

CHAPTER 4**BRYOGEOGRAPHIC REGIONS OF SOUTHERN AFRICA***Chapter Outline*

- A. Historical Perspective 110
 - I. Vascular plants 110
 - II. Bryophytes 119
 - III. Phytogeographic categories 122
- B. TWINSPAN Classification of Grid Squares 122
 - I. TWINSPAN complete classification 122
 - II. TWINSPAN 3+ and TWINSPAN 5+ classifications 126
 - Discussion 129
- C. Classification of the Bryogeographic Regions of Southern Africa 132
 - I. Introduction 132
 - II. Descriptions of Regions and Domains 133
 - 1. **Zambezi** Region 133
 - 1.1 Caprivi Domain 136
 - 1.2 Bushveld Domain 137
 - 2. **Afromontane** Region 138
 - 2.1 Drakensberg Domain 148
 - 2.2 Cape Domain 152
 - 3. **Karoo-Namib** Region 157
 - 3.1 Western Cape Domain 163
 - 3.2 Namaqua Domain 167
 - 4. **Highlands** Region 168
 - 4.1 Drakensberg Alpine Domain 173
 - 4.2 Upper Karoo Domain 176
- D. Indirect Gradient Analysis 177
 - I. Distribution of TWINSPAN regions in the ordination space 177
 - II. Compositional gradients 178

1. DCA scattergram of TWINSPAN 5+ grids	178
2. Geographic trends in the compositional gradients	178
III. Correlation with environmental variables	181
Discussion	186

A. Historical Perspective

Phytogeographic classifications have generally been based on the distribution of vascular plants only. The global phytogeographic classifications of Engler & Diels (1936), Good (1974) and Takhtajan (1986) have recently been compared by McLaughlin (1994). Detailed accounts of the history of phytogeographic divisions of (southern) Africa are given by Monod (1957), Werger (1978), Denys (1979), Friis (1986) and Iversen (1991). The latter provided an useful list of the most important phytogeographic classifications of Africa. A short synopsis for the southern African region is provided by Cowling & Hilton-Taylor (1997). Hilliard & Burtt (1987) reviewed the phytogeographic divisions of the southern KwaZulu-Natal Drakensberg. Some of the most important global and regional, contemporary classifications of floristic regions are briefly discussed here while regional subdivisions are generally considered under the relevant Regions and Domains (section C of this chapter). A distinction is made between phytogeographical classifications largely based on the geographic distribution of vascular plants and those based on the distribution of bryophytes.

I. Vascular plants

Known for his important plant collections, including bryophytes, from southern Africa (Dixon & Gepp 1923, Bayer 1971, Magill 1980, Gunn & Codd 1981, Codd & Gunn 1982), Antoni Rehman's contribution to the phytogeography of the region is not always appreciated (Zemanek & Zemanek 1990). In 1880 Rehman published *Phytogeographical conditions in South Africa* (Rehman 1880, in Polish) in which he described and mapped seven phytogeographic provinces in southern Africa (see map in Werger 1978):

The phytogeographic provinces of Rehman (1880)

Kalahari
 Highveld
 Monsoon Area
 Forest Region
 Roggeveld
 Karoo
 S.W. Cape

Frank White (1927-1994) of Oxford, United Kingdom (Gunn & Codd 1981, Angus & Chapman 1996) dominated the phytogeographic scene in Africa for the past 30 years. His early classifications (White 1965, 1970, 1971) were hierarchical and recognised six Regions in southern Africa, some of them represented by Domains:

Phytogeographic regions of southern Africa according to the hierarchical classification of White (1965, 1970, 1971)

1. Sudano-Zambezi Region, represented by the Zambezi Domain
2. Guineo-Congolian Region represented by the Usambara-Zululand Domain
3. Afro-montane Region
4. Afro-alpine Region (not mapped)
5. Karoo-Namib Region
6. Cape Region.

In 1976 White departed from a hierarchical classification system and introduced the rather confusing concepts of Regional centres of endemism, Archipelago-like centres of endemism, Regional mosaics, and Regional transition zones (White 1976). These phytogeographic categories are characterised as follows:

- 1) A regional centre of endemism has more than 50% of its species restricted to it and a total of more than 1000 endemic or near endemic species.
- 2) An archipelago-like regional centre of endemism only differs from the other regional centres of endemism in its fragmented distribution.
- 3) Regional transition zones separate regional centres of endemism and are characterised by less than 1000 endemic species, representing less than 50% of the total flora.
- 4) Regional mosaics cannot be categorized as any of the preceding and consist of a mosaic of distinct vegetation types and “.. a small amount of intermingling of otherwise distinct floras.” (White 1993).

In 1976 White (1976) also introduced a 7th phytochorion, the Kalahari-Highveld regional transition zone. In his publication *The Vegetation of Africa* (White 1983), which White himself called “A milestone in the history of African botany...”, he described the vegetation types of Africa and Madagascar “...within a regional chorological framework” (White 1983). With this publication White emphasized the similarities between the structural and floristic classifications of plants in the subregion. The following non-hierarchical phytochoria ‘of equal rank’ were now recognised by White (1976, 1983), see Fig. 17:

The non-hierarchical phytochoria of southern Africa according to White (1976, 1983).

Regional centres of endemism:

1. Zambezian
2. Karoo-Namib
3. Cape

Archipelago-like centres of endemism

1. Afro-montane
2. Afro-alpine (not mapped)

Regional mosaic

Tongaland-Pondoland

Regional transition zone

Kalahari-Highveld

The phytochorological classification of Africa by White (1976, 1983) is today widely accepted and forms the basis of other contemporary classifications, e.g. those of Goldblatt (1978) and Cowling & Hilton-Taylor (1997).

I largely agree with Linder (1990), who criticized the following aspects of White's phytochorological classifications:

- 1) The phytochoria are based on dominant taxa only.
- 2) The classification is influenced by historical developments in African phytogeography.

To these I would like to add that White's phytochorological classification is largely subjective and does not satisfy the current requirements of objectivity and repeatability.

Good (1974) recognised six Kingdoms (Boreal, Palaeotropical, Neotropical, South African, Australian, Antarctic) and 37 Regions in his phytogeographical classification of the world. His South African Kingdom, restricted to the south-western tip of Africa, contained a single Region, the Cape Region. The rest of southern Africa was covered by the South African and East African Steppe Regions, both of the Palaeotropical Kingdom. The South African Region is more or less restricted to the study area and described by Good (1974) as a transition zone between the 'tropical African flora' and the 'southern Mediterranean flora'. Good's East African Steppe Region is restricted to the north-eastern corner of South Africa and is characterised by savanna vegetation. The South African Region is subdivided into five 'parts' (Good 1974).

Phytogeographical division of southern Africa by Good (1974)

South African Kingdom

Cape Region

Paleotropical Kingdom

5) East African Steppe Region

6) South African Region

along the coast High veldt of the Transvaal and the Orange Free State

The Kalahari

The Karroo

Namaqualand and Damaraland

Natal and the eastern Cape Province.

In *A Classification of the Biogeographical Provinces of the World*, based on similarities in floral, faunal and ecosystem composition, **Udvardy** (1975) divided the world into eight biogeographic Realms instead of Kingdoms:

The Biogeographic Realms of Udvardy (1975)

Palaeartic Realm

Nearctic Realm

Africotropical Realm

Indomalayan Realm

Oceanian Realm

Australian Realm

Udvardy's (1975) Afrotropical Realm (Fig. 18) covers the whole of sub-Saharan Africa and is subdivided into 29 biogeographic Provinces, largely based on the classification of **Dasmann** (1974). Udvardy's biogeographical classification of Africa was followed in *The IUCN Directory of Afrotropical Protected Areas* (IUCN/UNEP 1987). It appears that 6 of these provinces are present in the FSA area (Fig. 18):

- 1) South African Woodland/savanna Province in the northern and eastern parts of the study area.
- 2) Cape Sclerophyll Province along the Cape Fold Mountains.
- 3) Namib Province along the Namibian coast.

- 4) Kalahari Province in the northern interior.
- 5) Karroo Province along the Cape west coast and interior.
- 6) South African Highlands covering Lesotho and the high altitude plateau along the eastern escarpment.

Werger (1978) analysed the phytogeographic divisions of Africa up to the mid 1970s and came up with a composite classification for southern and south-eastern Africa (Fig. 19). The whole area was divided into two main units: 1) Capensis restricted to the south-western corner and 2) the Palaeotropis Subkingdom in the remainder of the subcontinent. The following regions are recognised in the FSA area:

- 1) The Indian Ocean Coastal Belt represented by the Tongaland-Pondoland Regional Mosaic.
- 2) Sudano-Zambezian Region represented by the Zambezian Domain.
- 3) Afromontane Region.
- 4) Afro-alpine Region represented by the Austral Domain.
- 5) Karoo-Namib Region subdivided into four Domains and one Subdomain.
- 6) Capensis.

The first more or less objective, numerical phytogeographic classification of tropical and subtropical Africa was presented by Denys (1979, 1980). She based her classification on a factor analysis of plant distributions mapped in the *Distributiones Plantarum Africanarum* series, edited by P. Bamps (Denys 1979, 1980). This purely floristic approach included the liverwort family Frullaniaceae and the moss family Thuidiaceae. Denys (1980) identified the following Regions, Subregions and Domains in tropical Africa (Fig. 20):

The phytogeographic divisions of Denys (1980)

Guineo-Congolian Region

Upper-Guinea Domain

- Lower-Guinea Domain
- Congo Basin Domain
- 1) Holocene Guinea-Congolia/Sudania Transition Region
 - 2) Palaeotropical Sudanian Region
 - 3) Neotropical Southern Subregion
 - 4) Cape Kingdom Northern Subregion
 - 5) African Region of the Central African Lakes
 - 6) Tuluana Guinea-Congolia/Zambezia Transition Region
 - Zambezia Region
 - Region of the Indian Ocean Coastal Belt
 - Afromontane Region
 - Madagascan Region
- Occidental Domain
- Oriental Domain

Denys's classification largely confirmed the phytochoria of White (1983) but without clear support for his regional mosaics. Unfortunately her study excluded the largest part of southern Africa and only the Afromontane Region and a small part of the Zambezian Region is mapped in this area. The Afromontane Region was subdivided by Denys (1980) into seven Domains (see *Discussion* under the *Afromontane Region*, this chapter, and Fig. 21).

In a numerical analysis of the geographical distribution of Cape taxa **Oliver et al.** (1983) identified six phytogeographic areas or regions in the 'Cape Floral Region'. These regions, or 'elements' as they were called, were compared with the endem-centres of Weimarck (1941), which are not floristic regions but distribution centres within the Cape element. The six areas delimited by Oliver *et al.* (1983) are: 1) the Northern Centre, 2) the Peninsula Centre, 3) the South-western Centre, 4) the West Coast Centre, 5) the Bredasdorp Centre, and 6) the Southern Centre. These areas are generally below the level of Domain.

Takhtajan (1986) divided the world into six kingdoms:

- 1) Holarctic Kingdom (Holarctis).
- 2) Paleotropical Kingdom (Paleotropis).
- 3) Neotropical Kingdom (Neotropis).
- 4) Cape Kingdom (Capensis).
- 5) Australian Kingdom (Australis).
- 6) Holantarctic Kingdoms (Holantarctis).

The Cape Kingdom is the smallest of the six and restricted to the southernmost tip of Africa. The rest of sub-Saharan Africa is covered by the 'Paleotropical' Kingdom. The whole of southern Africa is divided into four of Takhtajan's 35 Regions, subdivided into subregions and provinces:

The phytogeographic subdivision of southern Africa by Takhtajan (1986)

- 1). The Cape Region in the extreme south-west represented by a single Cape Province.
- 2). The Karoo-Namib Region along the arid western coast, subdivided into 4 provinces (Namib, Namaland, Western Cape and Karoo) similar to the KarooNamib domains of Werger (1978).
- 3). The Sudano-Zambezian Region occupies subtropical Africa and is subdivided into a northern Sahelo-Sudanian Subregion and a southern Zambezian Subregion. The latter is represented in southern Africa by a single province, the Zambezian Province, which occupies much of the central and northern parts of the study area
- 4) The Uzambara-Zululand Region which runs along the southeastern coast of Africa and consists of a northern Zanzibar-Inhambane Province (not present in the study area) and a southern Tongoland-Pondoland Province.

In order to determine the conservation status of the Fynbos and Karoo Biomes **Hilton-Taylor & Le Roux** (1989) provided a combined structural and floristic classification of this area. Their map shows 25 "...biogeographic areas of the

fynbos, succulent karoo and Nama-karoo biomes.”. They explained that “The boundaries are based on Weimarck (1941), Oliver *et al.* (1983) and Hilton-Taylor (1987) with modifications based on Acocks (1953, 1975)”, therefore a mixture of floristic regions (Oliver *et al.* 1983, Hilton-Taylor 1987), floristic elements and distribution centres (Weimarck 1941), and vegetation types (Acocks 1953, 1975).

Phytogeographic patterns in the Corycinae, a group of orchids mainly distributed in southern Africa, were determined by Kurzweil *et al.* (1991). A numerical analysis of the data set “...to determine the relationships among the degree squares ...” revealed three main floristic regions in southern Africa, which Kurzweil *et al.* (1991) referred to as ‘centres’. They are: 1) the Namaqualand area, 2) the Cape Floristic Region, and 3) the Drakensberg. They also identified a number of floristic elements or ‘centres of endemism’ which are listed in Chapter 5 under *Historical Perspective*.

Oliver (1994) studied geographic distribution and endemism in the largely southern African subfamily Ericoideae (Ericaceae). Similarities and differences among the ericaceous floras of 12 subjectively chosen ‘centres’ were analysed using Jaccard’s coefficient and the classification program TWINSpan respectively. Oliver (1994) recognised five main areas or regions with distinct Ericoideae floras and high levels of species endemism which he called ‘Regional Centres of Endemism’. He suggested that the Cape Centre be included in a broad Afrotemperate Region.

The Regional Centres of Endemism based on the distribution of the subfamily Ericoideae (Ericaceae)

Herzog (1926) provided a comprehensive analysis of the geographic problems in his *Geographische Pflanzenwelt der Südafrika* and mentioned the bryogeographic classification of the Cape Centre. The *Regional Centres of Endemism* based on the distribution of the subfamily *Ericoideae (Ericaceae)* are briefly reviewed here:

- Cape Centre
- Drakensberg Centre
- Tropical Afromontane Centre
- Madagascan Centre
- North African/European Centre

In a recent review of the phytogeography of southern Africa **Cowling & Hilton-Taylor** (1997) adopted the floristic regions of **Goldblatt** (1978), who followed **White** (1976, 1978) with minor changes to the boundaries of the Cape Region. **Goldblatt** (1978) and **Cowling & Hilton-Taylor** (1997) have given their phytochoria the rank of Region except for the Kalahari-Highveld phytochorion which they called a Transition Zone after **White** (1976, 1978, 1983). Although the Afro-alpine Region is included within the Afromontane Region, **Cowling & Hilton-Taylor** (1997) admit that such an approach remains problematic. They recognise the following 6 regional phytochoria (see Fig. 22):

The phytogeographic regions of Goldblatt (1978) and Cowling & Hilton-Taylor (1997)

Zambezian Region
 Kalahari-Highveld Transition Zone
 Karoo-Namib Region
 Tongaland-Pondoland Region
 Afromontane Region
 Cape Region

II. Bryophytes

Werger (1978), in his historical review of phytogeographic divisions in Africa, mentioned the bryogeographic classifications of **Herzog** (1926) and **Ochi** (1973). These, as well as other bryogeographic classifications published since 1978, are briefly reviewed here.

Herzog (1926) provided the first comprehensive analyses of bryophyte distribution patterns in his *Geographie der Moose*. He did not include a map of his bryogeographic regions but **Miller** (1982) created a map from **Herzog's** descriptions (Fig. 23). The following six kingdoms were recognised by **Herzog** (1926):

Herzog's Florenreiche (Herzog 1926)

- Holarktisches Florenreich
- Neotropisches Florenreich
- Paläotropische Florenreich
- Australisches Florenreich
- Austral-antarktisches Florenreich
- Südafrikanisches Florenreich

According to the map in Miller (1982), Herzog's Südafrikanisches Florenreich included the whole of the FSA area. The recent vascular plant Kingdoms of Good (1974) and Takhtajan (1986) are remarkably similar to Herzog's Florenreiche.

Ochi (1973) based his bryogeographic division of Africa and adjacent islands on the geographic distributions of mosses in the subfamily Bryoideae (family Bryaceae). He took the geographic recording system of Van der Wijk *et al.* (1969) as a starting point to divide the area into four main regions (Fig. 24):

- 1) Afr I in the north (Sahara).
- 2) Afr II covering tropical and subtropical Africa, the west African islands, and eastern Indian Ocean islands including Madagascar, the Seychelles and the Mascarenes.
- 3) Afr III in the south.
- 4) KERG for the subAntarctic islands of Kerguelen, Prince Edward and Crozet.

Afr I was subdivided into two subregions and Afr II into five. The boundary between Afr II and Afr III is rather artificial but seems to enclose the whole of the study area in Afr III.

Miller (1982) adopted Good's classification of Floristic Regions (Good 1974) in his discussion of the phytogeography of the bryophytes. He found that the "...austral nature..." and "...high endemism rate" of the Cape bryoflora could not be

explained satisfactorily by contemporary hypotheses. Miller (1982) proposed that the Cape Fold Mountains represents a Gondwana island which caught up with the African mainland in the late Cretaceous or early Tertiary. Migration in and out of the unique flora of the “...long separated Cape Island” was supposed to be limited by ecological processes.

The rest of the study area is covered by the whole of Miller’s South African Region and the southernmost tip of his East African Steppe Region, both classified under the African Subkingdom of the Palaeotropical Kingdom (Miller 1982).

Schofield’s tentative Bryophyte floristic kingdoms (Schofield 1992) are essentially those of Herzog (1926), modified by incorporating recent distribution data. The floristic kingdoms are based on “...floristic similarity, with emphasis on families and genera unique to the Kingdoms, and on the degree of endemism, at the species level” (Schofield 1992). The following six bryofloristic kingdoms are recognised (Fig. 25):

Bryophyte floristic kingdoms of Schofield (1992)

- Holantarctic kingdom
- South African kingdom
- Australian kingdom
- Neotropical kingdom
- Palaeotropical kingdom
- Holarctic kingdom

Almost the whole of the FSA area is included in the South African Kingdom, the smallest of the six kingdoms. This kingdom was found to contain a “...highly distinctive bryoflora, especially in the mosses.” and is characterised by “...the endemic monotypic family Wardiaceae and at least 10 endemic genera, most of which are monotypic.” Schofield (1992) also pointed out that many of the endemic genera are small, short-lived mosses adapted to arid conditions, similar to many

genera in the Australian flora. He found that the (Schofield 1992) “Affinities of the South African flora are predominantly with continental Africa....”.

III. Phytogeographic categories

The following phytogeographic categories, in descending order, are widely used in hierarchical classifications of the world (See White 1970, Takhtajan 1986 and McLaughlin 1994):

1. Kingdom or Realm
2. Region
3. Province or Domain
4. District

3. Subdivisions of the main categories, viz. subkingdom, subregion, subprovince and subdistrict, are also used. The formal categories of Region and Domain are assigned to the bryogeographic regions described in this study.

B. TWINSpan Classification of Grid Squares

TWINSpan classification of grid squares into southern African floristic or phytogeographic regions (floristically homogeneous geographic areas or areas of similar floristic or species composition within southern Africa).

I. TWINSpan Complete classification

The TWINSpan Complete data set, consisting of the presence/absence of the 503 moss species/infraspecific taxa in each of the 416 grid squares, was divided into 11 groups after the 6th level of TWINSpan division. The dendrogram resulting from the TWINSpan Complete classification is shown in Fig. 26.

1. First level of division

The first and major TWINSpan Complete division separated grids 1816 D in northern Namibia and 2023 B near Maun in northern Botswana (Figs. 26 & 27, region 1/2 or end group 11) from the rest of the grids in the study area. These two grid squares are under-collected and contain a single species, *Plaubelia involuta* (Pottiaceae), a southern African endemic restricted to end group (or floristic region) 11.

2. Second level of division

At the second level of division, grid 3127 A in the Dordrecht area of the Eastern Cape province (Figs. 26 & 27, region 2/1 or end group 1) is split off from the remainder of the grids. This grid is distinguished by the narrow endemic *Pseudoleskeopsis unilateralis* (Leskeaceae), the only species recorded.

3. Third level of division

At the 3rd level of division grid 2818 B in southern Namibia was distinguished as floristic region (end group) 10 (Figs. 26 & 27) on the presence of the narrow endemic *Archidium dinteri* (Archidiaceae). Only this single species has so far been recorded from the locality.

4. Fourth level of division

It is only at the fourth level of division that the TWINSpan classification divides the remaining grids into two main groups (Fig. 26). Region 4/2 (fourth level of division group 2, consisting of end groups 2-5) represents the largest group of 287 grids that occupies the eastern part of southern Africa. Region 4/3 (end groups 6-9) form the smaller group of 135 grids, concentrated in the semi-arid to arid western and central parts of the study area (Fig. 28).

The groups have adjacent grids more or less grouped together along the eastern, southern and western borders of the study area. In the central and northern parts, however, the grids are non-contiguous, partly as a result of the many empty grids. The division line between the two groups is not very clear, mainly as a result of outliers and empty grid squares (Fig. 28).

5. Fifth level of division

At this level of division, region 5/2, consisting of 17 non-contiguous grids in the northern parts of southern Africa (Figs. 26 & 29), is separated from the rest of the eastern group (region 5/3). On the other side of the main division line region 5/5, consisting of 11 non-contiguous grids scattered down the centre of Namibia, from Otjiwarongo in the north to Augrabies in the south (Figs. 26 & 29), is split off from the western group (region 5/4).

After the fifth level of division the majority of grids still belong to one of the two main groups distinguished at the fourth level.

6. Sixth level of division

At the sixth and final level of division the grid squares have been divided into 11 end groups or regions (Fig. 26). Region 1 (grid 3127 A) has already been split off at the second level of division. At the first dichotomy TWINSpan separates end group or region 3 (three grids in northern Botswana and two grids in the north-eastern corner of the Northern province) from end group 2, consisting of grids scattered across the northern parts of the study area (Fig. 30). Region 3 is characterised by *Erpodium beccarii* (Erpodiaceae), a woodland epiphyte which occurs in all five of the grids. The next dichotomy separates a single grid square as region 4 from the rest of the grids in the large eastern group or region 5 (Fig. 30). This grid (2429 C) contains a single species, *Weisiopsis plicata* (Pottiaceae), which is restricted to three grids in the Northern province of South Africa .

Region 5, the largest floristic region distinguished by the TWINSpan Complete classification of grid squares, has several outliers in the central and northern regions of the study area (Fig. 30). These outliers are species poor grids, many with single species recorded from them (e.g. 1712 B, 1712 D, 1914 D, 1915 C, 1922 C, 2716 A, 2917 C, 2919 B and 3112 D), and are most probably under-collected. The rest of the grids in region 5 are more or less contiguous along the eastern and southern borders of the study area, from the Soutpansberg in the north to Table Mountain in the south-west (Fig. 30).

The other major group distinguished by TWINSpan at the 5th level of division (region 5/4), spread over the western and central parts of South Africa, is here subdivided into an eastern and a western region (Fig. 26). Region 6 is situated along the West Coast, roughly from Lüderitz on the Namibian Coast in the north to Malmesbury in the south and extending eastwards along the southern edge of the Great Karoo (Fig. 30). Several outlying grids to the east and north (e.g. 2117 D, 2217 D, 2516 A, 2525 C, 2616 C, 2624 C, 2720 C, 2926 B etc.) represent less than three species each. Region 7 is a high-altitude, low July and annual mean temperature area, scattered over the central parts of South Africa, from the Lesotho Highlands eastwards (Fig. 30).

The last dichotomy at the 6th level (Fig. 26) divides the already non-continuous region 5/5 into a northern group (region 8) and a southern group (region 9). Most of the grid squares in these two regions have less than three species recorded from them (2016 D, 2117 C, 2317 A, 2318D, 2426 D, 2417 C, 2417 D, 2718 B and 2820 C), while one grid contains less than five species (2216 D), and another (2116 D) six species (Fig. 30).

Discussion

From the results of the TWINSpan Complete classification it is clear that TWINSpan is sensitive to species-poor grids, especially those containing single narrow endemics or taxa of limited geographic distribution in the study area. This phenomenon, where instead of a first division in the middle, small groups of sample points are split off by TWINSpan from the main data set, was also reported by Gauch & Whittaker (1981) and Van Groenewoud (1992). The latter blamed the problem on the displacement of sample points along the ordinations (Van Groenewoud 1992) while in the case of Gauch & Whittaker (1981) it could have been caused by the presence of outliers. I therefore decided to remove some of the outliers from the TWINSpan Complete data set by deleting grids which contain less than three species, resulting in the TWINSpan 3+ data set, and grids with less than five species, resulting in the TWINSpan 5+ data set. The results of these two TWINSpan classifications are discussed next.

II. TWINSPAN 3+ and TWINSPAN 5+ classifications

For the TWINSPAN 3+ data run 128 grid squares with less than three species/infraspecific taxa each (Fig. 3) were deleted from the complete data set of 426 grids. An additional 47 grids with only three or four species/infraspecific taxa recorded (Fig. 3) were deleted for the TWINSPAN 5+ data run. Fortunately only two FSA endemics, *Plaubelia involuta* (Pottiaceae) and *Pseudoleskeopsis unilateralis* (Leskeaceae), restricted to two of the grids deleted for both data runs, were lost in the process.

2. Second level of division

The presence/absence data of 501 species/infraspecific taxa in 298 grid squares in the TWINSPAN 3+ data set was classified into 45 end groups or floristic regions (Fig. 31). The 251 grids in the TWINSPAN 5+ data set were divided into 39 floristic regions or end groups (Fig. 35). The results of the two TWINSPAN classifications are very similar and although the empty spaces increased compared to the TWINSPAN Complete classification, the floristic groups became more geographically homogeneous and the number of outliers decreased.

1. First level of division

The first and major TWINSPAN 3+ (and TWINSPAN 5+) division divides the grid squares into two main groups (Figs. 31 & 35), similar to the groups distinguished at the 4th level of division of the TWINSPAN Complete classification. Region 1/1 (end groups or regions 1-24 of the TWINSPAN 3+ classification) occupies the eastern and southern parts of the study area while region 1/2 (regions 25-45) is scattered over the arid and semi-arid western and central parts (Figs. 31 & 32). The only region 1/1 outliers that remain after the TWINSPAN 5+ classification are three grids in the Korannaberg and Langeberge of the Northern Cape Province, two grids in northern Namibia (Otjiwarongo-Otavi area) and two grids in the swamps of the Caprivi strip and northern Botswana (Fig. 36). The fate of these grids will only be decided by classifications based on more data from under-collected areas but I suspect that these areas will eventually prove to be continuous with the main areas occupied by region 1/1.

Region 1/2 is now more homogeneous than region 4/3 of the TWINSPAN Complete classification due to the elimination of species poor outliers. It has actually expanded, from the TWINSPAN Complete to TWINSPAN 3+ to TWINSPAN 5+, along the eastern and southern borders (Compare Figs. 28, 32 & 36). In central Namibia, however, the group has been reduced to four outliers. Many of the species-poor grids in the arid central parts of the study area have been deleted for the TWINSPAN 3+ and 5+ classifications and only two are left: grid 2822 C in the southern Langberge of the Northern Cape Province and grid 2824 D where the town of Kimberley is situated (Fig. 36).

2. Second level of division

At the second level of division regions 1/1 and 1/2 are subdivided into two groups each (Figs. 31 & 35). Region 1/1 is split into a large, more or less geographically coherent group (region 2/2) of 160 grids distributed along the southern and eastern parts of the study area, from Table Mountain in the south to the Soutpansberg in the north and a smaller group (region 2/1) of 64 grids scattered throughout the northern parts (Fig. 33). After the TWINSPAN 5+ classification region 2/1 extend as far south as KwaZulu-Natal (grid 3030 B) and the eastern Cape Province (grid 3224 D) with more outliers in The Okavango Swamps of Botswana, The Langeberg Mountains in the Northern Province and two grids in Namibia (Fig. 37).

The other dichotomy splits TWINSPAN region 1/2 into an eastern (region 2/4) and a western (region 2/3) group (Fig. 31). Most of the eastern region 2/4 grids are spatially continuous in and around the Highlands of Lesotho and the southern Free State, extending as far south as the mountains between Graaff-Reinet, Middelburg and Cradock in the Eastern Cape Province (Fig. 33). The remainder of the region 2/4 grids are scattered to the west of the main distribution with four outliers (grids 2822 C, 3221 B, 3119 B and 2416 A) remaining after the TWINSPAN 5+ classification (Fig. 37). Region 2/3 consists of 59 grids in the arid winter rainfall region, more or less contiguous along the south-western Cape coast as far north as Lüderitz in Namibia, with outliers to the east and north of the main area (Fig. 33).

3. Third level of division

Eight groups are distinguished at this level (Figs. 31 & 35). The first dichotomy splits eight grids in the extreme north of the study area (region 3/1) from the remainder of the northern group (region 3/2) (Fig. 34). The other dichotomy divides the large eastern group (region 2/2) into a small southern group of 18 grids (region 3/4) and a large northern group of 127 grids (region 3/3). Region 3/4 grids are centered in the south-western corner of the study area with outliers scattered to the east as far as the Eastern Cape Province (grid 3224 A) and north-eastern KwaZulu-Natal (2732 D). With the TWINSpan 5+ classification the grids in this group have actually increased to 21, all of them more or less continuous along the southern Cape Fold Mountains (Fig. 38). The KwaZulu-Natal outlier has been deleted and the Eastern Cape grid re-classified.

The large northern group of the TWINSpan 3+ classification (region 3/3) stretches from the Outeniqua Mountains in the south-western Cape to the Soutpansberg in the north (Fig. 34). The TWINSpan 5+ equivalent is even more geographically homogeneous and starts at the Alexandria grid to the east of Port Elizabeth (Fig. 38).

On the other side of the main division line the first dichotomy splits off a few northern grids (region 3/6) from the rest (region 3/5). The other dichotomy divides region 2/4 into an eastern (region 3/7) and a western (region 3/8) group (Figs. 34 & 38). The eastern group (region 3/7) is centered in the Highlands of Lesotho, with outliers to the south-west, while the adjacent western group (region 3/8) is most contiguous in the southern Free State with several outliers to the south and west.

TWINSpan goes on to classify the TWINSpan 3+ and TWINSpan 5+ grid squares into 45 and 39 end groups respectively after the 6th level of division (Figs. 31 & 35). However, it is at the 2nd and 3rd-levels of division that the groups are comparable with phytocoria at the subcontinental or regional scale.

Further discussion of the TWINSpan classification will therefore centre around the first three levels of division.

Discussion

Most of the bryogeographical regions identified by the TWINSpan 3+ and 5+ classifications are fairly geographically homogeneous with adjacent grids being grouped together. This suggests that there are clear geographically coherent patterns in the data. The increased homogeneity of the regions, from the TWINSpan Complete to the TWINSpan 5+ classification, suggests that the TWINSpan 5+ data set has resulted in the best classification of moss distribution patterns.

Unfortunately the removal of outliers from the TWINSpan Complete data set has resulted in the deletion of most grid squares in the arid north-western sector of the study area or the countries of Namibia and Botswana. This has made it impossible to present a clear picture of bryogeographic regions in this area. However, the DCA ordination made it possible to interpret the most obvious compositional gradients present in the data.

The first and major TWINSpan division line is not clearly distinguishable, especially in the central and northern parts of the study area, mainly due to the many empty grid squares but also as a result of the size of the grids or the grain chosen for this study (Figs. 32 & 36). This is to be expected in an exploratory, broad-scale analysis where the general pattern of division is more important than the precise boundaries between groups. However, the main discontinuity in the data appears to coincide with sections of major geological, geomorphological, climatic, and vascular plant vegetation and phytogeographic division lines in southern Africa.

Starting in the south, the main division begins at Table Mountain in the Cape Peninsula, turning slightly northwards up to 33° 30' latitude where it turns east to follow the northern boundary of the Cape Super Group (Truswell 1979, Kent 1980, Visser *et al.* 1984), the east-west axis of the southern Cape Fold Mountains (King 1963, Dingle *et al.* 1983, Partridge 1997), the boundary the Fynbos Biome (Rutherford & Westfall 1986, Low & Rebelo 1996, Rutherford 1997, Cowling &

Holmes 1992, Cowling *et al.* 1997) and the Cape (Floristic) region (Werger 1978, Cowling & Holmes 1992, Goldblatt 1978, Cowling & Hilton-Taylor 1997). From Port Elizabeth on the eastern Cape coast, where the first division line is interrupted by the dry Sunday's River Valley, it turns north to link up with and to follow the Great Escarpment (Wellington 1955, King 1963, Partridge & Maud 1987) and the continental watershed between drainage to the Indian Ocean and drainage to the Atlantic Ocean (Walton 1994). This line continues along the Great Escarpment of the Drakensberg Mountains, more or less coinciding with the border between the Afro-alpine and Afromontane regions (Werger 1978) all the way to the Maloti Mountains in northern Lesotho.

From the north-eastern Free State the division turns west to coincide with the border between the Nama-Karoo and Savanna Biomes (Rutherford & Westfall 1986, Low & Rebelo 1996, Rutherford 1997, Palmer & Hoffman 1997, Van Wyk & Van Wyk 1997) or Ecozone (McCullum 1994) and the boundary between the Karoo-Namib and Kalahari-Highveld regions (White 1983, Goldblatt 1978, Cowling & Hilton-Taylor 1997) or the boundary between the Karoo-Namib and Sudano-Zambezian regions (White 1965, 1971; Takhtajan 1986) right up to the northern border of Namibia.

The north-eastern part of the main division more or less coincides with the eastern limit of the karoo vegetation (see maps in Acocks 1953 and Nordenstam 1969). It also seems to follow, from the central part of the Northern Province all the way to the Angolan border, the general direction of the mean summer rainfall and mean annual rainfall isohyets (see rainfall maps in: Anon 1957; Le Roux 1967; Schulze & McGee 1978; Schulze 1997, 1997a; Barnard 1998), and the continental watershed between the inland drainage region or Kalahari Basin and the Atlantic Ocean drainage region (Walton 1994). It is most likely that in Namibia the 1st division line also coincides with the Great Escarpment (compare with physiographic maps in Barnard 1998) but this will only become clear once more sample points or grids are incorporated in the classification.

This main line therefore divides southern Africa into a temperate or austral moss flora (the Southern Flora of Acocks, 1971) represented by the the Karoo-Namib and

Highlands Regions on the one side, and a subtropical or palaeotropical moss flora (the Tropical Flora of Acocks, 1971) represented by the Zambezian and Afromontane (including the Cape) Regions on the other (Figs. 33 & 37). Whether this line represents the border between two Kingdoms, or the border between phytochoria of a lower rank, is not clear at this stage and should be determined by a much broader study including the whole of Africa and other southern temperate areas.

The main southern African division line of contemporary phytogeographic schemes (e.g. Good 1974, Miller 1982 Takhtajan 1986, Werger 1978, Jürgens 1991) is drawn much further south than the main TWINSPAN division and generally follows the boundary of the Cape Region (Goldblatt 1978, Cowling & Hilton-Taylor 1997) and the Fynbos Biome (Rutherford 1997). This line generally divides southern Africa into a Cape phytochorion (Kingdom) in the south and a Palaeotropical phytochorion (Kingdom) covering the rest of sub-Saharan Africa to the north. Herzog (1926) and Schofield (1992) on the other hand draw their main bryofloristic division line to include almost the entire study area in their southern division, the South African Kingdom.

The proposed subdivision of southern Africa into a Greater Cape Flora (Floristic Kingdom) in the south-west, including the western part of the Karoo-Namib region, the Cape region, and “ afromontane regions further east...”, as opposed to a Palaeotropis or Palaeotropical Kingdom in the rest of the area (Jürgens 1991), is not supported by this study. The whole of the Karoo-Namib Region is here included in the temperate or austral ‘kingdom’ while the fynbos and forest part of the Cape phytochorion belongs to a (sub)tropical or palaeotropical kingdom. I also don’t agree with Linder (1990) who argued that the temperate African phytochorion consists of the Afroalpine, Afromontane and Cape phytochoria (see discussions under the *Afromontane Region*). The temperate Afro-alpine region (Drakensberg Alpine Domain of this study) is clearly not closely related to the Afromontane region (including the Cape region) which belongs to the (sub)tropical phytochoria of Africa.

C. Classification of the Bryogeographic Regions of Southern Africa

I. Introduction

The bryogeographic classification presented here is based exclusively on the results of the TWINSPAN 3+ and TWINSPAN 5+ analyses. The classification is of course hierarchical and can be presented as a dendrogram (Fig. 39).

Most phytogeographic classifications have been hierarchical, as McLaughlin (1992) states: "...for reasons of convenience, not because analyses of plant distributions have revealed geographic patterns that are inherently hierarchical and hence best described by a hierarchical system." McLaughlin (1992), however, through analysis of 101 local floras of the western United States of America, has shown that a hierarchical classification system is not only an useful, but also a natural way of depicting floristic relationships.

The names assigned to the Regions and Domains are provisional because of the regional nature of this study but most of the names, especially those of the Regions, are well established and are not expected to change much. The floristic diversity and endemism in each of the phytochoria are summarised in Tables 14 & 15.

Hierarchical classification of the bryogeographic regions of southern Africa

1. Zambebian Region

1.1 Caprivi Domain

1.2 Bushveld Domain

2. Afromontane Region

2.1 Drakensberg Domain

2.2 Cape Domain

3. Karoo-Namib Region

3.1 Western Cape Domain

3.2 Namaqua Domain

4. Highlands Region

4.1 Drakensberg Alpine Domain

4.2 Upper Karoo Domain

II. Descriptions of Regions and Domains

1. Zambezian Region

Area

In southern Africa the Zambezian Region is at present most continuous in the Bushveld of the Northern Province with disjunctions in the Northern Cape, Eastern Cape, northern Botswana and Namibia (Fig. 37). This bryogeographical region seems to be associated with woodland, savanna or bushveld vegetation (White 1983, Low & Rebelo 1996, Scholes 1997) and therefore is largely restricted to the Savanna Biome (Rutherford & Westfall 1986, Low & Rebelo 1996, Rutherford 1997), or the Temperate Xerophytic Woods/Scrub biome (Olson *et al.* 1983).

The Zambezian Region consists of 39 grid squares (TWINSPAN 5+), largely discontinuous because of the many empty grids in the northern parts of the study area (Fig. 37). Significant outliers include grids 3030 B (Mkomazi River on the KwaZulu-Natal South Coast), 3224 D (Jansenville in the Eastern Cape), and 2722 A, 2722 D, & 2822 B (Langberge mountains the Northern Cape). These areas are known to have Bushveld or Thicket vegetation types (Low & Rebelo 1996) and fall in the Savanna Biome of Rutherford & Westfall (1986).

Several aspects of this phytochorion, such as the geology, physiography, climate, phytogeography, borders with other phytochoria, and vascular plant flora and vegetation, have recently been described by White (1965, 1983) Werger & Coetzee (1978) (in part), and Denys (1980). Useful synopses or reviews of the Zambezian Region have been provided by Goldblatt (1978), White (1993), Beentje *et al.* (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora

The moss flora (TWINSPAN 5+) of the Zambezi Region consists of 136 species/infraspecific taxa (27% of mosses in southern Africa) in 74 genera and 31 families which makes it the smallest of the regional floras (Appendix II,1). The largest family in this Region is Bryaceae with 21 species in seven genera. The second and third largest families are Pottiaceae with 17 species/infraspecific taxa in 10 genera and Dicranaceae with 15 species in five genera. *Fissidens* (Fissidentaceae) with 13 species, *Bryum* (Bryaceae) with 12 species and *Campylopus* (Dicranaceae) with 11 species are the largest moss genera in the Zambezi Region.

Characteristic of this flora is the prominence of woodland taxa in the families Fissidentaceae, Dicranaceae, Pottiaceae, Bryaceae, Erpodiaceae, Ptychomitriaceae and Meteoraceae. The woodland taxa include the diagnostic and important species (see lists) as well as more wide-ranging taxa like *Fissidens erosulus*, *Aulacopilum trichophyllum*, *Calymperes rabenhorstii*, *Octoblepharum albidum*, *Pseudocrossidium porphyreoneurum*, *P. replicatum*, *Syntrichia pagorum*, *Bryum capillare*, *Erpodium beccarii* and *Fabronia pilifera*.

None of the southern African moss families or genera are restricted or endemic to this region. Diagnostic species (species restricted to this Region in southern Africa but which may also occur in other parts of the world) are:

Diagnostic and endemic () Zambezi species*

Calymperes tenerum,

Erpodium grossirete

**Fissidens capriviensis*,

Fissidens capriviensis (Fissidentaceae) is the only true endemic (restricted to the FSA area and to this phytochorion) with *Calymperes tenerum*

(Calymperaceae) pantropical in distribution and *Erpodium grossirete* (Erpodiaceae) ranging northward as far as northeastern Zimbabwe.

Other important species, (species largely confined to this region in southern Africa), also called near-endemic elements by White (1993), include:

Important Zambezan mosses

Archidium acanthophyllum

Barbula eubryum

Erpodium coronatum *subsp.* transvaaliense

Ptychomitrium exaratifolium

Discussion

The Zambezan Region coincides with the southern section of the Zambezan regional centre of endemism of White (1976, 1983, 1993) and the Zambezan Region of Goldblatt (1978) and Cowling & Hilton-Taylor (1997). In the northern provinces of South Africa the bryogeographical region occupies the 'lowlands' in relation to the Soutpansberg, Drakensberg, Magaliesberg and Waterberg mountain ranges which fall in the Afromontane Region.

In Table 16 the numbers of moss taxa and endemics in the southern section of the Zambezan Region are compared with the figures available for vascular plants. Although the bryogeographical region is much smaller and therefore not directly comparable with the whole of the vascular plant region of White (1983) it is nevertheless interesting to look at the trends. Goldblatt (1978) gave a few figures for the southern African section of the phytochorion and these are also listed in Table 16.

Endemism is very low or absent at the family and genus level in both groups. The southern African section of the vascular plant region " is relatively depauperate " with only two endemic genera and few endemic species (Goldblatt 1978). Similarly only 27% of southern African mosses occur in this

phytochorion and endemism is even lower with no endemic families or genera and only one endemic species. Vascular plant endemism at the species level is higher (54%) for the whole region (White 1983).

Species of the Eastern Highlands and Afromontane Grassland Elements (distribution patterns) are most abundant in this region (Fig. 65) but none of the bryogeographic elements has its main centre of distribution in the Zambezi Region. As could be expected, species of the Cape Element are relatively scarce.

1.1 Caprivi Domain

Area

This Domain consists of a few grid squares in northern Namibia (TWINSPAN 3+ only), the Caprivi and Okavango swamps of northern Botswana, and the northern Province of South Africa (Figs. 34 & 38).

Composition of the moss flora

Only 22 mosses (4% of southern African mosses) belonging to 15 genera and 12 families make up the flora of the Caprivi Domain (Appendix II, 1a.), most of which belong to the acrocarpous orders of Dicranales, Pottiales and Bryales. The orders Andreaeales, Funariales, Hookeriales, Hypnobryales and Polytrichales are not represented in this domain.

The families Dicranaceae, Pottiaceae and Bartramiaceae are the largest with three species each while *Campylopus* (Dicranaceae) and *Philonotis* (Bartramiaceae) with three species each and *Fissidens* (Fissidentaceae), *Archidium* (Archidiaceae) and *Erpodium* (Erpodiaceae) with two species each are the best represented among the genera.

Diagnostic families or genera are absent. Of the two diagnostic species *Fissidens capriviensis* is endemic and *Erpodium grossirete* restricted to this Domain in southern Africa. Both are woodland species growing on the bark of trees.

Discussion

The already non-continuous Zambebian Region is further divided into what seems to be a northern (Caprivi) and a southern (Bushveld) Domain (Figs. 34 & 38). Whether these divisions are real and coincide with any of the vascular plant divisions reviewed by Werger & Coetzee (1978), or whether they are artifacts of insufficient data, remains to be seen. Another possibility is that the Caprivi Domain represents the Guinea-Congolia/Zambezia Transition Region, and the Bushveld Domain the Zambebian Region, both of Denys (1980).

The moss flora of the Caprivi Domain consists mostly of species in the Disjunct Cape Peninsula Subelement while species of the West Coast and Boland Subelements are absent from this area.

1.2 Bushveld Domain

Area

The Bushveld Domain is the largest of the two Zambebian divisions, distributed over 35 (TWINSPAN 5+) savanna grids in the northern provinces of South Africa and Namibia (Fig. 38). In South Africa it surrounds the northern part of the Drakensberg Domain or Afromontane Region. Outliers are discussed under the Zambebian Region.

Composition of the moss flora

The floristic composition of the Bushveld Domain is essentially the same as that of the Zambebian Region (minus *Fissidens capriviensis*, *Campylopus flaccidus*, *Octoblepharum albidum*, *Brachymenium*

systylium, *Erpodium grossirete* and *Aerobryopsis capensis*).

Octoblepharum is the only genus in the flora of the Zambezan Region not shared by the Bushveld Domain. The 130 species/infraspecific taxa, representing 73 genera in 30 families that occur in this domain are listed in Appendix II,1b. The families with the most specie/infraspecific taxa are Bryaceae with 20 species in seven genera, Pottiaceae with 17 species in 10 genera and Dicranaceae with 14 species in five genera. *Fissidens* (Fissidentaceae) and *Bryum* (Bryaceae) with 12 species each, *Campylopus* (Dicranaceae) with 10 species, and *Philonotis* (Bartramiaceae) with four species are the largest genera in the Bushveld Domain.

Calymperes tenerum (Calymperaceae) is the only diagnostic species (restricted to this Domain in southern Africa) but *Archidium acanthophyllum* (Archidiaceae), *Barbula eubryum* (Pottiaceae) and *Ptychomitrium exaratifolium* (Ptychomitriaceae) are also important woodland taxa largely restricted to this Domain. At present the Bushveld Domain lacks endemic moss taxa.

Discussion

As a subdivision of the Zambezan Region this Domain also is dominated by woodland taxa and can be compared with the southern section of the Zambezan regional centre of endemism (Region) of White (1976, 1983, 1993), Goldblatt (1978) and Cowling & Hilton-Taylor (1997). For more details see the discussions under the Zambezan Region and Caprivi Domain.

2. Afromontane Region

Area

The Afromontane Region, consisting of 113 grid squares (TWINSPAN 5+), is by far the largest of the four bryogeographic regions in southern Africa (Fig. 37). This region is most prominent in KwaZulu-Natal with extensions north

along the Great Escarpment to the Soutpansberg, and south-west as far as Table Mountain in the Western Cape. The Afromontane Region extends along the orogenic zone of southern Africa (see the map at Mountain Forum web site: www2.mtnforum.org/mtnforum/resources/stlas/atorafri.htm). The vascular plant vegetation of the southern Afromontane region "...is characterised by a recurring pattern of forest 'islands' in a 'sea' of grassland or heathland..." (Meadows & Linder 1993).

In the north the Afromontane Region runs along the Soutpansberg, Drakensberg and Magaliesberg mountain ranges, with an outlier in the Waterberg mountains of the Northern Province (Fig. 37). It continues south along the Great Escarpment and fans out in KwaZulu-Natal, reaching the Indian Ocean in the vicinity of Lake St. Lucia on the Zululand coast. In KwaZulu-Natal and the eastern Cape it occupies the Marginal Zone, more or less from the upper margin of the forests below the Great Escarpment down to the Indian Ocean. Near Port Elizabeth on the Eastern Cape coast this region is interrupted by a dry corridor along the Sundays River Valley (Cowling 1983) before it continues down the coast, covering the area between the sea and the top of the first mountain ranges, southward to the vicinity of Groot Brakrivier. In the south-western Cape the Afromontane Region is more or less restricted to the forest and mountain fynbos vegetation on the Cape Fold Mountains, as far west as Table Mountain in the Cape Peninsula and probably north to the Cederberg Mountains (TWINSPAN 3+, Fig. 33). The southern part of this region is therefore broken up into a series of isolated areas or Afromontane 'islands', surrounded by the Karoo-Namib Region along the drier river valleys and low-lying areas.

In general it can be said that all areas with indigenous forest, large or small, belong to the Afromontane Region. However, small Afromontane patches to the west of the main north-south axis (White 1978, Werger 1983) will probably not show up at a broad or macroregional scale.

Recent literature on the (southern) Afromontane region included discussions on the following topics: geology, physiography and climate (White 1978, 1983; Van Wyk 1994), phytogeography (White 1978, 1981; Van Wyk 1994, Cowling & Hilton-Taylor 1997), vascular plant flora and vegetation (White 1978, 1983; Denys 1980; Linder 1990; Van Wyk 1994) and the origin, evolution and relationships of the vascular plant flora (White 1981, 1983a; Werger 1983; Linder 1990, 1994; Iversen 1991; Meadows & Linder 1993). Useful reviews and summaries of the Afromontane Region were published by Goldblatt (1978), Meadows & Linder (1993), White (1993), Beentje *et al.* (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora

The Afromontane Region has the largest and most diverse moss flora of the four bryogeographic regions in southern Africa with 481 species/infraspecific taxa or 96% of the total moss flora (Appendix II,2). These species/infraspecific taxa are classified into 197 genera and 54 families. The largest families in the Afromontane Region, Pottiaceae with 61 species/infraspecific taxa in 24 genera, Dicranaceae with 48 species/infraspecific taxa in 14 genera, and Bryaceae with 40 species in nine genera are also the largest families in the study area. The genera *Fissidens* (Fissidentaceae) with 28 species, *Bryum* (Bryaceae) and *Campylopus* (Dicranaceae) with 19 species each and *Funaria* (Funariaceae) with 10 species are the most species-rich in this region.

Characteristic of this bryogeographic region is the abundance of pleurocarpous mosses in the Orders Isobryales, Hookeriales, Thuidiales and Hypnobryales. Most of the taxa in these groups occur in the forests, forest patches and wooded kloofs (White 1978, 1983; Cooper 1985; Geldenhuys & MacDevette 1989; McKenzie *et al.* 1990, Von Breitenbach 1990; Cooper & Swart 1992; Midgeley *et al.* 1997) that give the Afromontane region its unique character. Although the forests represent a small area of this region, at least 48% of mosses in the Afromontane Region (MOSS database) has been collected in forests or forest patches. It is generally accepted that these mesic

environments favour mosses with a pleurocarpous growth form (Vitt 1979, 1984; Buck & Vitt 1986).

None of the moss families in southern Africa is endemic to any of the bryogeographical regions. The only moss family endemic to southern Africa, the monotypic Wardiaceae, is found in both the Afromontane and the Karoo-Namib Regions but is largely restricted to the Afromontane Region. The following 11 families (phylogenetically arranged) are restricted to, and therefore diagnostic for the Afromontane Region:

Diagnostic families

- Seligeriaceae – Dicranales
- Splachnaceae – Funariales
- Eustichiaceae – Bryales
- Rhachithecaceae – Orthotricales
- Rhabdoweisiaceae – Orthotricales
- Fontinalaceae – Isobryales
- Cryphaeaceae – Isobryales
- Prionodontaceae – Isobryales
- Trachypodaceae – Isobryales
- Pterobryaceae – Isobryales
- Rigodiaceae – Thuidiales

The Isobryales is the best represented at the family level with five of its 12 families diagnostic for the region.

The 70 genera (34% of the total number of genera in southern Africa) restricted to the Afromontane Region in southern Africa are listed in Appendix II,5 (alphabetically and then phylogenetically arranged by family). Prominent among the orders, with regard to the number of diagnostic genera, are the Isobryales (13 or 48% of genera in this order), Hookeriales (5 or 63%), Thuidiales (11 or 55%) and Hypnobryales (14 or 48%). The families

Ditrichaceae (4), Pottiaceae (4), Pterobryaceae (5), Hookeriaceae (5), Amblystegiaceae (5) and Hypnaceae (4) are the best represented as far as the number of diagnostic genera is concerned.

Physcomitrellopsis of the family Funariaceae and *Quathlamba* of the Bartramiaceae are the only endemic genera. At a finer scale of analysis *Quathlamba* will probably be endemic to the Drakensberg Alpine Domain (Highlands Region) (see discussion under the Drakensberg Alpine Domain) while *Wardia* of the monotypic and endemic family Wardiaceae, now shared with the Karoo Namib Region, may actually be endemic to the Afromontane Region.

A total of 188 species/infraspecific taxa, or 39% of taxa in the Afromontane Region, is restricted to the region (Appendix II,6). Many of these may actually be endemic to the broader Afromontane Region. Some of the more widespread diagnostic species are:

A selection of widespread Afromontane diagnostic species (see Appendix II,6 for a complete list)

Callicostella tristis,
 Cyclodictyon vallis-gratiae
 Cyrtohypnum versicolor,
 Ectropothecium regulare
 Leucoloma rehmannii
 Lophidium pennaeforme
 Mittenothamnium pseudoreptans
 Oxyrrhynchium subasperum
 Pterobryopsis hoenelii
 Sematophyllum subpinnatum

True Afromontane endemics (mosses that are restricted to the southern African section of the Afromontane Region) are:

Afromontane endemics

<i>Archidium andersonianum</i>	<i>Macromitrium macropelma</i>
<i>Archidium julicaule</i>	<i>Meiothecium fuscescens</i>
<i>Archidium subulatum</i>	<i>Mielichhoferia subnuda</i>
<i>Brachythecium pinnatum</i>	<i>Oligotrichum afrolaevigatum</i>
<i>Brachythecium</i>	<i>Oligotrichum wageri</i>
<i>pseudopopuleum</i>	<i>Orthotrichum armatum</i>
<i>Brachythecium</i>	<i>Oxyrrhynchium confervoideum</i>
<i>pseudovelutinum</i>	<i>Oxyrrhynchium subasperum</i>
<i>Breutelia elliptica</i>	<i>Philonotis comosa</i>
<i>Breutelia tabularis</i>	<i>Physcomitrellopsis africana</i>
<i>Dimerodontium africanum</i>	<i>Pogonatum borgenii</i>
<i>Distichophyllum mniifolium</i>	<i>Pterobryopsis rehmannii</i>
<i>var. taylorii</i>	<i>Ptychomitriopsis africana</i>
<i>Ephemerum diversifolium</i>	<i>Quathlamba debilicostata</i>
<i>Fabronia eckloniana</i>	<i>Rhynchostegiella sublaevipes</i>
<i>Fabronia perciliata</i>	<i>Rhynchostegium</i>
<i>Fabronia wageri</i>	<i>subbrachypterum</i>
<i>Fissidens aciphyllus</i>	<i>Sematophyllum zuluense</i>
<i>Gymnostomum lingulatum</i>	<i>Stoneobryum mirum</i>
<i>Helicodontium lanceolatum</i>	<i>Streptocalypta pulchiretis</i>
<i>Isopterygium leucopsis</i>	<i>Ulota ecklonii</i>
<i>Isopterygium taxithelioides</i>	<i>Weissia cucullata</i>
<i>Isopterygium taylorii</i>	<i>Weissia humicola</i>
<i>Leskeella zuluensis</i>	<i>Zygodon dixonii</i>
<i>Leucobryum rehmannii</i>	<i>Zygodon leptobolax</i>
<i>Macrocoma pulchella</i>	

Species which are largely confined to, and widespread in the Afromontane Region include:

A selection of widespread Afromontane mosses

Aerobryopsis capensis	Neckera valentiniana
Atrichum androgynum	Pilotrichella pandurifolia
Brachymenium pulchrum	Pogonatum capense
Bryum andicola	Porothamnium stipitatum
Bryum viridescens	Porotrichum madagassum
Campylopus stenopelma	Racopilum capense
Ditrichum brachypodium	Rhodobryum commersonii
Entodon macropodus	Rhodobryum umbraculum
Funaria limbata	Schlotheimia ferruginea
Haplocladium angustifolium	Sematophyllum sphaeropyxis
Haplohymenium pseudo-triste	Squamidium brasiliense
Hypopterygium laricinum	Syrrhopodon gaudichaudii
Leucobryum acutifolium	

Discussion

The archipelago-like Afromontane Region was formally recognised as a separate phytochorion by White (1965). Later White (1978) divided his Afromontane archipelago-like regional centre of endemism into seven regional mountain systems. Denys (1980) adopted White's nomenclature for her seven Mountain Domains, which largely coincide with White's regional mountain systems.

The Afromontane regional mountain systems of White (1978) and the Mountain Domains of Denys (1980).

- 1) West African regional mountain system (Domain)
- 2) Ethiopian regional mountain system (Domain)
- 3) Kivu-Ruwenzori regional mountain system (Domain)
- 4) Imatongs-Usambara regional mountain system (Domain)
- 5) Uluguru-Mlanje regional mountain system (Domain)
- 6) Chimanimani regional mountain system (Domain)

7) Drakensberg regional mountain system (Domain)

The bryogeographic Region largely coincides with White's southernmost division of the Afromontane archipelago-like regional centre of endemism, the Drakensberg regional mountain system (White 1978), especially if the Magaliesberg extension and other satellite populations and transition zones are included. It also coincides with the Drakensberg Domain of Denys (1980), which includes two isolated areas in the southern and the southwestern Cape, and the Drakensberg Afromontane Regional System of Beentje *et al.* (1994), described as a regional centre of diversity in Davis *et al.* (1994). In KwaZulu-Natal and the Transkei the Afromontane Region, as described here, coincides with the Maputaland-Pondoland Region of Van Wyk (1994), extending from the Olifants-Limpopo Rivers (24°S) in the north to just beyond the Great Kei River (33°S) in the south. The bryogeographical Region is, however, more extensive and continuous than the vascular plant phytochoria and also displays a number of other important differences.

The Afromontane Region presented here includes, for the first time, much of the 'Capensis' or Cape (Floristic) region of Werger (1978), Taylor (1978), White (1976, 1983), Goldblatt (1978), Cowling & Richardson (1995), and Cowling & Hilton-Taylor (1997). A 'Cape' phytochorion is here only distinguished at the level of Domain (see 2.2, the Cape Domain). On the basis of strong floristic and ecological links between the Cape and Afromontane phytochoria (Levyns 1964, Goldblatt 1978, Cowling 1983, Hilliard & Burt 1987, Cowling & Richardson 1995), Linder (1990), and later Oliver (1994), proposed the establishment of a combined Afrotemperate Region, supporting an earlier suggestion by Wild (1964). However, until now this combined region has not been formally described or mapped.

The high plateau of Lesotho, or the Afro-alpine region, has generally been included in the Afromontane Region (Goldblatt 1978, Denys 1980, White 1983, Cowling & Hilton-Taylor 1997), or a combined Cape-Afromontane (Afrotemperate) phytochorion (Linder 1990, 1994; Oliver 1994). However,

the Afromontane Region recognised here excludes the high altitude areas on the Lesotho plateau or the Afro-alpine region. These areas form part of the temperate Highlands Region (see discussion under the *Drakensberg Alpine Domain*).

The bryogeographic classification does not support the recognition of a separate Tongoland-Pondoland regional mosaic (Region) or Province along the east coast of southern Africa, as described by Werger (1978), Goldblatt (1978), White & Moll (1978), White (1983), Takhtajan (1986) and Cowling & Hilton-Taylor (1997). According to the TWINSPAN classification the southern part of this vascular plant phytochorion falls into the Afromontane Region while the part north of Lake St. Lucia belongs to the Zambezian Region. This bryogeographic boundary is congruent with the southernmost Afromontane/Zambezian boundary of Denys (1980). The results of this study also doesn't support the notion put forward by Cawe *et al.* (1994) that the distinction between the 'subtropical' and 'afrotemperate' forests in the Transkei region of the Eastern Cape is indicative of two separate phytochoria, a 'subtropical region' along the coast and an 'afrotemperate region' further inland.

On the basis of the TWINSPAN classification of moss distributions I predict that the Afromontane Region, when mapped at a broad or (sub)continental scale, will prove to be more extensive and continuous throughout Africa than the archipelago-like region shown by White (1976, 1978), Goldblatt (1978), Denys (1980), or Cowling & Hilton-Taylor (1997). It may well form an almost continuous band, only interrupted by dry river valleys such as the Limpopo and Zambezi river valleys, from the Cape to Eritrea, and from Dar es Salaam to Luanda (Zaire-Zambezi watershed) with substantial outliers in west Africa, Madagascar and Yemen.

In Table 17 the Afromontane Region of this study is compared with two sets of vascular plant data: 1) The Afromontane archipelago-like regional centre of endemism of White (1983) (figures are not available for White's Drakensberg

regional mountain system or the Drakensberg Afromontane Regional System of Beentje *et al.* 1994), and 2) the Maputaland-Pondoland Region of Van Wyk (1994).

Endemism at the family level is low in both groups (much higher for vascular plants if the Cape Region is included) but endemism at the genus and species level is much higher for vascular plants than for mosses. The latter may of course change when the mosses of the whole Afromontane region are taken into account.

According to the TWINSPLAN classification (Fig. 39) the Afromontane Region, dominated by 'tropical' vascular plant taxa (White 1978), is closely related to the Zambezian Region which consists of savanna vegetation, a tropical vegetation type (Scholes 1997). Together they form a (sub)tropical phytochorion distinct from the temperate or austral phytochorion consisting of the Karoo-Namib and Highlands regions on the other side of the main TWINSPLAN division line. Goldblatt (1978), Linder (1990), Oliver (1994), and Cowling & Hilton-Taylor (1997) included the temperate Afro-alpine flora (see the *Highlands Region*) in their Afromontane Region and that is probably why they regarded the Afromontane Region as temperate rather than subtropical. The (sub)tropical affinity of the Afromontane Region is therefore in contrast to the suggestion by Linder (1990) that the combined Afromontane/Cape phytogeographic region be called the 'Afrotemperate Region'.

Three of the four bryogeographic elements (Cape, Afromontane Grassland, Afromontane Forest) have their main centres of distribution in the Afromontane Region (Fig. 65). The fourth element (Eastern Highlands) is also well represented in this region by secondary centres.

2.1 Drakensberg Domain

Area

This Domain represents the northern and largest division of the Afromontane Region, consisting of 92 grids of the TWINSPAN 5+ classification (Fig. 38). The position of the southern boundary differs between the TWINSPAN 3+ and 5+ classifications. In the TWINSPAN 3+ classification the Drakensberg Domain extends as far south as the forests around George in the Western Cape Province (Fig. 34) while the TWINSPAN 5+ classification draws the border with the Cape Domain between Port Elizabeth and Grahamstown in the Eastern Cape Province (Fig. 38).

The vascular plant flora of the Drakensberg Domain is described in Denys (1980). Otherwise the literature references given under the Afromontane Region also apply here.

Composition of the moss flora

The 409 species/infraspecific taxa that occur in the Drakensberg Domain are listed in Appendix II,2a. These mosses belong to 179 genera in 50 families. As with the Afromontane Region, the families Pottiaceae (53 species/infraspecific taxa in 21 genera), Dicranaceae (40 species/infraspecific taxa in 13 genera) and Bryaceae (36 species in eight genera) are the largest in the moss flora of the Drakensberg Domain.

In southern Africa the following eight families (16% of families in this domain) are diagnostic (restricted to this domain in southern Africa) for the Drakensberg Domain:

Diagnostic families

Seligeriaceae – Dicranales

Splachnaceae – Funariales
 Eustichiaceae – Bryales
 Rhachithecaceae – Orthotricales
 Rhabdoweisiaceae – Orthotricales
 Prionodontaceae – Isobryales
 Trachypodaceae – Isobryales
 Rigodiaceae – Thuidiales

The genera *Fissidens* (Fissidentaceae) with 24 species, *Bryum* (Bryaceae) with 18 species and *Campylopus* (Dicranaceae) with 17 species are the largest in this Domain. The following 45 genera (25% of genera in this Domain) are restricted to the Drakensberg Domain:

Diagnostic genera

Abietinella	Levierella
Aongstroemiopsis	Micropoma
Astomiopsis	Orthostichopsis
Blindia	Physcomitrellopsis
Callicostella	Pinnatella
Campyliadelphus	Plagiobryum
Chrysohypnum	Plagiopus
Conostomum	Platyhypnidium
Cratoneuron	Prionodon
Entodontopsis	Pterobryopsis
Eustichia	Quathlamba
Herpetineuron	Raiiella
Hyophila	Rhabdoweisia
Jaegerina	Rhachithecium
Lepidopilidium	Rhacopilopsis
Leptoischyrodon	Rigodium
Leptoterigynandrum	Saelania
Leskeella	Sanionia

Stoneobryum	Trichosteleum
Streptocalypta	Tristichium
Tayloria	Vittia
Trachypodopsis	Weisiopsis
Trachypus	

The genus *Physcomitrellopsis* (Funariaceae), endemic to the Afromontane Region, is also endemic to the Drakensberg Domain. The 153 species/infraspecific taxa restricted to this Domain (the diagnostic species) represents 37% of the mosses in this domain and are listed in Appendix II,2c. Of these the following 28 species (7%) are endemic to the Drakensberg Domain:

Drakensberg endemics

Archidium julicaule	Orthotrichum armatum
Dimerodontium africanum	Oxyrrhynchium confervoideum
Fabronia eckloniana	Oxyrrhynchium subasperum
Fabronia perciliata	Physcomitrellopsis africana
Fissidens aciphyllus	Pogonatum borgenii
Gymnostomum lingulatum	Pterobryopsis rehmannii
Helicodontium lanceolatum	Ptychomitriopsis africana
Isopterygium leucopsis	Quathlamba debilicostata
Isopterygium taxithelioides	Rhynchostegiella sublaevipes
Leskeella zuluensis	Rhynchostegium subbrachypterum
Mielichhoferia subnuda	
Oligotrichum afrolaevigatum	
Oligotrichum wageri	

Sematophyllum	Streptocalypta
zuluense	pulchiretis
Stoneobryum mirum	Weissia humicola
	Zygodon dixonii

Quathlamba debilicostata (Bartramiaceae), here listed as endemic to the Drakensberg Domain, may actually be endemic to the Highlands Region and the Drakensberg Alpine Domain (see discussion under the Highlands Region).

Discussion

This phytochorion is most similar to the Drakensberg regional mountain system of White (1978) including the Magaliesberg extension and the transition zone in KwaZulu-Natal but excluding the satellite populations and islands of Afromontane vegetation in the south-western Cape. It also coincides with, and is named after, the northern part of Denys's Drakensberg Domain (Denys 1980), excluding the two Cape 'islands' in the southern and south-western Cape.

The border between the two Domains of the Afromontane Region is situated in the south-eastern Cape, a geological, topographic, climatic and vegetation transition zone known for its phytogeographic complexity (Goldblatt 1978, Werger 1978a, Werger & Coetzee 1978, Gibbs Russell & Robinson 1981, White 1983, Cowling 1983, Kopke 1988, Nicol 1988, Palmer 1990, Hoffman & Cowling 1991). It is a region of convergence for five vascular plant phytochoria (Cowling & Hilton-Taylor 1997), all four of the bryogeographic Regions (Figs. 33 & 37), and six of the eight bryogeographic Domains (Figs. 34 & 38). It is therefore not surprising that the phytogeographic delimitation of the area is unsettled (Cowling & Hilton-Taylor 1997), and that the bryogeographic boundaries differ between the TWINSPAN 3+ and TWINSPAN 5+ classifications. However, the TWINSPAN 5+

classification (Fig. 38), which is perhaps the better of the two bryogeographic classifications, draws the main phytogeographic boundary in more or less the same place (along the Sundays River Valley east of Port Elizabeth) as recent classifications based on the distributions of vascular plants (White 1976, 1983; Goldblatt 1978; Werger 1978; Cowling & Hilton-Taylor 1997).

In Table 18 the moss flora of the Drakensberg Domain is compared with the flora of the Maputaland-Pondoland Region (Van Wyk 1994). Although a much greater number of southern African mosses (81%) occurs in this region than vascular plants (29-33%), endemism in the Drakensberg moss flora is rather low (7%) compared to that of vascular plants (c. 20%).

2.2 Cape Domain

Area

The Cape Domain occupies 18 TWINSPAN 3+, or 21 TWINSPAN 5+ grid squares in the mountains of the south-western Cape (see Third level of TWINSPAN 3+, 5+ classification, this chapter, and Figs. 34 & 38). The Cape Region based on vascular plants covers an area of c. 71000 km² (White 1983) or 90000 km² (Bond & Goldblatt 1984, Rebelo 1994a, Cowling & Hilton-Taylor 1997), depending on what figure you accept.

The TWINSPAN 5+ phytochorion is not spatially continuous but forms four distinct areas (Fig. 38) along the Cape Fold mountains. In the east around Alicedale and Grahamstown (grids 3326 A & B), where the Cape Supergroup (Hammerbeck & Allcock 1985) disappears beneath the Karoo sediments, the Cape mosses form an 'island', separated from the rest of the Cape Domain by an intrusion of the Western Cape Domain along the drier Sundays River Valley. For a discussion of the phytogeographically complex eastern Cape area, see

the *Drakensberg Domain*. The Langeberg Mountains of the Western Cape Province (grids 3320 D and 3321 C) represent another Cape island in a sea of Karoo-Namib or Western Cape mosses along the intermontane, low rainfall valleys of the Klein Karoo (Fig. 38).

The western part of the TWINSPAN 5+ phytochorion falls into the *winter* rainfall region while the eastern part falls into the *all year* rainfall region (see Rainfall Seasonality map in Schulze, 1997). The TWINSPAN 3+ phytochorion (Fig. 34) is largely restricted to the south-western part of the Cape where a mediterranean-type climate (Goldblatt 1978) prevails.

The geology, physiography, climate, vegetation, phytogeography, and composition and origin of the vascular plant flora of the Cape phytochorion have been the subjects of several recent studies and reviews, notably those by White (1976, 1983), Werger (1978), Taylor (1978), Goldblatt (1978), Oliver *et al.* (1983), Bond & Goldblatt (1984), Meadows (1985), Takhtajan (1986), Cowling & Holmes (1992), Cowling *et al.* (1992), Deacon *et al.* (1992), Linder *et al.* (1992), Rebelo (1994a), Cowling & Richardson (1995), and Cowling & Hilton-Taylor (1997). Several aspects of the Fynbos Biome, largely equivalent to the Cape region but based on plant growth form, have been described by Rutherford & Westfall (1986), Low & Rebelo (1996), Rutherford (1997) and Cowling, Richardson & Mustart (1997).

Composition of the moss flora

The moss flora of the Cape Domain consists of 284 species/infraspecific taxa in 127 genera and 44 families (Appendix II,2b). This represents 59% of species/infraspecific taxa in the Afromontane Region and 57% of all the mosses in southern Africa. Pottiaceae (33 species/infraspecific taxa in 17 genera), Dicranaceae (29/11) and Bryaceae (23/7) are the most species-rich among the families in this Domain while *Fissidens* of the family Fissidentaceae

with 14 species/infraspecific taxa, *Bryum* (Bryaceae) and *Campylopus* (Dicranaceae) with 13 species each, and *Fabronia* (Fabroniaceae) and *Funaria* (Funariaceae) with eight species each are the largest genera.

The Fontinalaceae (Isobryales), probably introduced from Europe (Magill & Van Rooy 1998), is the only diagnostic family for this domain. The monotypic family Wardiaceae, usually associated with the Cape region, is shared with the Western Cape Domain (see discussion under the Afromontane Region).

The genera *Cheilothela*, *Ulota*, *Fontinalis*, *Distichophyllum*, *Meiothecium* and *Polytrichastrum* are restricted to the Cape Domain but none is endemic to the phytochorion. Lists of diagnostic (35) and endemic (19) species/infraspecific taxa follows.

Diagnostic mosses of the Cape Domain

<i>Andreaea nitida</i>	<i>Bryum donianum</i>
<i>Archidium</i>	<i>Calymperes levyanum</i>
<i>andersonianum</i>	<i>Campylopus bicolor</i>
<i>Archidium subulatum</i>	<i>Cheilothela chilensis</i>
<i>Barbula calycina</i>	<i>Distichophyllum</i>
<i>Brachythecium</i>	<i>mniifolium var.</i>
<i>pinnatum</i>	<i>mniifolium</i>
<i>Brachythecium</i>	<i>Distichophyllum</i>
<i>populeum</i>	<i>mniifolium var. taylorii</i>
<i>Brachythecium</i>	<i>Drepanocladus</i>
<i>pseudopopuleum</i>	<i>sendtneri</i>
<i>Brachythecium</i>	<i>Ephemerum</i>
<i>pseudovelutinum</i>	<i>diversifolium</i>
<i>Breutelia elliptica</i>	<i>Fabronia wageri</i>
<i>Breutelia tabularis</i>	<i>Fissidens splachnifolius</i>
<i>Bruchia eckloniana</i>	

Fissidens	Meiothecium
stellenboschianus	fuscescens
Fontinalis antipyretica	Philonotis comosa
var. gracilis	Philonotis vagans
Fontinalis squamosa	Polytrichastrum
Isopterygium taylorii	formosum
Leucobryum rehmannii	Ulota ecklonii
Macrocoma pulchella	Weissia cucullata
Macromitrium	Zygodon leptobolax
macropelma	

Cape Domain endemics

Archidium andersonianum
Archidium subulatum
Brachythecium pinnatum
Brachythecium pseudopopuleum
Brachythecium pseudovelutinum
Breutelia elliptica
Breutelia tabularis
Distichophyllum mniifolium var. taylorii
Ephemerum diversifolium
Fabronia wageri
Isopterygium taylorii
Leucobryum rehmannii
Macrocoma pulchella
Macromitrium macropelma
Meiothecium fuscescens
Philonotis comosa
Ulota ecklonii
Weissia cucullata
Zygodon leptobolax

Discussion

The remarkable richness of the vascular plant flora in the Cape region (Bond & Goldblatt 1984, Cowling & Holmes 1992, Cowling *et al.* 1992, Cowling & Richardson 1995) has contributed greatly to its recognition as one of the vascular plant (and bryofloristic) Kingdoms of the world (Good 1974; Miller 1982, Takhtajan 1986; Cowling & Holmes 1992, Rebelo 1994a, Cowling & Richardson 1995). However, the Cape phytochorion based on the distributions of southern African mosses is rather less distinctive and is only separated from the rest of the Afromontane Region at the 8-group level, or rank of Domain (Fig. 39).

The Cape Domain is more or less restricted to the Afromontane Forest and Mountain Fynbos vegetation types (Campbell 1985, Low & Rebelo 1996) on the Cape Fold Mountains. Although forest areas in the south-western Cape are usually classified as Afromontane and fynbos areas as Cape, Manders (1991) has challenged the concept of fynbos and forest as distinct and mutually exclusive vegetation types. Goldblatt (1978) included "...a substantial forest element related to the Afromontane forest,..." in his Cape Region but also "...Karoo-Namib elements in the drier valleys", which are excluded here. Furthermore, Fynbos-like vegetation occurs throughout sub-Saharan Africa, Madagascar and the Mascarenes, often in association with Afromontane forest (Cowling & Richardson 1995).

The Cape phytochorion as defined here therefore excludes the renosterveld of the lowlands or coastal plains and the succulent karoo shrubland of the intermontane valleys, which are included in the Karoo-Namib Region. The Cape Domain, as a subdivision of the Afromontane Region, forms part of a (sub)tropical African flora (see Discussions under the *TWINSpan 3+*, and *TWINSpan 5+* classifications and the *Afromontane Region*, this chapter), and is not

closely related to the temperate western part of the Karoo-Namib Region (the Succulent Karoo Region) as proposed by Jürgens (1991).

Although a relatively great number of southern African mosses (57%) occurs in the Cape Domain, endemism is absent at the family and genus levels, and relatively low at the species level (12%) compared to the 68% of vascular plants (Table 19).

3. Karoo-Namib Region

Area

This is the second largest bryogeographical region in southern Africa (Figs. 33 & 37), more or less congruent with the Karoo-Namib regional centre of endemism of White (1983), which extends over an area of 661,000 km². This Region consists of 61 grid squares (TWINSPAN 5+), more or less contiguous in the south-western corner or the winter rainfall arid region of the study area, from Port Elizabeth in the Eastern Cape to Lüderitz in southern Namibia (Fig. 37). Both the TWINSPAN 3+ and 5+ classifications show three northern outliers in central Namibia. In the south the Karoo-Namib Region borders on three Afromontane archipelagos or islands on the Cape Fold mountains and follows the dry intermontane valleys down to the coastal plain between Gansbaai in the west, and Mossel Bay in the east (Figs. 33 & 37).

The geology, physiography, climate, phytogeography, vegetation, and flora, including the origin of the Karoo-Namib flora, have recently been studied or reviewed by Goldblatt (1978), Werger (1978a), White (1983), Takhtajan (1986), Hilton-Taylor (1987, 1994), Jürgens (1991) and Cowling *et al.* (1998, 1999).

Composition of the moss flora

The flora of the Karoo-Namib Region is composed of 196 species/infraspecific taxa (39% of the total moss flora) representing 93 genera and 37 families (Appendix II, 3). Largest among the Karoo-Namib families is

the Pottiaceae with 38 species/infraspecific taxa in 19 genera, the Dicranaceae with 19 species/infraspecific taxa in 10 genera and the Bryaceae with 16 species in five genera. The genus *Fissidens* (Fissidentaceae) with 11 species is the best represented in this region followed by *Bryum* (Bryaceae) with 10 species and *Campylopus* (Dicranaceae) and *Funaria* (Funariaceae) with seven species/infraspecific taxa each.

Characteristic of the Karoo-Namib moss flora is the prominence of xerophytic mosses in the families Archidiaceae, Ditrichaceae, Dicranaceae, Pottiaceae, Grimmiaceae, Ephemeraceae, Funariaceae and Bryaceae, adapted to survive life in the (semi) arid conditions of this region. The life strategies as well as morphological and physiological adaptations in arid land mosses have been discussed by During (1979, 1992), Magill (1981, 1987), Vitt (1981, 1984), Bell (1982), Scott (1982), Longton (1988), Frey (1990), Frey & Kürschner (1988, 1991, 1995), Zander (1993), and Eldridge & Tozer (1996). The two main strategies involved are:

1. *Desiccation tolerance*. Perennial gametophyte growth, associated with physiological desiccation resistance (poikilohydric mosses). These mosses usually display some of the following morphological features:
 - a) densely papillose leaf surfaces, which allegedly provide capillary channels for rapid uptake and transport of water, b) revolute or involute leaf margins, which may encourage water movement from leaf tip to base, c) robust, thickened costae which provide mechanical support during desiccation and may aid in water uptake, d) hyaline hair points, which increase the water-receiving area, e) hyaline or partly hyaline leaves which act as protective coverings for the green, photosynthetic parts, f) small squarrose leaf cells which reduce the ratio of cell surface area to volume, and g) leaves that change position markedly between dry and wet conditions, often tightly twisted or rolled when dry and squarrose when wet.

These features allow the mosses to maintain physiological processes for extended periods. Perennial mosses in arid regions can also survive in a dehydrated state with low water potentials, considerable heat tolerance and the capability to resume physiological processes very quickly after re-hydration. Examples of mosses in the Karoo-Namib Region that can tolerate the arid conditions are: *Pseudocrossidium*, *Syntrichia* and *Tortula* spp. (Pottiaceae), *Grimmia* spp. (Grimmiaceae), *Bryum argenteum* (Bryaceae) and *Orthotrichum* spp. (Orthotrichaceae).

2. *Dessication avoidance*. Ephemeral life strategy, associated with a reduction in the life cycle and stature of the plants. Rapid production of sporophytes during a short growth period and survival in the form of stress-tolerant diaspores. 'Ephemerals' are characterised by one or more of the following features: a) cleistocarpous, gymnostomous capsules, b) shortened seta, c) small, bulbiform gametophore, d) increased spore size, and e) adaxial leaf growths such as lamellae or filaments.

The following are examples of mosses in the Karoo-Namib Region which possess features characteristic of an ephemeral life style: *Archidium* spp. (Archidiaceae), *Pleuridium* spp. (Ditrichaceae), *Aloina bifrons*, *Acaulon* spp., *Crossidium spiralifolium*, *Phascum peraristatum*, *Pottia* spp. (Pottiaceae), *Bryobartramia novaevalesiae* (Bryobartramiaceae), *Chamaebryum pottioides* and *Gigaspermum repens* (Gigaspermaceae), *Ephemerum* spp. (Ephemeraceae), and *Cygnicollum immersum* and *Goniomitrium africanum* (Funariaceae).

Although the ephemeral life style is probably a recent adaptation to arid conditions (Vitt 1984), in southern Africa brought about by the rifting of Gondwana and the northward drifting of the African plate (Axelrod & Raven 1978, Audley-Charles *et al.* 1981, Pitman III *et al.* 1993, White 1994), many of the acrocarpous families to which these mosses belong show Pangaeian distributions (Vitt 1984).

Xerophytic Pottiaceae with bulbiform gametophores, assimilation filaments/lamellae or thickened costae, hyaline hairpoints, a dimorphic rhizoid system, and reduced peristomes have been classified under the Xeropottioid life syndrome by Frey (1990) and Frey & Kürschner (1988, 1991, 1995). This group of mosses is particularly well represented in the Karoo-Namib Region by species of *Aloina*, *Crossidium*, *Didymodon*, *Pseudocrossidium*, and *Tortula*, all from the Pottiaceae. Many taxa in this group are distributed in mediterranean and temperate to hot, semi-arid to arid areas of the world. This distribution pattern is described as the Xerothermic Pangaeon by Frey (1990).

The genera *Acaulon*, *Crossidium*, *Cygnicollum*, *Leucoperichaetium*, *Microcrossidium* and *Pottia* are diagnostic for the Karoo-Namib Region. All but two (*Leucoperichaetium* and *Cygnicollum*) belong to the Pottiaceae. Only two genera, *Cygnicollum* of the family Funariaceae and *Microcrossidium* of the Pottiaceae, or 2% of genera in this region, are endemic to this phytochorion.

Of the 14 diagnostic species only *Acaulon leucochaete* (also known from Australia), *Archidium amplexicaule* (present in South America) and *Bruchia queenslandica* (Mexico and Australia) are not true endemics.

Diagnostic and endemic () species of the Karoo-Namib Region*

- Acaulon leucochaete
- *Acaulon recurvatum
- *Andreaea bistratosa
- Archidium amplexicaule,
- Bruchia queenslandica
- *Crossidium spiralifolium
- *Cygnicollum immersum
- *Fabronia breutelii

**Leucoperichaetium eremophilum*

**Microcrossidium apiculatum*

**Oligotrichum tetragonum*

**Pleuridium papillosum*

**Pottia namaquensis*

Other important species which are mainly distributed in this region include:

Important species

Aloina bifrons

Bryobartramia novae-valesiae

Desmatodon longipedunculatus

Henediella longipedunculata

Ephemerum namaquense

Funaria clavata

Ischyrodon lepturus

Orthotrichum incurvomarginatum

Phascum peraristatum

Tortula splachnoides

Ptychomitrium crassinervium

Tetrapterum tetragonum

Syntrichia chisosa

Ptychomitriopsis aloinoides

Discussion

With increased collecting this bryogeographic region is sure to cover most of the (semi-)arid south-western part of southern Africa. This area "...is in a state of severe water stress even during the rainy season" (Jury *et al.* 1997) and the moss flora is remarkably adapted to survive the harsh conditions. The Karoo-Namib Region, and in particular the Succulent Karoo (Region), supports a very rich vascular plant flora, including "...the world's largest succulent flora..." (Cowling *et al.* 1998).

The Karoo-Namib Region described here more or less coincides with the Karoo-Namib regional centre of endemism (Region) of White (1965, 1971, 1976, 1983), Wickens (1976), Goldblatt (1978), Takhtajan (1986) and Cowling & Hilton-Taylor (1997), or the larger Karoo-Namib Region of Werger (1978). Subdivision of this region is discussed under the Western Cape Domain.

The northern and eastern borders of this Region also coincide with the borders of major vascular plant vegetation types (based on growth form) and 'ecozones' (defined by factors such as geology, rainfall, vegetation and soil). The northern border, situated just north of the Namibian town of Lüderitz, coincides with the boundary between the Succulent Karoo and Desert Biomes (Rutherford & Westfall 1986, Rutherford 1997) or Ecozones (McCullum 1994). However, the outliers in central Namibia might indicate that this Region extends into southern Angola as in the case of the vascular plant phytochorion (Werger 1978, White 1983). The eastern border of the Karoo-Namib Region, which coincides with the border between the Succulent Karoo and Nama-Karoo Biomes (Rutherford & Westfall 1986, Rutherford 1997) or Ecozones (McCullum 1994), runs parallel to the Atlantic coastline, following the Great Escarpment for most of the way. Hilton-Taylor & Le Roux (1989: 203) provided an useful map of the phytogeographic subdivisions or "...the biogeographic areas..." of the Fynbos, Succulent Karoo and Nama-Karoo Biomes in South Africa.

The presence of this bryofloristic region along the dry intermontane valleys and the southern coastal plain of the Cape region might point to a high degree of affinity between the karroid shrublands of the Karoo-Namib Region and the shrublands usually included in the Cape Region (see Hilton-Taylor 1987), particularly the South and South-west Coast Renosterveld of Low & Rebelo (1996). White (1983) recognised that "...large enclaves of Karoo..." vegetation exist within the boundaries of the Cape Region.

Although 39% of southern African mosses occurs in the Karoo-Namib Region compared to the 29% of vascular plants, endemism is much lower in the mosses with only 6% of species restricted to this region compared to the 35–50% of vascular plants (Table 20). Endemism at the genus level is also low in mosses with only two (2%) endemic genera.

The moss flora of the Karoo-Namib Region consists mostly of xerophytic species in the Cape Element, and to a lesser degree the Eastern Highlands Element (Fig. 65). None of the bryogeographic elements has its centre of distribution in this region and the Afromontane Forest Element is poorly represented.

3.1 Western Cape Domain

Area

The largest of the two Karoo-Namib divisions, the Western Cape Domain covers an area of 54 grid squares (TWINSPAN 5+), only seven northern grids less than the Karoo-Namib Region. (Fig. 38). It is more or less restricted to the winter rainfall region (see rainfall seasonality map in Schultze 1997) and is known as a region of unparalleled succulent plant diversity (Hilton-Taylor 1994, Cowling *et al.* 1998).

The geography, flora, vegetation, and phytogeography of the Western Cape Domain (Succulent Karoo) have been discussed by Werger (1978a), Jürgens (1991), Hilton-Taylor (1987, 1994, 1996), Hilton-Taylor & Le Roux (1989), Milton *et al.* (1997), and Cowling *et al.* (1998, 1999).

Composition of the moss flora

The moss flora of the Western Cape Domain is almost identical to that of the Karoo-Namib Region and only six species (*Fissidens subobtusatus*, *Barbula bolleana*, *Funaria rhomboidea*, *Bryum*

capillare, *B. cellulare* and *Ptychomitriopsis aloinoides*) are not shared between the two phytochoria. The 190 species/infraspecific taxa in this Domain represent 93 genera and 37 families (Appendix II,3a). This moss flora also is characterised by the presence of a substantial number of mosses with an ephemeral life style (see discussion under the *Karoo-Namib Region*).

As in the case of the *Karoo-Namib Region*, the families Pottiaceae (37 species/infraspecific taxa in 19 genera), Dicranaceae (19 species in 10 genera) and Bryaceae (14 species in five genera) are the largest families while *Fissidens* (Fissidentaceae) with 10 species, *Bryum* (Bryaceae) with eight species and *Campylopus* (Dicranaceae) with seven species are the largest among the genera.

The genera and species which are diagnostic and endemic to the *Karoo-Namib Region* are also diagnostic and endemic to the Western Cape Domain. Other important species, mainly distributed in this Domain, are listed under the *Karoo-Namib Region*.

Diagnostic and endemic () genera of the Western Cape Domain*

Acaulon
 Crossidium
 *Cynicollum
 Leucoperichaetium
 *Microcrossidium
 Pottia

Diagnostic and endemic () species of the Western Cape Domain*

Acaulon leucochaete
 *Acaulon recurvatum
 *Andreaea bistratosa

- Archidium amplexicaule
- *Archidium dinteri
- Bruchia queenslandica
- *Crossidium spiralifolium
- *Cygnicollum immersum
- *Fabronia breutelii
- *Leucoperichaetium eremophilum
- *Microcrossidium apiculatum
- *Oligotrichum tetragonum
- *Pleuridium papillosum
- *Pottia namaquensis

Discussion

Monod (1957) subdivided the Karoo-Namib Region into three domains: the Karoo Domain, Namaqualand Domain and Namib Domain. Subsequent authors (Troupin 1966, Aubréville 1975) have followed this subdivision with adjustments to the boundaries. Werger (1978a) divided the Karoo-Namib Region into the following four domains (called provinces by Takhtajan, 1986) and 1 subdomain:

Domains of the Karoo-Namib Region (Werger 1978a)

1. Namib Domain
2. Namaland Domain
3. Southern Kalahari Subdomain
4. Western Cape Domain
5. Karoo Domain

Jürgens (1991) proposed a new subdivision of the Karoo-Namib Region into 1) a Succulent Karoo Region all along the west coast and 2) a Nama Karoo Region inland from the Succulent Karoo and Cape Floristic Regions. His Nama Karoo Region is further divided into three domains: the Eastern Karoo, Namaland and Damaraland-Kaokoland

Domains, the Namaland Domain in turn into the Namaland and Namib Subdomains, and lastly the Namib Subdomain is divided into a Namib and an Eastern Gariiep District (Jürgens 1991). However, the results of this study show that Jürgens's Succulent Karoo Region is not closely related to the fynbos part of the Cape Region and therefore can't form part of a proposed Greater Cape Flora or Floristic Kingdom (see discussions in this chapter under *TWINSPAN 3+ and TWINSPAN 5+ classifications* and the *Cape Domain*).

More moss distribution data is needed to critically compare the bryofloristic and vascular plant subdivision of the Karoo Namib Region but at this stage it appears that the Western Cape Domain of this study coincides with the Succulent Karoo Region of Jürgens (1991) and the Western Cape Domain of Hilton-Taylor (1994). The boundaries of the Western Cape Domain also are more or less congruent with those of the ecologically defined Succulent Karoo Biome (Rutherford & Westfall 1986, Hilton-Taylor 1996, Rutherford 1997, Milton *et al.* 1997).

The Karoo-Namib Region or Western Cape Domain (Succulent Karoo) has been subdivided into a number of small areas or phytochoria with high concentrations of endemic species, so-called centres of endemism (see discussion under *Centre of endemism*, Chapter 1), also referred to as geographical areas, biogeographic areas, or bioregions (Werger 1978, 1978a; Hilton-Taylor 1987, 1994, 1996; Hilton-Taylor & Le Roux 1989; Cowling *et al.* 1999). These are generally below the level of Domain and therefore not considered here.

Although 38% of southern African mosses occur in the Western Cape Domain compared to the 20% of vascular plants, endemism is much lower in the mosses with only 6% of species restricted to this region compared to the 40% of vascular plants (Table 21). Endemism at the genus level is also lower in mosses with only 2% of genera compared

to the 8% of vascular plants. Cowling *et al.* (1998) have recently argued that the Succulent Karoo (Region) "...represents a major extratropical centre of plant biodiversity" and "...is home to the world's largest succulent flora...".

3.2 Namaqua Domain

Area

This Domain is scattered over seven grid squares (TWINSPAN 5+) situated in the most arid part of southern Africa (Fig. 38), generally receiving less than 300 mm of rain per annum. As a result of the many empty grids in this area it is not possible to draw exact boundaries for this domain.

The phytogeography, flora and vegetation of the Namaqua Domain have been described by Werger (1978a) and Jürgens (1991).

Composition of the moss flora

The Namaqua Domain has the smallest moss flora (TWINSPAN 5+) of all the domains with only 20 species in 15 genera and 10 families (Appendix II,3b), none of which is diagnostic or endemic to the phytochorion.

The presence of xerophytic taxa and the absence of pleurocarpous taxa is striking. The families Pottiaceae (six species in five genera), Bryaceae (four species in two genera) and Funariaceae (three species of *Funaria*) are the best represented in the region. The genera *Bryum* (Bryaceae) and *Funaria* (Funariaceae) with three species each, followed by *Pseudocrossidium* (Pottiaceae) with two species are the largest in the Namaqua Domain.

Discussion

Although the boundaries of the Namaqua Domain are poorly defined as a result of insufficient collecting or sampling, this domain appears to coincide with, and is therefore named after, the Namaqualand (Namaland) Domain (Province) of Monod (1957), Werger (1978, 1978a), Takhtajan (1986) and Jürgens (1991).

4. Highlands Region

Area

The Highlands Region consists of 39 TWINSPAN 5+ grid squares covering the high altitude areas of the Interior Plateau (Fig. 37). It is almost spatially continuous from the north-eastern Free State, through Lesotho and the southern Free State, to the Sneeuberge mountain range in the Eastern Cape Province. Outliers occur in the Nuweveldberge mountains between Beaufort West and Fraserburg in the Great Karoo, the Hantamsberg mountains in the Northern Cape Province, and the Naukluft mountains in central Namibia. Another isolated and rather low altitude grid square (2822 C) is found in the Northern Cape Province and represents a single collecting locality on the southernmost tip of the Langeberge mountains.

The region has a temperate climate with summer rainfall, hot summers and cold winters with severe frost and occasional snowfalls. The vascular plant vegetation can be classified into alpine and subalpine belts (Killick 1963, 1978). The exact position of the border between the Highlands and Afromontane, and Highlands and Karoo-Namib regions is obscured by the broad-scale used and the many empty grids but it seems to follow the Great Escarpment.

The geology, physiography, climate and vascular plant flora and vegetation of this phytochorion should be more or less the same as that of the Kalahari-Highveld transition zone as described by White (1983) including the

Drakensberg (Afro-alpine) Region of Killick (1978, 1994), summarised by Goldblatt (1978), Beentje *et al.* (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora

The moss flora of the Highlands Region is made up of 152 species/infraspecific taxa (30% of the total moss flora) in 71 genera and 29 families (Appendix II,4). The families Pottiaceae (37 species/infraspecific taxa in 16 genera), Bryaceae (21 species in five genera) and Dicranaceae (11 species in five genera) are the largest in this Region. The largest genera are *Bryum* (Bryaceae) with 15 species, *Fissidens* (Fissidentaceae) with nine species and *Syntrichia* (Pottiaceae) with eight species/infraspecific taxa.

The Highlands moss flora differs from the closely related Karoo-Namib flora mainly in the absence of families such as Sphagnaceae, Bryobartramiaceae, Wardiaceae and ephemerals such as *Bruchia*, *Acaulon*, *Crossidium*, *Microcrossidium*, *Pottia*, *Leucoperichaetium* and *Cygnicollum*, and the presence of families such as the Mniaceae, Thuidiaceae, Amblystegiaceae and additional taxa in the Leskeaceae. The moss flora reflects the severity of the climate and most of the mosses exhibit xeromorphic characters.

There are no diagnostic or endemic families or genera in this region. Two of the three diagnostic species/infraspecific taxa, *Syntrichia austroafricana* (Pottiaceae) and *Physcomitrium spathulatum* var. *sessile* (Funariaceae), are endemic to the Highlands Region while *Pterygoneurum macleanum* (Pottiaceae) is also known from southern and western Australia.

Diagnostic and endemic () species/infraspecific taxa*

**Syntrichia austroafricana*

Pterygoneurum macleanum

**Physcomitrium spathulatum* var. *sessile*

There may actually be more diagnostic and endemic taxa than identified by TWINSPAN which, as a result of the scale used, fall into predominantly Afromontane grids covering both sides of the KwaZulu-Natal/Lesotho escarpment. Examples are: *Quathlamba debilicostata* (Bartramiaceae), endemic to the escarpment cliffs at Sani Pass but classified as Afromontane, and *Anomobryum drakensbergense* (Bryaceae), endemic to Highlands (2927 B, 2928 B, 3028A) as well as borderline Afromontane grids (2929 A, 2929 C). Other important species which are mainly distributed in this region are:

Important species

Bryoerythrophyllum recurvirostrum

Bryum turbinatum

Didymodon trivialis

Encalypta ciliata

Encalypta vulgaris

Ptychomitrium cucullatifolium

Ptychomitrium diexaratum

Weissia dieterlenii

Discussion

At the turn of the previous century the high altitude areas of the Central Plateau were included in a Kalahari or a Highveld region by several phytogeographers (Rehman 1880, Phillips 1917). Later on these high altitude areas were included in several subdivisions of the Sudano-Angolan or Sudano-Zambezian Region (e.g. Lebrun 1947, Monod 1957, Troupin 1966, Takhtajan 1986). Weger (1978, 1983) included the eastern part of the Kalahari/Highveld area (excluding the Afro-alpine Region) in his Sudano-Zambezian Region and the western part or the southern Kalahari (Leistner 1967) in his Karoo-Namib Region as the Southern Kalahari Subdomain.

Since the recognition of a separate Afromontane region by White (1965, 1970) the high plateau of Lesotho (Afro-alpine region) has generally been regarded

as a subdivision or part of the Afromontane region (Goldblatt 1978; Denys 1980; White 1981, 1983; Cowling & Hilton-Taylor 1997).

In 1976 White re-instated the Kalahari-Highveld region, excluding the Afro-alpine region on the high plateau of Lesotho, as the Kalahari-Highveld transition zone (White 1976, 1978, 1983). This classification has been followed by Goldblatt (1978) and Cowling & Hilton-Taylor (1997).

The Highlands Region identified here (Fig. 37) is very much restricted to (and is named after) the Highlands of Lesotho and surrounding high altitude areas, including the Afro-alpine or Drakensberg Alpine Region of Killick (1978, 1994). It is therefore most unlikely that this region includes the sandy Kalahari basin, or areas below c.1500 m in altitude, as in the case of the Kalahari-Highveld transition zone of White (1978, 1983), Goldblatt (1978) and Cowling & Hilton-Taylor (1997).

To speculate on the full extent of this Region may be premature but I predict that it will be present on all the high altitude, temperate areas throughout Africa, generally above c.1700 m but increasing in altitude towards the equator and decreasing in altitude towards the poles. It is therefore likely that this region occupies a series of isolated high altitude areas forming an archipelago-like region, similar to the Afromontane Region of White (1978) and Denys (1980). In the southern part of Africa this Region may also be present on isolated mountain peaks of the northern Drakensberg of Mpumalanga and the Northern Province, the Eastern Highlands and Limpopo Escarpment in Zimbabwe, Mount Mulanje and the Nyika Plateau in Malawi, the highlands around Windhoek (e.g. the Auas Mountains) and perhaps other isolated peaks in the Erongo and Brandberg mountains of Namibia, and the central or Bié Plateau in Angola.

Killick (1978) listed a number of 'subalpine' areas in the southern part of Africa that could also be included in this phytochorion (e.g. Amatole and Bosberg mountains in the Eastern Cape Province, Chimanmani and

Gorongosa Mountains in Mozambique, and the Zomba plateau in Malawi) but concluded that Mt. Mulanje in Malawi could be “...the only subalpine vegetation in southern Africa outside South Africa”. Many of these high altitude areas are under-explored (Touw 1974, Killick 1978, White 1993, O’Shea 1997) and additional collecting, taxonomic studies and phytogeographic analysis should greatly improve the delimitation of the Highveld as well as other phytogeographic regions in Africa.

Udvardy (1975) identified five Highlands provinces in Africa (Fig. 18):

1. Ethiopian Highlands
2. Guinean Highlands
3. Central African Highlands
4. East African Highlands
5. South African Highlands

These phytochoria appear to cover at least some of the high altitude areas in Africa which are likely to form part of an African ‘Highlands’ region.

Udvardy’s South African Highlands Province (Fig. 18) covers the high altitude plateau along the eastern escarpment of South Africa, from Mpumalanga down to the Eastern Cape (Udvardy 1975).

From Table 22 it is evident that endemism is extremely low or absent in the mosses as well as the vascular plants of the Highlands Region. Goldblatt (1978) estimates that c.15 genera “...are confined to this region,...” and White (1983) found that “There are very few endemic species and the greater part of the interior has a very poor flora.”. Of course the vascular plant flora considered by Goldblatt (1978) and White (1983) does not include the Drakensberg (Afro) Alpine flora (see the *Drakensberg Alpine Domain*, this Chapter) which may change the figures. Endemism may also be higher in the moss flora of this Region (see *Composition of the moss flora*). The Eastern Highlands Element dominates the moss flora of this region (Fig. 65).

4.1 Drakensberg Alpine Domain

Area

The Drakensberg Alpine Domain consists of 20 high altitude grid squares (TWINSPAN 5+) contiguous on and around the high plateau of Lesotho (Fig. 38). An outlying group of three grids is found in the Sneeuberge mountains between the towns of Graaff-Reinet and Middelburg in the Eastern Cape Province and a single outlier occurs in the Hantamsberg mountains north of Calvinia in the Northern Cape Province (Fig. 38). The TWINSPAN 3+ classification shows another outlier: grid 3322 B in the Swartberg mountains north of De Rust in the Western Cape Province (Fig. 34).

The climate is severe (broadly classified as temperate with summer rainfall) with cool to hot temperatures in summer and cold to freezing in winter. The vegetation of the high plateau of Lesotho (mostly above 2750 m) lies in the Alpine belt (Killick 1963) and has recently been described as tundra (Killick 1997). Geologically this Domain is associated with basalt of the Drakensberg Formation.

The historical background, geology, climate, phytogeography, flora, ecology and vegetation of this region have been described by Killick (1963, 1978, 1990, 1994, 1997) and Schmitz (1984).

Composition of the moss flora

The moss flora of the Drakensberg Alpine Domain consists of 142 species/infraspecific taxa in 67 genera and 27 families (Appendix II, 4 a), only 10 species/infraspecific taxa, four genera and two families less than the Highlands Region. The family Pottiaceae is the largest with 36 species/infraspecific taxa in 16 genera followed by Bryaceae with 20 species in five genera and Dicranaceae with 11 species in five genera. *Bryum* (Bryaceae) with 14 species, *Fissidens* (Fissidentaceae) with eight, and *Syntrichia* (Pottiaceae) and *Funaria* (Funariaceae) with

seven species each are the largest genera in the Drakensberg Alpine Domain.

Syntrichia austroafricana and *Pterygoneurum macleanum*, both of the family Pottiaceae, are diagnostic for the Drakensberg Alpine Domain with *Syntrichia austroafricana* the only endemic taxon (see *Composition of the moss flora* under the *Highlands Region*). Some taxa now classified as Afromontane endemics may actually belong here (see *Composition of the moss flora* under the *Highlands Region*). Important Highland species (see list there) are also largely restricted to this domain.

Discussion

The recognition of a separate Afro-alpine region is one of the controversies in southern African phytogeography (Killick 1978, Cowling & Hilton-Taylor 1997). Since its proposal by Hauman (1955), based on Hedberg (1951), the existence of a distinct, discontinuous Afro-alpine Region has generally been acknowledged, but often as a subdivision or 'impoverished' part of the Afromontane region (Weimarck 1941; Troupin 1966; White 1976, 1978, 1981, 1983; Goldblatt 1978; Denys 1980; Cowling & Hilton-Taylor 1997). This study clearly shows that the Afro-alpine region, or the Drakensberg Alpine Domain as it is named here, is a distinct temperate phytochorion not closely related to the subtropical Afromontane Region.

The Drakensberg Alpine Domain is more or less congruent with, and is named after, the Afro-alpine and Drakensberg Alpine Regions of Killick (1978, 1994). More or less restricted to areas above 2000 m (see altitude map in Schulze 1997), this domain will probably combine with a couple of closely related domains to occupy the highest mountains of Africa, increasing in altitude towards the equator and decreasing in altitude towards the poles. It is still uncertain at what

level this phytochorion will combine with the Afro-alpine Region of east and north-east tropical Africa (Hedberg 1965, 1994). Friis (1994) found that the Afromontane and Afro-temperate floras of the Sudan, Ethiopia and Somalia occupy the 'high land' above c. 1400–1500 m but he did not distinguish between the two.

The Drakensberg Alpine Domain also coincides with the Eastern Mountain Region of Phillips (1917), renamed the South-eastern Mountain Regional Mosaic by Hilliard & Burtt (1987). However, the boundaries of the (South) Eastern Mountain Region were subjectively drawn and are rather artificial (a lower limit of between 1050 m and 1200 m in the case of Phillips, 1917, and 1800 m in Hilliard & Burtt, 1987). This has resulted in the inclusion of (sub)tropical forest elements on the KwaZulu-Natal side of the Drakensberg escarpment which gives the (South) Eastern Mountain region a distinct Afromontane flavour.

If compared to structural classifications of vascular plant vegetation, the Highlands Region occupy more or less the same geographic area as the Steppe biome of Olson *et al.* (1983). The bryogeographic classification also seems to support the inclusion of the high plateau of eastern Lesotho in the Nama-Karoo Biome by Rutherford & Westfall (1986).

Although only about 8% of vascular plant species in southern Africa occur in the Drakensberg Alpine Domain (Region) compared to the 28% of mosses, endemism is much higher at an estimated 30% compared to only 1% in mosses (Table 23).

4.2 Upper Karoo Domain

Area

The Upper Karoo Domain represents the western half of the Highlands Region, scattered over 20 grid squares in the Free State, southern Lesotho, Eastern and Northern Cape Provinces and Namibia (Fig. 38). This domain occupies a lower altitude and lower rainfall area than the Drakensberg Alpine Domain.

Composition of the moss flora

The moss flora of the Upper Karoo Domain is relatively small and consists of 63 species in 32 genera and 15 families (Appendix II,4 b). The families Pottiaceae with 18 specie/infraspecific taxa in 11 genera, Bryaceae with 12 species in two genera and Funariaceae with eight species/infraspecific taxa in three genera are the best represented in this domain. The largest genera are: *Bryum* (Bryaceae) with 11 species, *Funaria* (Funariaceae) with six species and *Fissidens* (Fissidentaceae) with five species.

None of the taxa are diagnostic, endemic or largely restricted to the Upper Karoo Domain. *Pseudocrossidium crinitum*, *Tortula atrovirens* and *Trichostomum brachydontium* of the Pottiaceae, and *Bryum argenteum*, and *B. pycnophyllum* of the Bryaceae are the most widespread, and the most frequently collected taxa in this but also in other domains. *Ptychomitrium cucullatifolium* (Ptychomitriaceae) is widespread and largely restricted to this domain as well as the closely related Drakensberg Alpine Domain.

Of the relatively few pleurocarpous mosses present in the Highlands Region only six species (four in the family Leskeaceae, one in Fabroniaceae and one in Meteoriaceae) remain in this domain. The pleurocarpous Orders Hookeriales and Hypnobryales, as well as the

Sphagnales, Andreaeales and Polytrichales have not been recorded from this domain.

Discussion

The composition of the Upper Karoo moss flora reflects the increasing aridity in the Highlands Region, from the Drakensberg Alpine Domain in the east to the Upper Karoo Domain in the west.

D. Indirect Gradient Analysis (Ordination of Grid Squares)

The DCA ordinations of the TWINSPAN 3+ and TWINSPAN 5+ databases yielded four axes each with eigenvalues as listed in Table 24. These eigenvalues are only relative measures of the variation accounted for by each axis. The gradient length is a measure of change in species composition of the grids along the ordination axis and a full turnover of species composition occurs in about 4 SD (Gauch 1982).

I. Distribution of TWINSPAN regions in the ordination space

Fig. 40 shows the positions of the TWINSPAN 5+ grids squares on DCA ordination axes 1 and 2, the two axes with the highest eigenvalues. Each grid is also classified according to the TWINSPAN Region it belongs to.

The grids are roughly grouped according to the TWINSPAN analysis and the groups show a large degree of coherence but do not display distinct discontinuity. The Zambezian grids are widely dispersed but more or less grouped together in the top left hand corner of the scatter diagram while the Afromontane grids are clustered towards the bottom left hand corner. These two regions overlap along axis 1. The Highlands grids occupy a central position towards the top of the scatter diagram while the Karoo-Namib grids are widely scattered all along the right hand sector of the plot, overlapping with the other regions along axis 2. The Highlands and Karoo-Namib regions overlap along axis 1. The main TWINSPAN division line is only weakly distinguishable along the first axis, dividing the Zambezi and

Afromontane grids on the left of the scattergram from the Highlands and Karoo-Namib grids on the right.

II. Compositional gradients

1. DCA scattergram of TWINSPAN 5+ grids

Axis 1

There is a clear gradient from Zambezi and Afromontane grids with low values on the one hand to Karoo-Namib and Highlands grids with high values on the other (Fig. 40). The main TWINSPAN 5+ division line runs between these two groups but is not clearly distinguishable as a result of some overlap between the groups. The compositional gradient along the first axis is therefore from grids along the northern, eastern and southern border of the study area to inland and western grids.

Axis 2

Afromontane and Karoo-Namib grids, and to a lesser degree Zambezi grids, are widely dispersed along the 2nd axis which causes considerable overlap among the regions (Fig. 40). There is, however, a gradient from Afromontane and Karoo-Namib grids with relatively low scores to Highlands and Zambezi grids with higher values. This represents a compositional gradient from eastern and southern coastal grid squares to inland and northern grids.

The geographic trends of change in the floristic composition along the first 4 DCA axes are further investigated through Figs. 41–48.

2. Geographic trends in the compositional gradients

Axis 1

The first DCA axes of the TWINSPAN 3+ and TWINSPAN 5+ ordinations have eigenvalues of 0.477 and 0.466, while the gradient lengths are 5.19 and 4.63 standard deviation (SD) units respectively (Table 24). The relatively high eigenvalues of the 1st as well as the other ordination axes indicate that a high

percentage of total variance is accounted for by the axes which, however, does not guarantee ecological (phytogeographical) meaningful results (Gauch 1982).

The relatively high gradient lengths indicate total turnover of taxa along the 1st axis. In both cases the main compositional gradient is from low grid scores in the east and north-east of the study area, gradually increasing towards the south and west, to high scores along the west coast and adjacent interior (Figs. 41 & 45). Grids with low scores in the central and northern parts of the study area, e.g. 1723 C, 2723 A and 2527 B, should be regarded as outliers.

The species composition therefore changes from east to west in longitudinal bands more or less parallel to the coast line (Figs. 41 & 45).

Axis 2

The lower eigenvalues of 0.374 and 0.322 respectively (Table 24) show that axis 2 explains less of the variation in the data than axis 1 (Table 24). Although the relatively high gradient lengths of 4.84 and 4.54 SD (Table 24) indicate complete turnover of species there is less change in species composition along this axis. The TWINSpan 3+ ordination results show that most grids have low scores and fall into the first two class intervals, thus many of the distribution ranges of taxa cover almost the whole gradient represented by this axis (Fig. 42). Complete turnover of species in the TWINSpan 3+ data set is only achieved through grids 2732 D and 2632 D with extreme positive scores. These two grids are outliers already identified as such by the TWINSpan classification of grid squares (see *TWINSpan 3+ and TWINSpan 5+ classifications*). The TWINSpan 3+ grid scores change from low scores in the extreme northern inland regions of the study area to higher scores in the southern and southwestern coastal areas (Fig. 42).

Change in the TWINSpan 5+ species composition along the 2nd axis is more gradual but in the opposite direction than the TWINSpan 3+ results (Fig. 46). The gradient runs from low values in the southern and coastal parts of the study area gradually increasing towards the interior and extreme northern grid squares. The

three eastern grids with extreme low scores (3229 A, 2632 D and 2731 D), although situated more or less on the coast, are probably outliers.

DCA axis 2 therefore represents a latitudinal north-south gradient in the floristic composition of the grids.

Axis 3

The lower eigenvalues of DCA axes 3 and 4 (Table 24) indicate that each captures only about half of the phytogeographic information accounted for by DCA axis 1. Complete turnover in TWINSpan 3+ species composition (gradient length = 4.28 SD) is only achieved through the inclusion of three outliers (3424 A, 3424 B, and 2931 A) with extreme low scores on the 2nd axis (Fig. 43). The rest of the grid scores gradually increase from the south-west to western and eastern coastal areas ranging into the northeastern lowveld and escarpment, to high altitude areas of the eastern and southern escarpments and central plateau.

There is less change in the TWINSpan 5+ species composition along this axis and most grids fall into the first three divisional classes (Fig. 47). A gradient length of 3.74 SD is only achieved through the inclusion of a few grids with high scores in the arid Northern Cape Province and southern Namibia (3221 B, 2718 C, 2918 B, 2615 C and 2716 D). The gradient is different from that of the TWINSpan 3+ ordination and contrasts grids in the central and northern bushveld parts of the study area with grids scattered over a large area in the southeastern part of southern Africa (Fig. 47).

Axis 4

The gradient lengths of 5.01 and 5.21 SD respectively give a false impression of the change in species composition along the 4th ordination axis. Many of the TWINSpan 3+ grids have intermediate scores on the 4th axis and full species turnover is only achieved through grids 3222 D and 3024 A, the only grids in their divisional class of extreme low scores (Fig. 44). This axis contrasts some of the alpine and adjacent afro-montane grids (low scores), on and around the high altitude central plateau, with high scoring grids scattered in the central and

northern bushveld areas of South Africa. This gradient is more or less the same as, but in the opposite direction, of the TWINSPAN 5+ gradient along the 3rd DCA axis.

Most of the TWINSPAN 5+ grids belong to one divisional class of intermediate scores which indicates little change in species composition along the 4th axis (Fig. 48). Full species turnover is only achieved through a few outliers with extreme low scores on the one end (3229 A, 2731 D, 2528 B) and extreme high scores on the other (2632 D and 1723 C). This axis contrasts 'bushveld' grids in central and northern south Africa with a few grids along the eastern escarpment. The low scoring grids along the Transkei coast (3030 A, 3129 C & D, 3128 D, 3228 B & C, and 3229 A) is probably the result of recent collecting and uneven taxonomic representation in the database. The grids with extreme low and high scores can be regarded as outliers.

It appears that the 3rd and 4th ordination axes represent the same floristic gradient that runs both altitudinally and latitudinally in southern Africa.

III. Correlation with environmental variables

Axis 1

The following environmental variables correlate in varying degrees with the main east-west gradient along the first DCA ordination axis:

1. **Solar radiation** (based on Clemence's Equation) for the **summer** months, roughly from November to March (Schulze 1997a). The values are low in the east and south, gradually increasing in more or less longitudinal bands to high values in the western interior.
2. **Mean annual precipitation** (Anon 1957, B.R. Schulze 1965, Schulze & McGee 1978; Schultze 1997, 1997a). Highest values in the east, gradually increasing towards the south and west in longitudinal bands.

3. **Coefficient of variation of annual precipitation** (Schulze 1997a) which measures the natural year to year variability of rainfall. The higher the mean annual precipitation the lower its inter-annual variability and vice versa. Therefore low percentages in the east and south, gradually increasing in longitudinal bands to high percentages (> 40%) in the Northern Cape and southern Namibia.

4. **Mean or median rainfall** for the **summer** months, roughly from October to March. Highest rainfall figures are generally recorded in the eastern and, to a lesser degree, the southern parts of the study area gradually decreasing in more or less longitudinal bands to very low figures in the west (Schulze 1997a).

5. **Daily mean (and minimum) relative humidity** in **spring** and **autumn**, particularly the month of March (Schulze 1997a). Lowest percentages occur in the western interior with a gradual increase towards the east. Low values are also recorded on the high plateau of Lesotho.

6. **Potential evaporation** (A-pan equivalent), and to a lesser degree **Reference Evapotranspiration** (FAO Penman-Monteith Method), over southern Africa in **December** (Schulze 1997a). The following climatic and physiographic variables were used by Schulze and Maharaj (Schulze 1997a) to estimate potential evaporation over South Africa.: 1) maximum daily temperature, 2) extraterrestrial radiation, 3) altitude, 4) median monthly rainfall and 5) evaporation regions. Low values occur in the east and south with a southeast-northwest increase towards high values in the western interior.

7. **Median annual simulated runoff** with high values in the east and south decreasing towards low values in the west (Schulze 1997a). Runoff patterns reflect a combination of rainfall and soil characteristics.

A number of environmental classifications and indices (usually including some moisture parameter) not mentioned here, also show an east-west gradient (see Schulze & McGee 1978; Schulze 1997, 1997a; Jury *et al.* 1997), but these are mostly applicable to vascular plants.

Axis 2

The following environmental parameters correlate more or less with the latitudinal north-south gradient along the 2nd DCA ordination axis:

1. **Solar radiation** (based on Clemence's Equation) for the **winter** months, roughly from May to September (Schulze 1997a). The values are low in the south and east increasing in bands running more or less parallel to the coast line to high values in the northern interior.
2. **Temperature Range** (Diurnal) for the **winter** months of May - August (Schulze 1997, 1997a). Low values occur along the coast extending northwards into the lowveld, increasing in latitudinal bands to high values in the northern interior.
3. **Daily mean (and minimum) relative humidity** in the **winter** months, roughly from May to September (Schulze 1997a). Low values (%) are recorded in the northern interior of southern Africa, gradually increasing in latitudinal bands parallel to the coastline to high values along the south-western, southern and eastern coast, extending into the eastern lowveld.
4. **Potential evaporation** (A-pan equivalent), and to a lesser degree **Reference Evapotranspiration** (FAO Penman-Monteith Method), which includes temperature based information, over southern Africa in **spring**, and in particular the month of September (Schulze 1997a). Low values occur in the south-west and south, gradually increasing latitudinally to high values in the northern interior.

Axis 3

Although DCA ordination axes 3 & 4 are phytogeographically less important than the first two DCA axes, the gradients along these axes are nevertheless interpretable.

The following parameters are related to the gradient along the 3rd axis of the **TWINSpan 3+** ordination (Fig. 43):

1. **Altitude** (Schulze 1997a), from low altitudes along the coastal plain (in particular the southwestern Cape and Maputaland where the coastal plain is at its widest) extending into the lowveld and the Limpopo River valley, to higher altitudes along the escarpment and interior plateau.
2. **Means of daily minimum temperature (°C)** for the **winter** months of May, June, July, and August (Schulze 1997a), with low axis scores corresponding to high daily minimum temperature and vice versa.
3. The gradient along the 3rd axis of the **TWINSpan 3+** grid ordination is also broadly related to most of the **frost**, and some of the **chill unit** parameters mapped in Schulze (1997a).

Two climatic parameters that might explain the floristic gradient along the 3rd axis of the **TWINSpan 5+** ordination (Fig. 47) are:

1. **Means of daily maximum temperature (°C)** for **spring** with low means in the southern sector of the study area and high means (corresponding to low means on the ordination axis) in the northern and central interior (Schulze 1997a).
2. **Means of daily minimum temperature (°C)** in **summer** with low minimum temperatures along the southern escarpment and adjacent areas, and higher minimums in the northern parts, particularly the north-eastern sector of South Africa (Schulze 1997a).

Axis 4

The **TWINSpan 3+** gradient along the 4th axis (Fig. 44) seems to be related to:

1. **Means of daily maximum temperature (°C)** for the months of **spring**, with low maximums along the southern escarpment and adjacent parts of southern

Africa, and high maximum temperatures in the northern and central parts (Schulze 1997a).

2. **Daily mean temperature (°C)** for the **summer** months, with low temperatures in the south, especially on the high plateau of Lesotho, increasing towards the central and northern parts of the study area.

3. **Mean annual temperature (°C)**, low means occur on the high plateau of Lesotho and the southern escarpment, gradually increasing towards the coast and interior, with high mean temperatures in the northern and central parts of South Africa (Schulze 1997a).

4. **Heat units (°days)** for the **summer** months of October to March, with 10 °C as base (Schulze 1997a). Low values occur on the high lying areas of the central plateau and along the escarpment with higher values in the northern and central parts of the study area.

The change in species composition along the 4th axis of the **TWINSPAN 5+** ordination (Fig. 48) might be explained by:

1. **Means of daily maximum temperature (°C)** in **spring** or, to a lesser degree, the **Means of daily minimum temperature (°C)** in **winter** with low temperatures more or less corresponding with high axis scores and vice versa.

2. **Mean annual temperature (°C)** with low degrees corresponding to high values on the ordination axis and vice versa.

3. **Heat units (°days)** for the **summer** months of October to March, with 10 °C as base (Schulze 1997a). Low axis scores correspond more or less to high degree days and vice versa.

Discussion

The DCA ordination supports the TWINSpan classification of grid squares in that the bryogeographic Regions generally cluster together in ordination space. The distribution of grids along the first axis repeats the general pattern of the major TWINSpan division: a gradient from sub-tropical Zambezi and Afromontane grids with low scores on the one side to temperate Karoo-Namib and Highlands grids with high scores on the other.

Over wide (broad) landscapes climatic gradients are generally considered to have greater influence on the distribution of plants, including bryophytes, than edaphic factors (Belland 1987, Woodward 1987, Mielke 1989, Pederson 1989, Hill & Dominguez Lozano 1994, McLaughlin 1994, Bates 1995, Akin in Schulze 1997, and references in O'Brien 1993). This hypothesis has also been proposed for southern Africa (Adamson 1938, Werger 1983), where the major climatic gradient runs from east to west, or from humid to hyper-arid (Schulze & McGee 1978; Partridge 1997; Schulze 1997, 1997a). At a broad scale, Ellery *et al.* (1991) recently confirmed that there exists a high degree of correlation between climate and the distribution of biomes in southern Africa, in particular the grassland biome, and O'Brien (1993) found that climate accounts for a large percentage of the "...west-to-east pattern of increasing species richness." More examples are mentioned later on in the Discussion.

Most of the climatic factors that might be related to the main east-west change in floristic composition of mosses in southern Africa are associated with moisture. Of these the mean annual precipitation (MAP) gives the best fit. This is not surprising as it is well known that humidity can have a strong influence on the composition of bryophyte floras (Richards 1984a, Gradstein & Pocs 1989, Gradstein *et al.* 1989). Climatic and in particular rainfall variability over southern Africa can be explained by a number of factors including latitudinal displacements of major easterly and westerly wind belts, meridional displacements of the African tropical-temperate cloud band and convergence zone, and changes in sea-surface temperature fields (Tyson 1999). According to Schulze (1997a) physiography is one of the most important factors influencing the spatial distribution of MAP in southern Africa.

A water or moisture gradient, and in particular rainfall, has long been accepted as probably the most important climatic variable determining the diversity and distribution of (vascular) plants in southern Africa (Adamson 1938; Liversidge 1962; Schulze & McGee 1978; Tainton 1981; Werger 1983, Meadows 1985; Schulze 1997, 1997a). The following are examples of recent studies lending support to this hypothesis, not only for southern Africa but also for other parts of Africa:

1. Linder (1991) showed that rainfall is the best predictor of species richness in the south-western Cape.
2. O'Brien (1993) found that woody plant species richness increases with an increase in moisture.
3. Kornas (1993) and Dzonko & Kornas (1994) have shown that the humidity (rainfall) gradient is the main factor influencing the differentiation of pteridophyte floras in tropical Africa.
4. Cawe (1994) found a high degree of correlation between rainfall and Acocks' veld types in the Transkei.
5. The most important environmental factors which determine the vegetation zonation on Mt. Kilimanjaro, Tanzania are the rainfall and the temperature (Pocs 1994).
6. In a quantitative analysis of the vegetation-environment relationships in the southern Langeberg Mountains, McDonald *et al.* (1996) found that rainfall is one of the major environmental gradients determining the distribution patterns of plant communities.
7. Cowling *et al.* (1997b) found that warm, moist and aseasonal environmental conditions are responsible for high plant diversity in the "...tropical-derived savanna and grassland flora,...".

The latitudinal north-south gradient along the 2nd DCA ordination axis is more difficult to interpret but appears to be related to temperature, and in particular the effect of temperature on the availability of moisture. Factors affecting temperature include latitude, altitude, continentality, seasonality, topography, and longitude in those regions with an east-west alignment (Schulze 1997a).

Axes 3 & 4 of the DCA ordination seem to represent the same floristic gradient, running both altitudinally and latitudinally, which is related to several temperature parameters and indices. Together with precipitation, temperature was singled out by Adamson (1938) as an important climatic factor influencing the distribution of southern African plants.

The species composition of the southern African moss flora can therefore be explained by two main climatic factors, precipitation (moisture) and temperature, acting independantly and in combination. This hypothesis should now be tested by 1) employing a direct gradient analysis as performed by Canonical Correspondence Analysis (CCA), a multivariate gradient analysis that relates species composition directly to measured environmental variables, and 2) by experimentation.