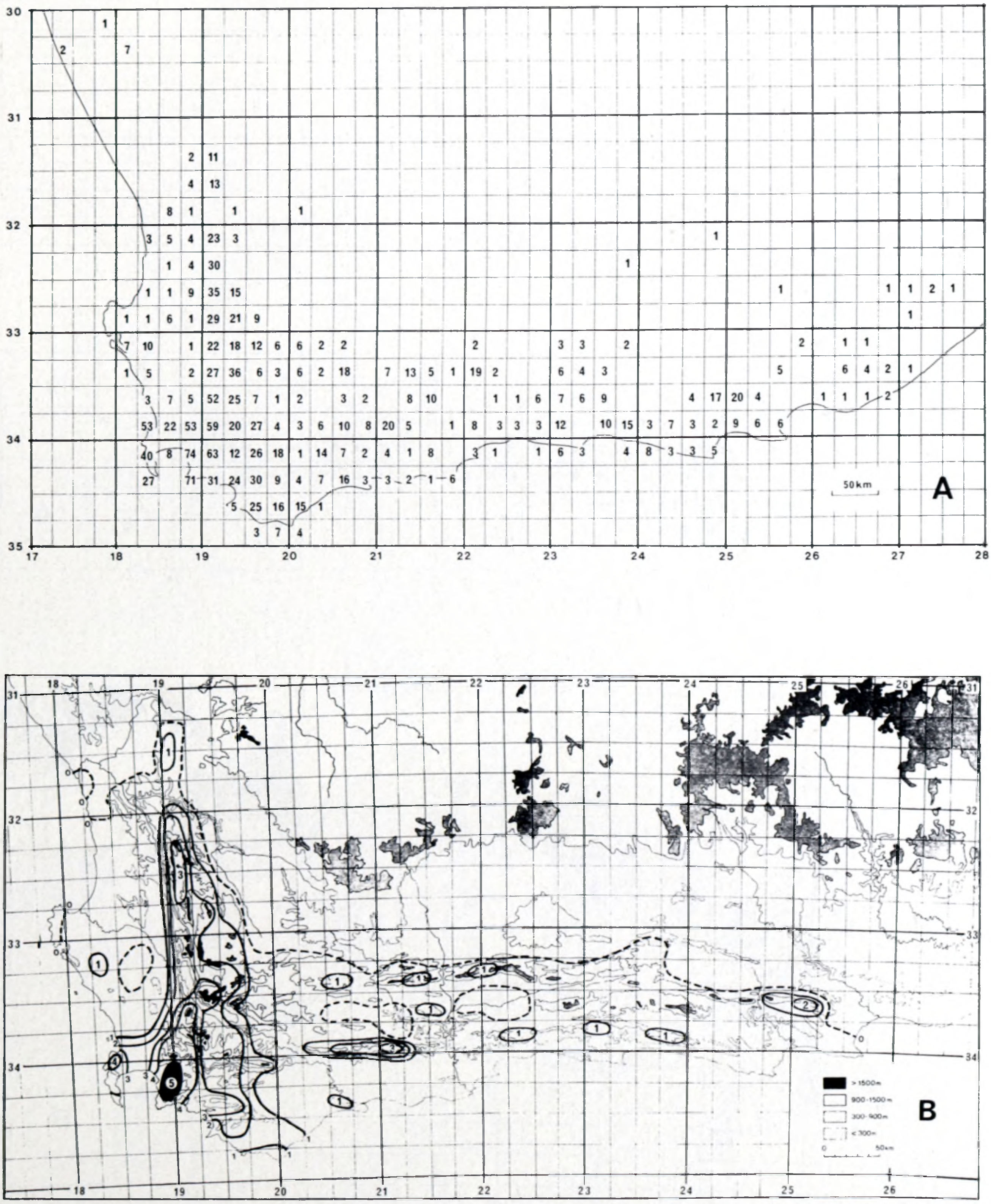

FIG. 4.—Distribution of Restionaceae. A, the number of species per grid square; B, as isoflors (0–1 = 0–9 species; 1–2 = 10–19 species; 2–3 = 20–39 species; 3–4 = 30–49 species; 4–5 = 50–69 species; 5 = 70 species→).

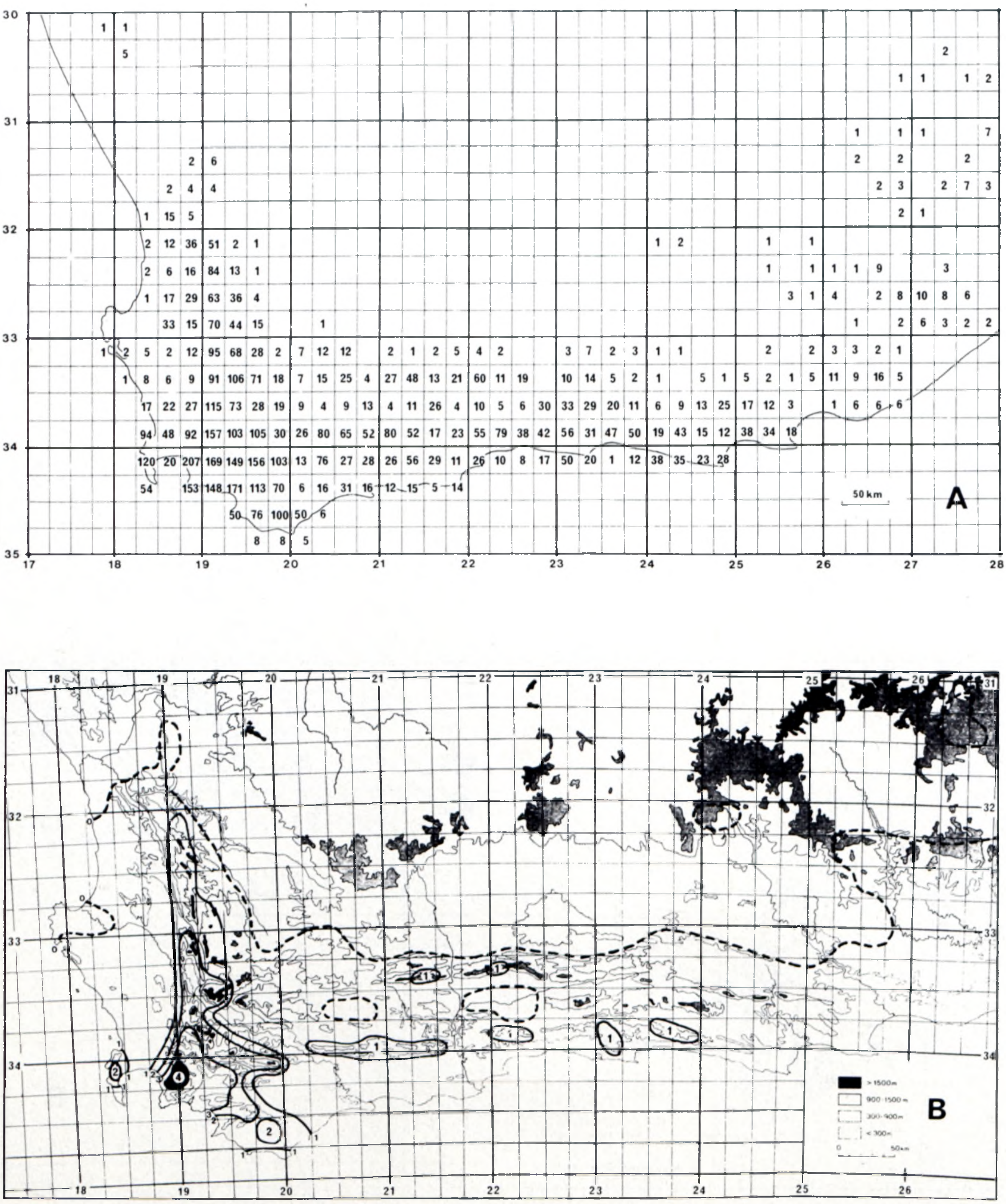

FIG. 5.—Distribution of Ericaceae. A, the number of species per grid square; B, as isoflors (0–1 = 0–49 species; 1–2 = 50–99 species; 2–3 = 100–149 species; 3–4 = 150–199 species; 4 = 200 species→).

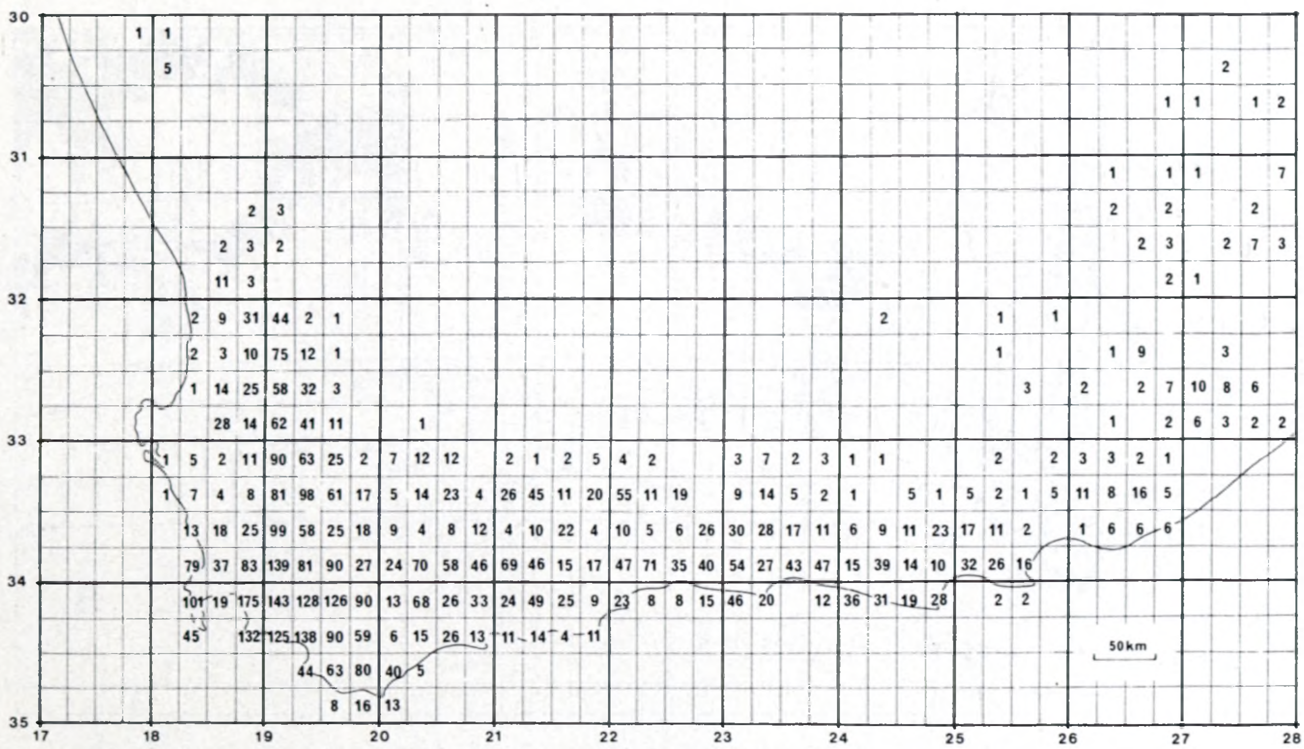

FIG. 6.—Distribution of the genus *Erica* with the number of species per grid square.

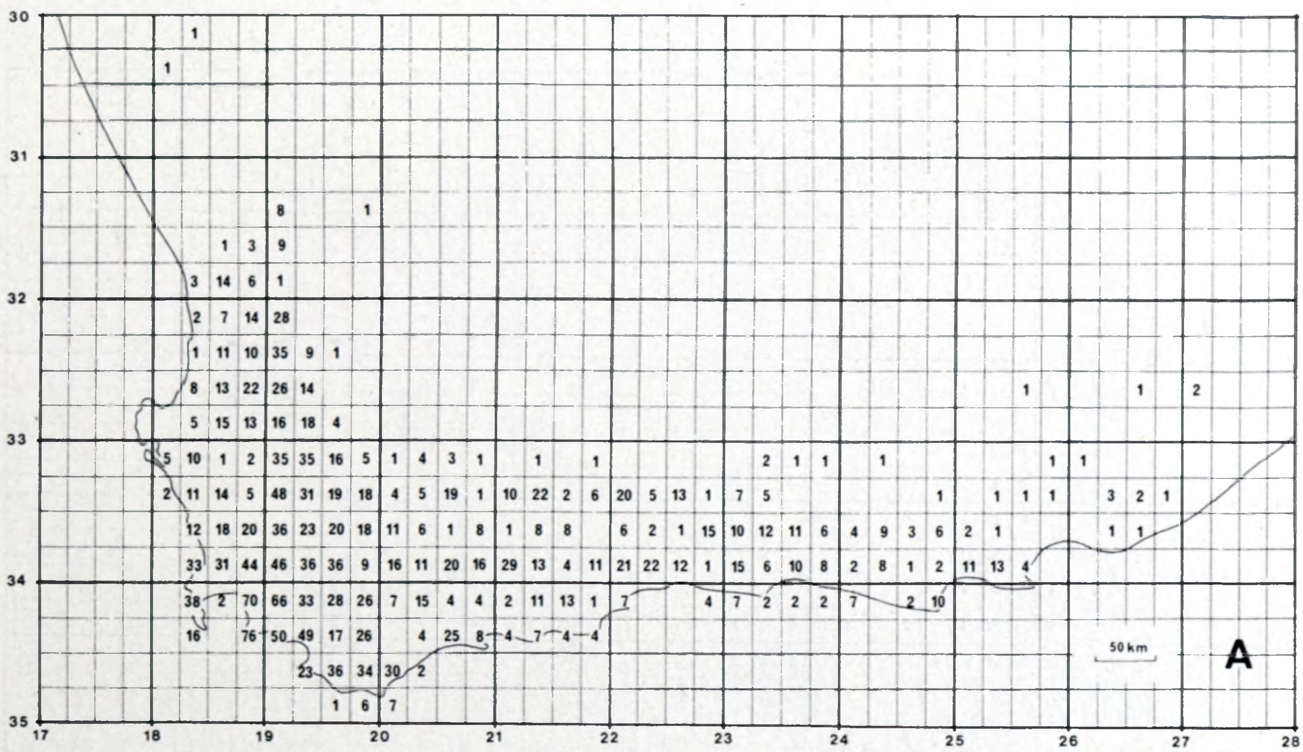

FIG. 7A.—Distribution of Proteaceae. The number of species per grid square.

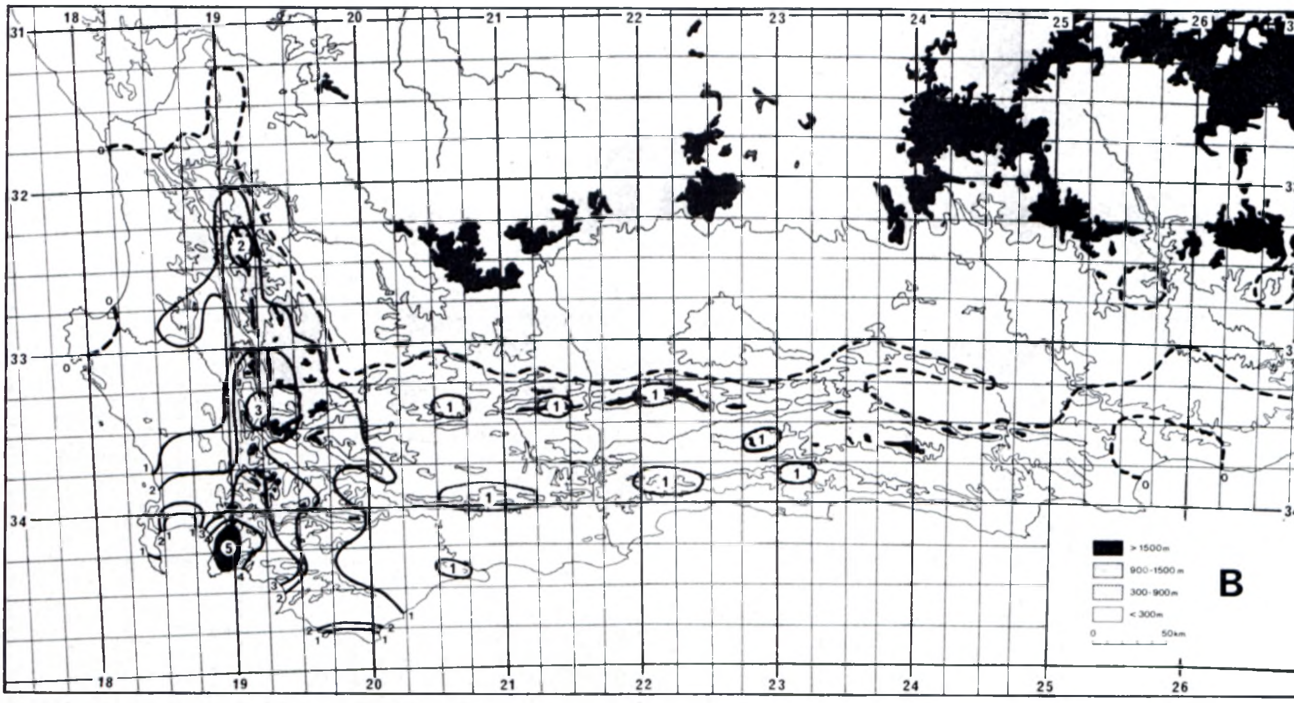

FIG. 7B.—Distribution of Proteaceae. As isoflors (0–1 = 0–14 species; 1–2 = 15–29 species; 2–3 = 30–44 species; 3–4 = 45–59 species; 4–5 = 60–69 species; 5 = 70 species→).

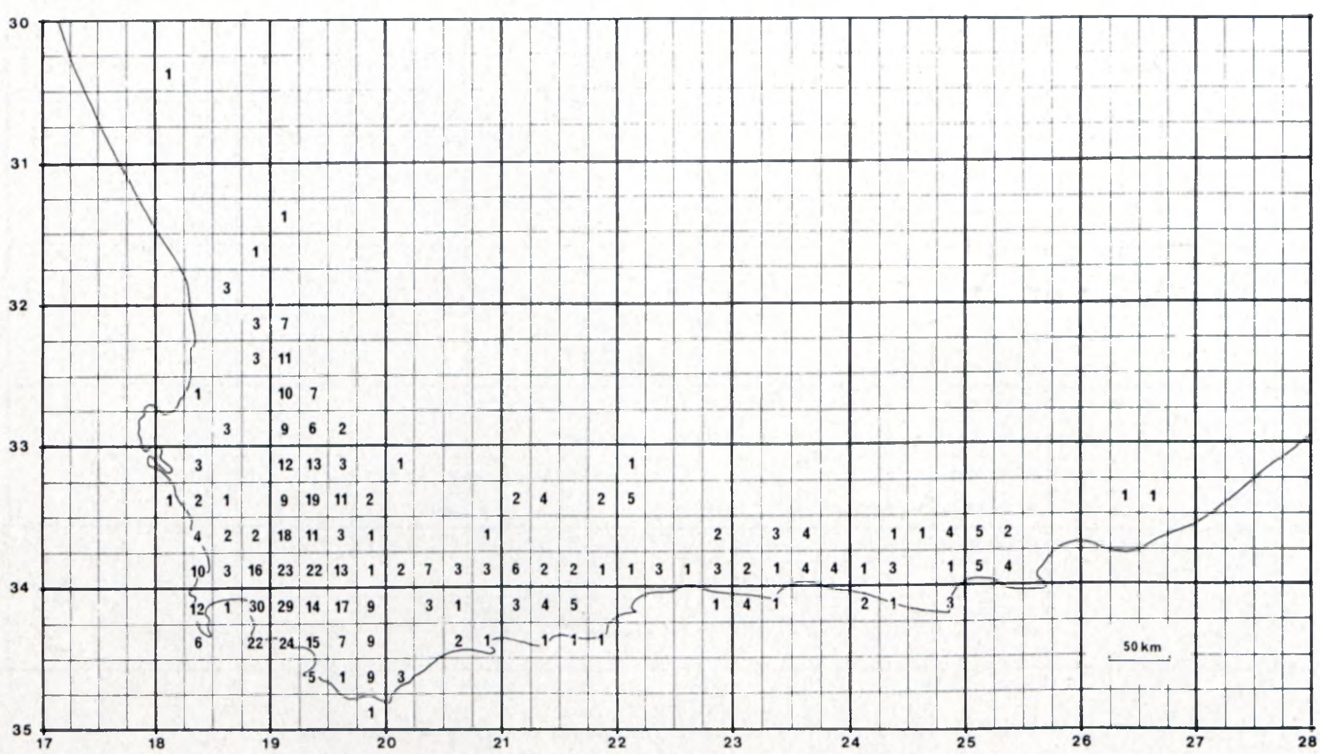

FIG. 8.—Distribution of Bruniaceae with the number of species per grid square.

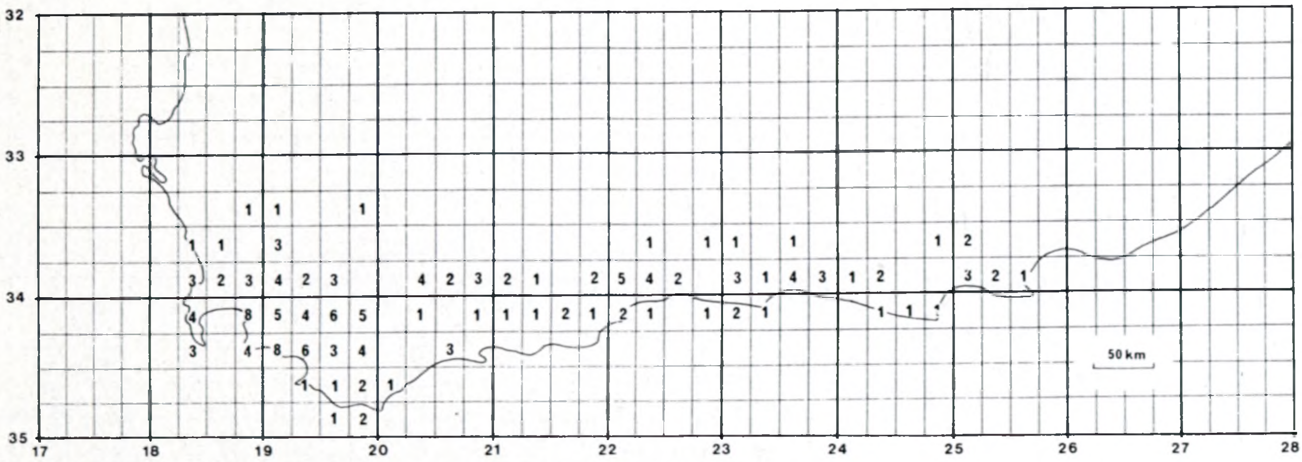

FIG. 9.—Distribution of Penaeaceae with the number of species per grid square.

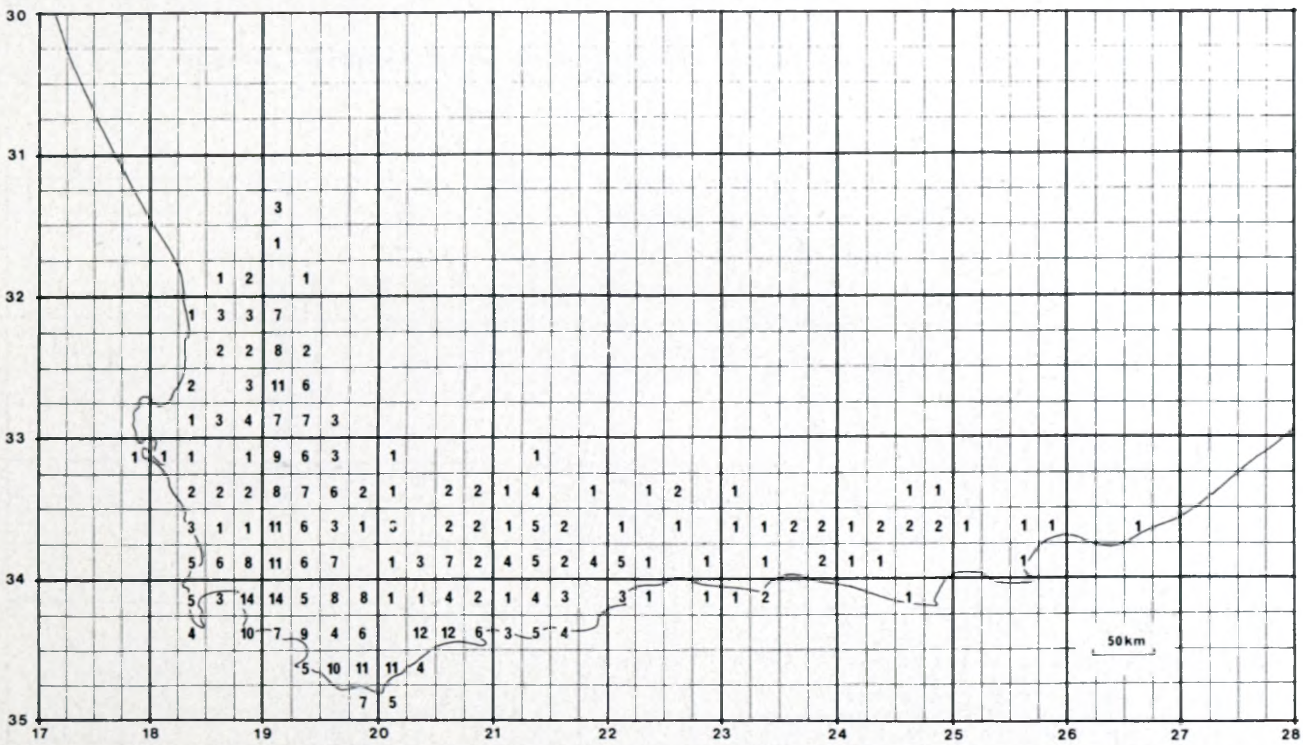

FIG. 10.—Distribution of the tribe Diosmeae (Rutaceae), excluding the genus *Agathosma*, with the number of species per grid square.

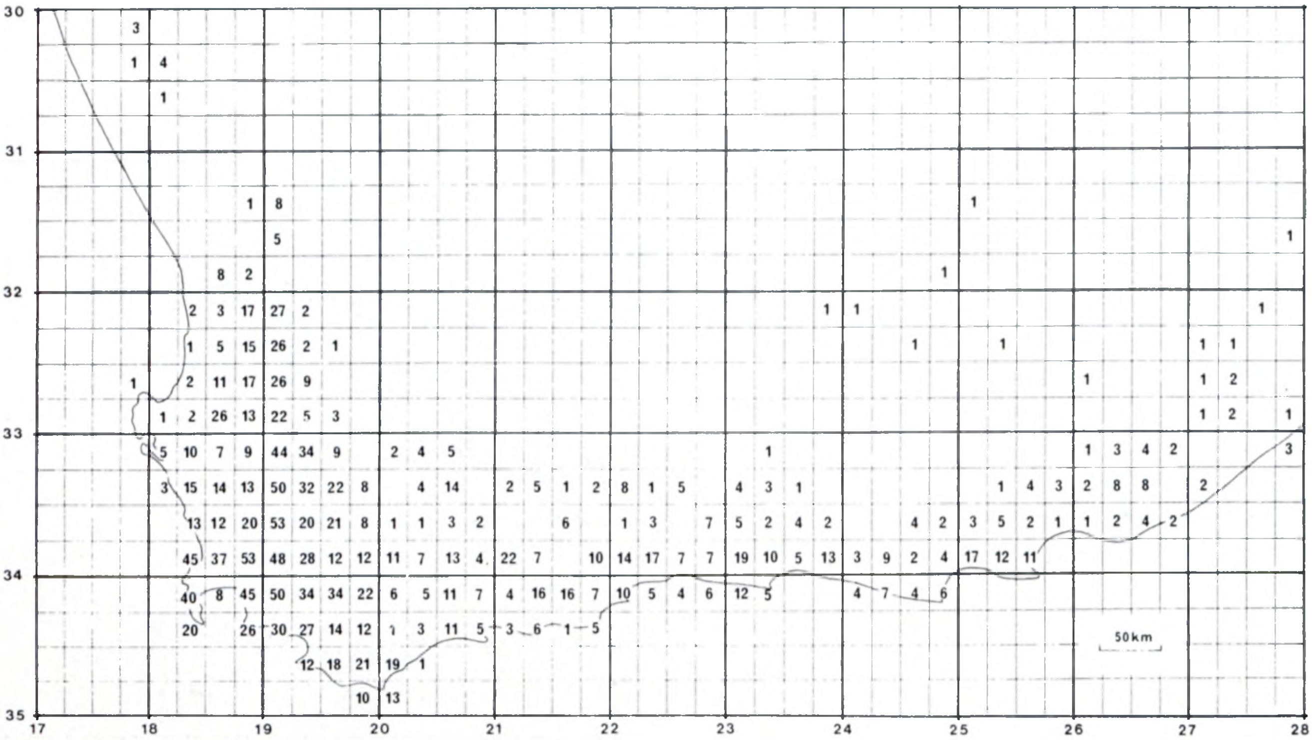

FIG. 11.—Distribution of the genus *Aspalathus* (Fabaceae) with the number of species per grid square.

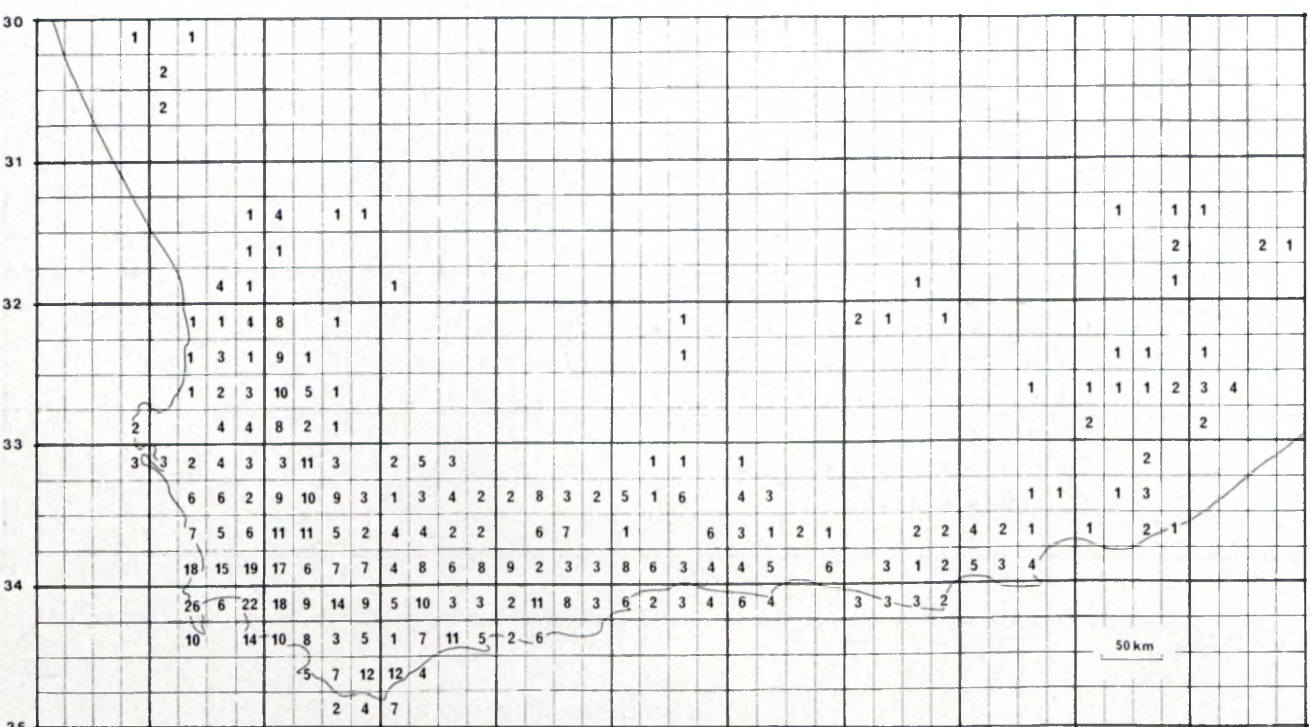

FIG. 12.—Distribution of the genus *Muraltia* (Polygalaceae) with the number of species per grid square.

highest point again within a very short distance. The precipitation pattern varies from summer drought regime to all-year rainfall on the summits caused by deposition of moisture from south-easterly clouds which is not recorded in the annual rainfall figure above (Marloth, 1904; Boucher, 1978).

The maps also indicate that there is a species richness gradient (1) from the Hottentots-Holland northwards to the Cedarberg, where there is a slight centre of richness (2) south-eastwards to the Bredasdorp/Agulhas area (3) eastwards along the main chain of mountains of the southern Cape, i.e. Langeberg/Outeniqua/Tzitzikama, to Port Elizabeth (4) an inland gradient along the Swartberg Range and (5) a centre of richness on the Cape Peninsula.

A word of caution should be expressed when looking at these results. To some extent the patterns produced are artifacts produced by uneven collecting. Herbarium records depend on the accessibility and 'popularity' of areas. Areas such as the Cape Peninsula, Sir Lowry's Pass, central Cedarberg are well collected. This is very evident in the eastern parts such as the Witteberg, Seven Weeks Poort, Swartberg Pass, Meirings Poort, Garcia's Pass and the Outeniqua/Montagu Pass. However, one could extrapolate these figures to the rest of the mountain ranges without affecting the results unduly.

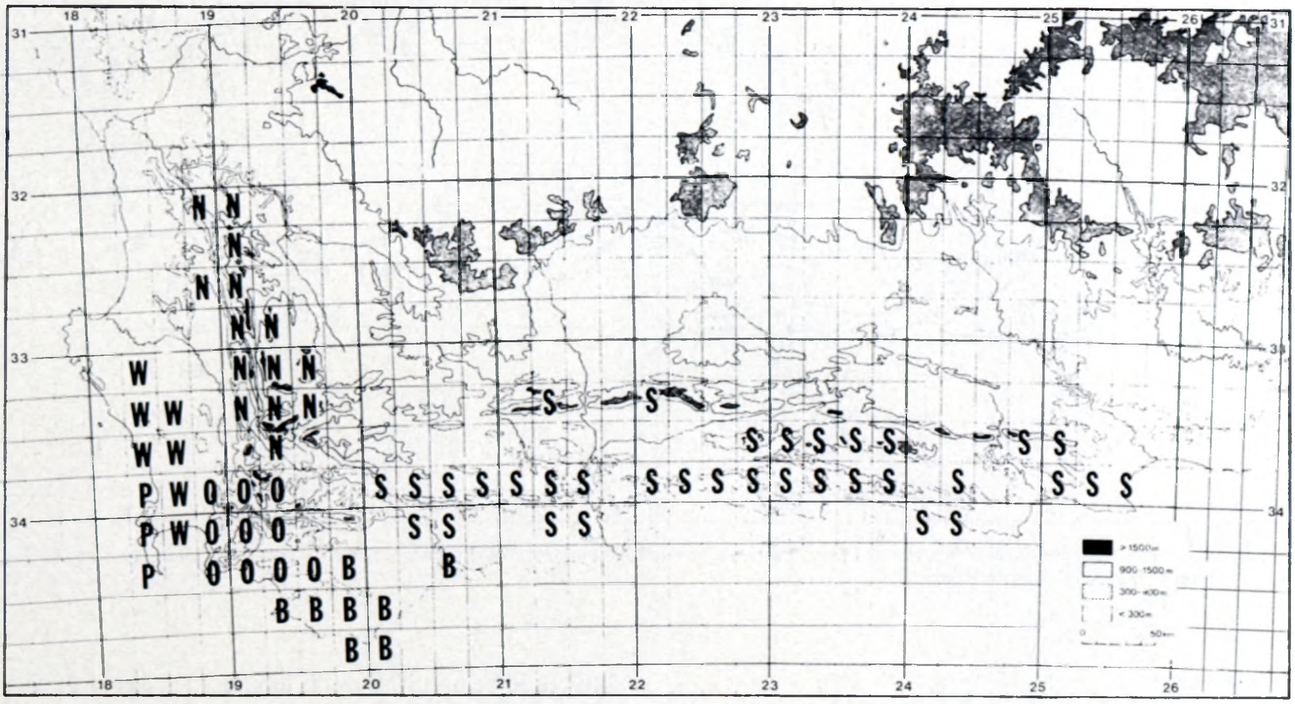

FIG. 13.—Phytogeographical centres in the Cape Flora as indicated by the present survey (N. Northern; W. West coastal; P. Peninsula; O. South-Western; B. Bredasdorp; S. Southern).

Phytogeographical centres

The next section of the program PHYTOTAB 20 grouped the grid localities wherever possible into large or small units which were then visually checked for grouping. The resulting six basic groups were plotted onto a grid map (Fig. 13). These groups covered six distinct separate areas which will be referred to as the Northern Centre, the Peninsula Centre, the South-western Centre, the West Coast Centre, the Bredasdorp Centre and the Southern Centre. Several areas of grid squares were not grouped in this program, due either to inadequate sampling and records or to their being intermediate between centres. The coastal flats of the north-west certainly group with the West Coast centre, and the southern coastal flats should be included with the Bredasdorp Centre.

The Rivier Zonder Eind mountains are probably intermediate between the South-western and Southern Centres, whereas the Robertson to Witteberg mountains are probably intermediate between the Northern, South-western and Southern Centres. Outliers in Namaqualand, the Karoo mountains and Eastern Cape mountains would be related to their nearest centres. These six centres agree with the major edaphic and climatic systems in the south-western and southern Cape outlined in Table 1.

On the whole, these centres agree with the centres defined by Weimarck (1941). (Fig. 14). His North-western Centre is clearly the same as ours.

We have a grouping equivalent to his South-western Centre which is bounded by the Berg River in the north and the Breede River in the east, but with a slight discrepancy in the Tulbagh area. However, very distinct groupings occurred within our centre that turn out to be equivalent to Weimarck's subcentres, i.e. Cape Peninsula, West Coast Flats, Central South-western Mountains and Bredasdorp.

The main discrepancy lies with the centres to the east where we are unable, in the preliminary sort, to obtain any really significant groupings. There were slight indications of groupings in the Langeberg, the Tzitzikama/Kouga area and the far south-east.

TABLE 1.—Phytogeographical centres indicated in this survey with the main edaphic and climatic conditions prevailing in each one (TMS = Table Mountain Sandstone)

Centre	Substrate	Climate	Rainfall (mm p.a.)
Northern	TMS mountains	Summer drought	300–1600 North 3000 South
West Coast	Recent TMS sand	Summer drought	200–500
Peninsula	TMS mountains	Winter rains Summer clouds	600–2400
South-Western	TMS mountains	Winter rains Summer clouds	700–3600
Bredasdorp	Recent calcrete and sand	Summer drought	300–700
Southern	TMS mountains	All year rain	300–1400

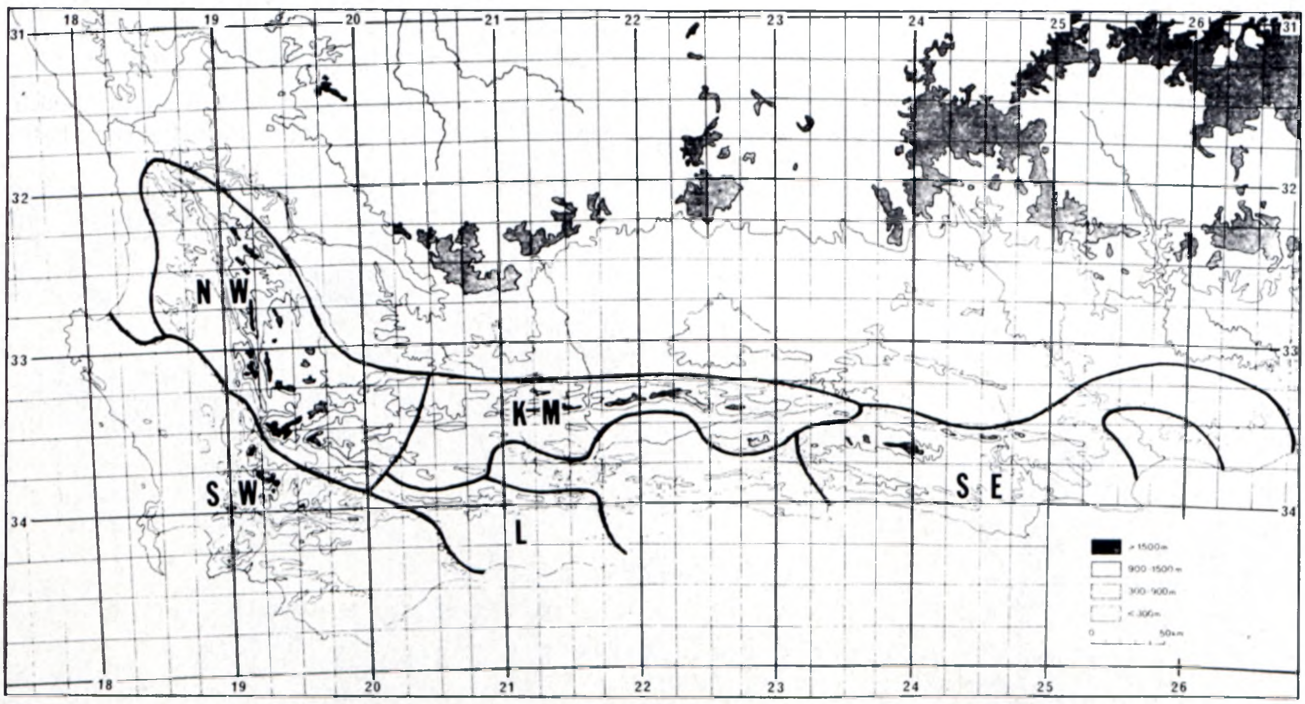

FIG. 14.—Phytogeographical centres in the Cape Flora according to Weimarck, 1941 (NW, North-western; SW, South-western; L, Langeberg; KM, Karoo Mountain).

Endemism

The Cape Flora is renowned both for the high degree of endemism to the Cape Floral Region and for a high degree of endemism locally. From a literature survey, Weimarck (1941) showed that of the 3 692 species represented within the Cape Flora 3 536, i.e. 95,8%, are endemic. Table 2 gives a summary of the endemism in the families and genera included in the present survey. With some 2 183 species endemic in the Cape Region out of an estimated total of 2 235 species represented in Africa a figure of 98% is obtained. This extremely high figure is unusual for a continental region being associated more with island floras. Raven & Axelrod (1978) give a figure of 47,7%, 2 125 out of 4 452 species, for the Californian Floristic Province. In South-western Australia endemism was estimated at 68%, 2 450 out of 3 637 species (Marchant, 1973), but could be up to 75–80% as genera are enlarged in new revisions (Hopper, 1979).

The impressive nature of the endemism in the Cape Flora is twofold; first is the large number of endemic species, but second and perhaps more remarkable, are the seven endemic families with one, the Bruniaceae, having as many as 75 species. These families are taxonomically distinct and some are isolated (Goldblatt, 1978) and are therefore good examples of ancient relics.

Local endemics should be treated with caution. Dahlgren (1963c) pointed out a comment made by Van Steenis that 'local endemic species loose their endemic character as soon as they are found elsewhere.' This is certainly true in the case of the Cape Flora, where more intensive collecting has brought to light new records but, on the whole, with

TABLE 2.—Endemism in the groups covered by this survey

	Genera in Africa	Endemic in Cape survey area	Species in Africa	Endemic in Cape survey area
Proteaceae (excl. *Faurea)*	12	9	393	336(85,5%)
Restionaceae	12	10	±400	386(95%)
Ericaceae-Ericoideae	24	19	826	765(93%)
Bruniaceae	12	12	75	74(95%)
Penaeaceae	7	7	21	21(100%)
Grubbiaceae	1	1	3	3(100%)
Geissolomataceae	1	1	1	1(100%)
Retziaceae	1	1	1	1(100%)
Rutaceae-Diosmeae (excl. *Agathosma)*	10	10	237	237(100%)
Aspalathus	—	—	255	251(98%)
Muraltia	—	—	115	108(94%)
Total			2235	2183(98%)

such a high degree of endemism, this is not likely to affect the overall picture to any extent.

Stebbins & Major (1965) state that discussions on endemism must involve the primary distinction between relic and newly evolved endemics. The endemism in the Cape Flora is high at species level, but also at generic and even at family level, the latter indicating the palaeoendemic nature of the Flora as a whole. It is difficult, however, to distinguish the relative age of the various centres. There is some indication that both the West Coast and Bredasdorp Centres are younger than the inland 'mountain' centres (Rourke, 1972; Oliver, 1977). Only one genus *Platycalyx* (Ericaceae) is known to be endemic to the coastal flats. This indicates that the coastal centres are neo-endemic centres relative to the 'montane' centres in which several families and genera are endemic i.e. Geissolomataceae, Roridulaceae and Retziaceae. This agrees with the known geological history of the coastal flats (Hendey, 1981). Analysis of the species covered in this survey into palaeo- or neoendemics is not possible at this stage, due to the incomplete state of our taxonomic knowledge of many of the genera.

CONCLUSIONS

There are four major phytogeographical patterns in the Cape Flora: (1) a concentration of species and diversity in the mountains of the south-western Cape with the number of species per unit area decreasing from this centre outwards, (2) a high degree of endemism to the Cape Floral Region both at specific and generic level and to a small extent family level, (3) the lack of generic endemism to the two coastal centres and (4) the existence of six centres within the Cape Floral Region which are correlated to the major edaphic and climatic systems within the region.

From an analysis of the phytogeographical patterns within the Cape Floral Region not much light is shed on the history of the Flora. Much of the present overall pattern, i.e. the delimitation of the centres and the high species numbers in the South-western Centre can be accounted for by ecological factors. The high taxonomic level of the regional endemism and the high degree of development of the centres indicate a remarkable evolutionary history *in situ* taking into account the relatively young age of the area as it exists at present and of its characteristic floral elements. This does not mean that the total area occupied by the Cape Flora did not fluctuate in the past as suggested by various authors (Levyns, 1964; Axelrod & Raven 1978), only that it has occupied the present area and has had sufficient time to develop into a very distinctive and complex flora.

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