

CHAPTER 5**FLORISTIC ELEMENTS IN THE MOSS FLORA OF SOUTHERN AFRICA***Chapter Outline*

- A. Historical Perspective 190
 - I. Vascular plants 191
 - II. Bryophytes 203
- B. TWINSPLAN 3+ Classification of Species 206
 - 1. First level of division 206
 - 2. Second level of division 210
 - 3. Third level of division 210
 - Discussion 211
- C. Classification of the Bryofloristic Elements of Southern Africa 213
 - I. Introduction 213
 - II. Descriptions of Elements and Subelements 214
 - 1. Eastern Highlands Element 214**
 - 1.1 Mont Aux Sources Subelement 216
 - 1.2 Widespread Subelement 217
 - 2. Cape Element 220**
 - 2.1 West Coast Subelement 222
 - 2.2 Boland Subelement 225
 - 3. Afromontane Grassland Element 227**
 - 3.1 Disjunct Cape Peninsula Subelement 229
 - 3.2 Drakensberg Subelement 230
 - 4. Afromontane Forest Element 231**
 - 4.1 Widespread Afromontane Subelement 235

4.2 Tropical Afromontane Subelement 237

D. World Distribution Elements 240

E. DCA Ordination of Species 241

1. TWINSPAN elements 242

2. Distributional gradients 242

Discussion 245

A. Historical Perspective

Since numerical programs generally perform classification or ordination on areas (grid squares or releves) and species simultaneously, the description and interpretation of floristic elements have become an integral part of phytogeographic investigations. Recent examples involving vascular plants and ferns include studies by Gill *et al.* (1985), Pederson (1990), Myklestad & Birks (1993), Dzwonko & Kornas (1994) and Heikkinen *et al.* (1998). Good examples of bryophyte distribution (floristic) elements are those described by Proctor (1967) and Belland (1987). More examples are listed in Chapter 2 under *Numerical Analysis*.

In southern Africa phytogeographic elements have received much less attention than phytogeographic regions (phytochoria), so much so that in recent reviews of southern African phytogeography by Werger (1978) and Cowling & Hilton-Taylor (1997) no mention is made of phytogeographic elements within the FSA area. Where phytogeographic elements have been described for southern Africa it has generally been for certain plant groups only (e.g. Nordenstam 1969, Acocks 1971, Kurzweil *et al.* 1991), for limited geographic areas (e.g. Weimarck 1941, Hilliard & Burt 1987, Linder *et al.* 1992), or both (e.g. Geldenhuys 1994). An exception is the world distribution elements described for families and genera in the vascular plant flora of the entire FSA region by Goldblatt (1978). Some of the more recent studies describing biogeographic elements at the subcontinental scale or below are briefly discussed here:

I. Vascular plants

Weimarck (1941) recognised a number of world distribution (phytogeographic) elements in the Cape flora:

- Cape element
- Karoo element
- Afromontane element
- Subtropical–tropical African element
- Mediterranean element
- North-hemispherical temperate element
- Antarctic element
- Cosmopolitan element

He subdivided the Cape element, “...i.e. genera having their actual centre within the region.”, into 17 ‘phytogeographical groups’ defined as “...species with equivalent or nearly equivalent distribution areas.” (Weimarck 1941). These species groups were divided into two main groups: 1) Species endemic to the Cape proper, and 2) Species also occurring outside the Cape proper. Weimarck’s (1941) elements were therefore based on the distribution of vascular plant genera which occur in the Cape (the Cape flora) while his ‘phytogeographical groups’ were based on the distribution of species belonging to genera of the the Cape element.

Weimarck’s (1941) subdivision of the Cape element into phytogeographical (species) groups

A. Species Endemic in the Cape Proper

1. The Cape Ubiquists
2. The Cape Ubiquists with a Knysna Interval
3. The Karoo-Mountain–Western Group
4. The Southern Group

5. The Southern Species with a Knysna Interval
6. The Western Group
7. The Lange Berg–South-Western Group
8. The South-Western Endems
9. The North-Western Endems
10. The Lange Berg Endems
11. The Karroo-Mountain Endems
12. The South-Eastern Endems

B. Species occurring (also) outside the Cape Proper

13. The Cape–Drakensberg Group
14. The Drakensberg Endems
15. The Drakensberg–Tropical African Mountain Group
16. The Montane Endems within Tropical Africa
17. The Madagascar Endems

Weimarck (1941) has further identified a number of distribution centres, some subdivided into subcentres: 1) within the Cape proper, and 2) outside the Cape proper. Distribution centres located within the Cape area are called ‘endem-centres’:

The Cape endem-centres and subcentres of Weimarck (1941)

1. The South-Western Centre
 - a. The Cape Peninsula Subcentre
 - b. The Frensch Hoek Subcentre
 - c. The Bredasdorp Subcentre
 - d. The Hottentotsholland Subcentre
2. The North-Western centre
 - a. The Great Winterhoek Subcentre
 - b. The Cedarberg Subcentre
 - c. The Kamiesberg Subcentre

- d. The Hantam–Roggeveld Subcentre
- 3. The Lange-Berg centre
- 4. The Karoo-Mountain centre
- 5. The South-Eastern centre
 - a. The Zitzikamma Subcentre
 - b. The Cockscomb Subcentre
 - c. The Zuurberg Subcentre

Distribution centres and subcentres of the Cape element outside the Cape Proper

- 6. The Drakensberg Centre
- 7. The Tropical African Mountain Centre
 - a. The Inyangani Subcentre
 - b. The Mlanja Subcentre
 - c. The Rungwe Subcentre
 - d. The Katanga Subcentre
 - e. The Kenya Subcentre
 - f. The Kivu Subcentre
 - g. The Abessinian Subcentre
 - h. The Angolan Subcentre
 - i. The Cameroon Subcentre
- 8. The Madagascar Centre

Weimarck (1941) has also classified the 17 phytogeographical groups (elements) in the Cape element according to the number and location of the distribution centres covered by each: 1) Species that occur in two or more Cape endem-centres (phytogeographical groups 1 to 7), 2) elements whose distributions coincide with one of the endem-centres (phytogeographic groups 8 to 12), and 3) species with distribution centres outside the Cape area (phytogeographical groups 13 to 17).

Gaps in the distributions of the Cape species are described as 13 ‘intervals’ by Weimarck (1941). He distinguished between two kinds of intervals: 1) the intervals within the Cape proper (intervals 1-5) and 2) the intervals outside the Cape proper (intervals 6-13):

Intervals in the geographic distribution of the Cape element according to Weimarck (1941)

A. The Intervals within the Cape Proper

1. The North-Western Interval
2. The Doorn River Interval
3. The Tulbagh Interval
4. The Karoo Interval
5. The Knysna Interval

B. The Intervals outside the Cape Proper

6. The Kaffraria Interval
7. The Limpopo Interval
8. The Zambesi Interval
9. The Nyasa Interval
10. The East African Interval
11. The Rudolph Interval
12. The Upper-Zambesi–Kassai Interval
13. The Congo Basin Interval

In conclusion Weimarck (1941) compared the Cape element with other African elements, i.e. the Forest element, Karroo element, and the Afro-montane element. Within the latter he identified 5 ‘distribution-types’.

Distribution types within the Afromontane element of Weimarck (1941)

1. A ubiquitous group, distributed in west as well as east Africa
2. An eastern group, from Ethiopia to the Drakensberg
3. A southern group, limited to the southern mountains in Africa
4. A northern group, distributed in northern tropical Africa
5. A number of groups with species endemic in one or two adjacent subcentres

The criticisms of Weimarck's centres listed by Cowling *et al.* (1992) are largely unfounded. Weimarck (1941) clearly stated that his aim was to delimit species groups and endem-centres within the Cape element. It is also clear that his phytogeographic groups and centres are floristic elements and phytogeographic centres, and not biogeographic areas or "...phytogeographical regions..." as suggested by Cowling *et al.* (1992).

Levyns (1954) found that the genus *Muraltia* has a geographic distribution characteristic of the Cape Element. The magisterial divisions of Caledon, the Cape and Paarl-Stellenbosch were identified as the most species rich.

In 1962 Stuckenberg (1962) described the 'montane palaeogenic element' based on the distributions of palaeogenic invertebrates. He also recognised this element in other insect as well as plant groups and regarded it as an ancient distribution pattern (Stuckenberg 1962). This element was divided into two main centres of distribution: 1) the Cape Centre comprising the Cape Fold mountains, and 2) the Eastern Highlands Centre along the eastern escarpment. The Eastern Highlands Centre was subdivided into three subcentres: 1) The Basutoland–Drakensberg Highlands and Eastern Plateau Slopes, 2) The Amatola Range, and 3) The Eastern Transvaal Subcentre.

The montane palaeogenic element of Stuckenberg (1962)

- Cape Centre

- Eastern Highlands Centre
 1. Basutoland-Drakensberg Highlands and Eastern Plateau slopes
 2. Amatola Range
 3. Eastern Transvaal Subcentre

Liversidge (1962) identified nine ‘generalised distribution patterns’ of southern African birds and related these to the vascular plant vegetation.

Dahlgren (1963) identified *Aspalathus* as belonging to the Cape element of Weimarck (1941). He somewhat modified Weimarck’s (1941) system to classify the species into floristic elements.

Croizat (1965) identified four main ‘biogeographic centres’, or “...centres of massing and form-making,...” in southern Africa. These were formally described as: 1) Barberton Centre, 2) Gariep Centre, 3) Caledon Centre, and 4) Albany Centre.

In his article *Die florengebiere von Südwestafrika* **Volk** (1966) recognised a number of elements and centres in the flora of Namibia but did not make a clear distinction between floristic regions and elements.

Although Zimbabwe falls outside the borders of the FSA region, many of the broad-scale phytogeographic elements described for that country by **Wild** (1968) range into the FSA area. However, from his statement “ All elements above, except the montane and submontane elements (including the Cape element), are merely subdivisions of the Sudano-Zambesian phytogeographical region or Zambesian domain as defined by **White** (1965) and earlier authors.” it is clear that **Wild** (1968) confused the distinction between floristic elements and floristic regions.

The principle phytogeographic elements of the Zimbabwe flora according to Wild

13. The Upper Karoo (1968)

14. The Southern Karoo (1968)

1. Cape element
2. Afro-montane element
3. High rainfall forest element
4. Forest or forest-savanna element
5. Medium altitude woodland or savanna-woodland elements
6. Low altitude savanna or savanna element on more basic soils
7. Kalahari Sand element

Nordenstam (1969) studied distribution patterns in the genus *Euryops* (Asteraceae), which has its main distribution area in southern Africa. Five main 'phytogeographical groups' and 24 subdivisions are described in detail. Subdivision of the 'Cape Species' was largely based on the classification of Weimarck (1941).

Phytogeographical Groups in the genus Euryops (Nordenstam 1969)

Nordenstam (1969) studied

of diversity and A. Cape Species

1. The Cape Ubiquists
2. The Karoo Mountain–Western Group
3. The Southern Group
4. The Western Group
5. The Langeberg–Southwestern Group
6. The Southwestern Endemics
7. The Northwestern Endemics
8. The Langeberg Endemics
9. The Karoo Mountain Endemics
10. The Southeastern Endemics

B. South African (Extra-Cape) Species

11. The Western Upper Karoo Endemics

12. The Roggeveld–Cape Karroo Group
 13. The Upper Karroo Group
 14. The Sneeuwbergen Endemics
 15. The Sneeuwbergen–Drakensbergen Group
 16. The Sneeuwbergen–Cape Group
 17. The Drakensbergen Endemics
 18. The Karroo Ubiquists
 19. The Namaqualand–Cape Group
 20. The Namaqua Group
 21. The Vanrhynsdorp Karroo Endemics
 22. The Gariep Endemics
 23. The Highveld Group
 24. The Kaffraria–Transkei Group
- C. East Tropical African Species
- D. Ethiopian Species
- E. Somali–Arabian Species

Nordenstam (1969) also identified a number of ‘phytogeographical centres’ or centres of diversity and endemism in southern Africa, which are listed under *Historical Perspective*, Chapter 3. In conclusion Nordenstam (1969) identified three trends in the floristic plant geography of southern Africa: “(i) Increasing number of floristic units. (ii) Increasingly physiognomic classification. (iii) Tendency to particularize the Cape Flora.” which he correctly thought “...somewhat hampered the understanding of the floristic phytogeography of the South African Region.”

Acocks (1971) described nine South African distribution patterns or ‘types of distribution’ in a selection of 44 ecologically important grasses:

Patterns of distribution in certain ecologically important grasses (Acocks 1971)

The North-eastern distribution of tropical and sub-tropical species

The south-eastern type of distribution

The Kalahari type of distribution

The north-western type of distribution

The Karoo type of distribution

The east-central type of distribution

The south-coastal and mountain type of distribution

The western type of distribution

The south-western type of distribution

Clayton (1975) used a clustering program to delimit floristic elements in the mountain grasses of Africa. The species groups were called “Chorological Regions” in one place and “chorological elements” in another. A mixture of categories (Sub-kingdom, element, Region and endemic centre) was used in the classification and some of the floristic elements were compared to floristic regions described by others. This confusion between floristic elements and regions continued in a paper on the “generalized distribution patterns of grass species in the Old World” by **Clayton & Cope** (1979). However, in an earlier paper Clayton (1974) drew a clear distinction between areas of the world with characteristic floras of grass genera (regions) and grass genera with similar distribution patterns (elements).

In *An analysis of the flora of southern Africa...* **Goldblatt** (1978) identified a number of distribution patterns in the ‘phanerogamic families and genera’ of the FSA area:

World distribution elements in the phanerogamic families and genera of southern FSA area: the Cape region of southern Africa (Goldblatt 1978)

Cosmopolitan/Pantropic (22.8%)

Paleotropic (13.7%)

African-Madagascan (6.2%)

African (19.1%)

African-Eurasian (4.2%)

African-New World (2.5%)

African-Australian and South America (1.2%)

Endemic (30.2%)

Goldblatt (1978) recognised three main distribution patterns “...among the genera of southern and tropical Africa.”: 1) tropical taxa, 2) arid elements of the Karoo-Namib and Kalahari, and 3) a Cape -Afromontane group of “...temperate southern African genera, mostly centered in the Cape, which extend outside southern Africa mainly in highland areas...”.

Denys (1979) described a number of phylogeographic elements in tropical Africa, based on a factor analysis of distribution maps published in the *Distributiones Plantarum Africanarum* series. Some of these elements (which includes a few bryophytes) range into the northern provinces of South Africa.

Cowling (1983) has subjectively classified vascular plant species in the south-eastern Cape into 12 ‘phytochorological groups’ based on the distribution of the species in the phytogeographic regions (phytochoria) of White (1982). These elements were classified as follows: 1) species endemic to a particular phytochorion (four groups), 2) species linking two usually adjacent phytochoria (six groups), 3) tropical wides (one group), and 4) widespread species (one group).

Linder (1983) delimited centres of endemism, overlap regions, and outliers within the distribution range of the Disinae (Orchidaceae). Two centres are recognised within the FSA area: the Cape centre and the Natal-Transvaal centre. The geographic distribution of this group shows that it belongs to the Afromontane element.

In a phytogeographic analysis of the flowering plants of the southern Drakensberg, **Hilliard & Burt** (1987) described six 'classes of distribution' based on the world distributions of the genera, and 10 'species groups', some subdivided into subgroups, based on the geographic distributions of species.

Almborn (1988) identified the following distribution patterns in selected lichens of South Africa: 1) Ubiquitous species with a more or less worldwide distribution, 2) Steppe and desert species, 3) Montane species, 4) Oceanic species, 5) Tropic-oceanic species, 6) Maritime species, 7) Endemic species of South Africa.

The eight 'species groups' described in the vascular plant flora of the the Karoo Nature Reserve near Graaff-Reinet by **Palmer** (1990) are based on the distribution of differential species (of the plant communities) in the Biomes of Rutherford & Westfall (1986). These species groups can therefore be regarded as ecological rather than floristic elements.

Van Wyk (1990) classified the vascular plant flora of the Pondoland Centre into four floristic elements: Afromontane, Endemic sandstone, Cape, and Mixed tropical elements.

Hoffmann & Cowling (1991) described seven 'generalised tracks' in the vascular plant flora of the lower Sundays River Valley (Eastern Cape Province) based on the distribution of species relative to the phytochoria of White (1983).

The generalised tracks in a sample flora of the lower Sundays River valley, Eastern Cape (Hoffmann & Cowling 1991)

WID - widespread species

TRW - tropical widespread species

TZL - Tongaland-Pondoland – Zambezian linking species

TEN - Tongaland-Pondoland endemics

TKL - Tongaland-Pondoland – Karoo-Namib linking species

KEN - Karoo-Namib endemics

KZL - Karoo-Namib – Zambezian linking species

Species of the Coryciinae (Orchidaceae) were subjectively classified into a number of floristic groups or 'centres of endemism' by **Kurzweil et al.** (1991). These floristic elements were equated to the floristic regions delimited by a numerical classification of grid squares (see *Historical perspective*, Chapter 4), which is of course not possible. From the descriptions of the species groups, where they compared their groups with established phytochoria, it is evident that **Kurzweil et al.** (1991) confused the distinction between floristic elements and floristic regions. The Coryciinae is widespread in the more temperate parts of southern Africa and forms part of the Afrotropical Track (**Kurzweil et al.** 1991).

Centres of endemism in the geographic distribution of the Coryciinae according to Kurzweil et al. (1991)

Drakensberg

Central African Centre

Karoo-margins species

Cape Floristic Centre

Ubiquitous

Southern group

Northern group

SW. Cape

W. Cape

SW.- and S. Cape

Lotononis of the Fabaceae is a southern African genus with a temperate distribution in Africa (**Van Wyk** 1991). The centres of diversity and endemism are listed under *Historical Perspective* in Chapter 3.

Linder *et al.* (1992) identified three world distribution elements or 'tracks' in the Cape flora: 1) the Gondwana track, 2) the African track, and 3) the boreal track. For phytogeographic patterns within the Cape flora they referred to the 'centres' of Weimarck (1941) and Cowling *et al.* (1992).

Geldenhuis (1994) summarized the geographical distribution of southern Cape forest species "...by means of 18 categories which describe the western and eastern distribution limits of the species". These categories were combined into "...five species groups which represent separate geographical regions." or 'generalised tracks'. The phrase: "...which represent separate geographic regions". is confusing and should rather read: *with distinctive distribution patterns*. Geldenhuis (1994) also discussed the ecology of the groups and the origin and evolution of the southern Cape forest flora.

Generalized tracks in the southern Cape forest species (Geldenhuis 1994) with the percentage of the total flora represented by each

Western Cape group (15%)

Southern Cape group (4%)

Eastern Cape group (25%)

Afromontane group (21%)

Transgressor group (35%)

II. Bryophytes

The most recent attempt to identify distribution (floristic) elements in the bryophytes of the world is *Phytogeography of the Bryophyta* by Schuster (1983). He divided his world distribution elements into seven main groups, subdivided into a number of subelements.

The main distribution elements in the bryophytes of the world according to Schuster (1983)

- Laurasian Patterns
- Gondwanalandic Patterns
- Tropical Distribution Patterns
- Bipolar Ranges
- 'Cosmopolitan' Ranges
- Anomalous Distribution Patterns
- Man-Dispersed Taxa

In the publication series *East African bryophytes* (**Bizot & Pocs** 1974, 1982; **Ochyra & Pocs** 1985a; see the British Bryological Society Website:

www.rbge.org.uk/bbs/eab.htm for a list of all 15 publications in the series) and *Results of a bryogeographical expedition to east Africa* (**Bizot et al.** 1979, 1985; **Ochyra & Sharp** 1988) mosses and liverworts of tropical and subtropical Africa were assigned to floristic elements, many of which are applicable to southern Africa mosses. These elements refer to the total or world distributions of African mosses.

Little work has been done on the phytogeography of southern African bryophytes. **Schelpe** (1953) studied the distribution of bryophytes in three vegetation zones (Montane Forest, Fynbos and Subalpine *Erica* Zones) of the KwaZulu-Natal Drakensberg. **Magill & Vitt** (1981) found that the moss genus *Macrocoma* (Orthotrichaceae) fits into an Afromontane distribution pattern.

In 1988 **Russell & Van Rooy** (1988) identified the following world distribution patterns in the bryoflora of Namibia:

- Cosmopolitan (7% of the total bryoflora),
- Widespread (15%),
- Southern and Eastern Africa (14%),

Southern Africa (33%),
SWA/Namibia endemic (11%), and
Disjunct/anomalous (20%).

In the same year **Russell & Van Rooy** (1988a) referred to a few distribution patterns in the moss flora of the eastern Cape forests.

Dilg & Frahm (1997) identified three broad-scale phytogeographic elements in the epiphytic bryophytes of the southern KwaZulu-Natal Drakensberg. They are: 1) species distributed in temperate and subtropical Africa, 2) species distributed in tropical Africa, and 3) cosmopolitan taxa.

Hodgetts *et al.* (1999) briefly discussed the following 'phytogeographical patterns' or world distribution elements in the moss flora of Lesotho and adjacent Drakensberg Mountains:

1. The circum-subantarctic pattern of Seki (1974)
2. The South Africa distribution pattern of Seki (1974) or the tropical alpine element of a wider tropical Afro-American distribution after Gradstein *et al.* (1983)
3. Bipolar distributions
4. The East African or Afromontane element
5. African elements
6. Cosmopolitan elements
7. Endemics of the high Drakensberg

They found that a considerable number of Drakensberg species belongs to the East African or Afromontane element.

B. TWINSPAN 3+ Classification of Species

TWINSpan 3+ classification of southern African moss species into floristic or phytogeographic elements (groups of species with similar spatial or geographic distributions within southern Africa).

The dendrogram resulting from the TWINSpan 3+ classification of moss species is shown in Fig. 26.

1. First level of division

The first and major TWINSpan division splits the TWINSpan 3+ data set into two large groups or elements (Fig. 49). Element 1/1 (first level of division, first group from the left in the TWINSpan 3+ classification of species) is the smallest of the two main elements with 131 species; the larger element 1/2 consists of 370 species (Appendices III,1 & III,2). The differences in the taxonomic composition of these two main elements are striking.

Element 1/1: Consists mostly of acrocarpous taxa in the Orders Dicranales, Pottiales, Funariales, Bryales and Orthotrichales (see Magill & Van Rooy, 1998 for a *Conspectus of classification*) of which the Pottiales is particularly well represented. The families Encalyptaceae, Bryobartramiaceae, Grimmiaceae and the endemic family Wardiaceae are restricted to this group. Most of the taxa in this element are xerophytic and therefore adapted to life in the semi-arid conditions of the main distribution area. Most of the ephemerals (see discussion under the *Karoo-Namib Region, Chapter 4*) such as six of the *Archidium* species, all four of the *Pleuridium* species, *Aloina bifrons*, *Acaulon recurvatum* and *A. leucochaete*, *Crossidium spiralifolium*, *Microcrossidium apiculatum*, *Pottia namaquensis*, *Bryobartramia novaevalesiae*, *Chamaebryum pottioides*, *Gigaspermum repens*, *Ephemerum namaquense* and *E. rehmannii*, *Cygnicollum immersum*, and *Goniomitrium africanum* (Appendix III,1) are part of this element. Pleurocarpous mosses of the Order

Hookeriales are absent from this element and the Orders Isobryales, Thuidiales and Hypnobryales are poorly represented.

Element 1/1 is mainly distributed in the south-western, winter-rainfall part of the study area as well as the high altitude, temperate areas of the interior plateau (Fig. 50). Two main centres of distribution are recognised within this element and Stuckenberg (1962) suggested that they be called the Cape Centre and the Eastern Highlands Centre:

- **Cape Centre:** The main distribution centre of this element is located in the south-western Cape Fold Mountains (Fig. 50), in particular Table mountain (grid 3318 C with 64 species), the mountains at Stellenbosch (3318 D with 54 species), the mountains of the Boland (3319 C with 51 species) and the Cedarberge at Clanwilliam (3218 B with 47 species).
- **Eastern Highlands Centre:** Consists of the high plateau of Lesotho, in particular grid 2828 D, the Mont Aux Sources – Oxbow area with 40 species (Fig. 50). Stuckenberg (1962) divided this centre into three subcentres: 1) The Basutoland–Drakensberg Highlands and Eastern Plateau Slopes, 2) The Amatola Range. and 3) The Eastern Transvaal Subcentre.

Other areas with relatively high species concentrations are (Fig. 50):

- the Bokkeveldberge at Niewoudtville (grid 3319 A),
- the mountains at Springbok (2917 D),
- the mountains of the Richtersveld, in particular grid 2927 A,
- the highlands at Windhoek in Namibia (2217 B),
- the Outeniqua Mountains between George and Oudsthoorn (3322 A & C),
- the high altitude Karoo mountains around Graaff Reinet (3224 A & B, 3124 D) and Middelburg (3024 B, 3025 C) and further north to Reddersburg in the southern Free state (2926 A),

- and the Witteberge in the Zaaron–Lady Grey area (3027 A & C).

Element 1/2: The other main TWINSPAN division consists of 370 species (Appendix III,2). The pleurocarpous Orders Isobryales, Hookeriales, Thuidiales and Hypnobryales are restricted or largely restricted to this element in southern Africa. It is generally accepted that pleurocarpous mosses are much more abundant in stable, mesophytic (forest) habitats than acrocarps (Vitt 1979, 1984; Buck & Vitt 1986). In mesic environments (Buck & Vitt 1986) “...competitive interactions, broad niche overlap and long growing seasons...”, as well as epiphytic habitats, give advantage to pleurocarpous mosses with their ability to form mats through continuous growth of the gametophyte (Vitt 1984, Buck & Vitt 1986).

Acrocarpous taxa adapted to subtropical forest/woodland environments, such as species of *Leucobryum*, *Calymperes*, *Syrrhopodon* and *Rhodobryum* are also restricted to this element. Many of the xerophytic Orthotrichaceae, adapted to habitats on trees and rocks within the Afromontane forest areas (e.g. *Macrocoma*, *Macromitrium* and *Schlotheimia* species) form part of this element. The following families, mostly pleurocarpous, have all their southern African representatives confined to the subtropical element:

Families restricted to the main subtropical, mesophytic element (Element 1/2)

Seligeriaceae	Cryphaeaceae
Splachnaceae	Leucodontaceae
Mniaceae	Prionodontaceae
Eustichiaceae	Trachypodaceae
Erpodiaceae	Pterobryaceae
Rhachithecaceae	Meteoriaceae
Rhabdoweisiaceae	Leptodontaceae
Racopilaceae	Neckeraceae
Fontinalaceae	Thamnobryaceae

Hookeriaceae	Brachytheciaceae (in 67 species) to
Stereophyllaceae	Entodontaceae
Leskeaceae	Plagoptheciaceae with 93 species
Thuidiaceae	Catagoniaceae
Rigodiaceae	Sematophyllaceae (with 24
Amblystegiaceae	

Element 1/2 is widely distributed in the northern, eastern and southern subtropical (mesic) or Afromontane areas of southern Africa (Fig. 51). The main centres of distribution are:

- **Mpumalanga Centre.** The ‘eastern Transvaal’ or Mpumalanga escarpment in the Graskop – Blyderivierspoort area (grid 2430 D with 163 species) and the Nelspruit – Sabie area (2530 B with 104 species). Croizat (1965) formally named this centre the Barberton Centre.
- **KwaZulu-Natal Centre.** Situated in the KwaZulu-Natal Drakensberg and Midlands area, in particular the montane forests in the Pietermaritzburg – Karkloof area (grids 2930 C with 150 species and 2930 A with 106 species) and the ‘High Berg’ from Mont Aux Sources in the north to Sehlabathebe in the south (grids 2828 D with 126, 2829 C with 102, 2929 A with 124, and 2929 C with 121 species). This centre might therefore be subdivided into two subcentres (Fig. 51): 1) the Drakensberg Subcentre and 2) the Midlands Subcentre.

Other areas of relatively high species concentrations include:

- The entire escarpment of the northern provinces, from the Soutpansberg in the north (grid 2230 C with 68 species) to Swaziland in the south (grid 2631 A with 76 species).

- The Magaliesberg, from Pretoria in the east (grid 2528 C with 67 species) to Rustenburg in the west (grid 2527 C with 56 species).
- Montane forests in the Eshowe – Empangeni grids (2831 C with 93 species and 2831 D with 63 species).
- The montane forests in the King William's Town area (grid 3227 C with 84 species), the southern Cape or 'Knysna' forests (Van der Merwe 1998), especially in the Outeniqua Mountains at George (grid 3322 C with 80 species).
- The montane forest on the eastern slopes of Table Mountain (, grid 3318 C with 122 species, which is the main secondary centre of distribution.

2. Second level of division

At the second level of the TWINSpan 3+ division the two main centres (Cape and Eastern Highlands) in the south-western, xerophytic element (element 1/1) are neatly separated as species groups or elements 2/1 and 2/2 (Fig. 49). Element 2/1 consist of 47 species, centred on the high interior plateau of Lesotho (Fig. 52). Element 2/2 consist of 84 species, mainly distributed in the south-western corner of the study area (Fig. 53).

The other dichotomy splits the widespread, subtropical group of species (element 1/2) into element 2/3 of 63 species, centred on the Mpumalanga escarpment, KwaZulu-Natal Drakensberg and Midlands, and the mountains of the Cape Peninsula and Boland (Fig. 54), and element 2/4, by far the largest of the 4 elements, with 307 species, widely distributed along the escarpment of the northern provinces, KwaZulu-Natal, and down to the southern Cape (Fig. 55). The group has it's highest species diversity on the Mpumalanga escarpment, the northern part of the KwaZulu-Natal Drakensberg and Natal Midlands, and Table Mountain in the south-western Cape.

3. Third level of division

The four elements delimited at the 2nd level of division are here subdivided into eight groups (Fig. 49):

- 1) Element 2/1 is split into element 3/1, a group of 35 species with restricted distributions, and a smaller element 3/2 consisting of 12 species with wide geographic distributions (Figs. 56 & 57).
- 2) Element 2/2 with its south-western Cape distribution is subdivided into element 3/3 consisting of 57 species with a 'west coast' distribution, and element 3/4 with 27 species restricted to the southern part of the distribution range (Figs. 58 & 59).
- 3) Element 2/3 is split into a small group of 11 species (element 3/5), largely absent from the KwaZulu-Natal Drakensberg, and a larger group of 52 species (element 3/6), centred in this area (Figs. 60 & 61).
- 4) Element 2/4 is divided into a widespread group of 49 species (element 3/7) and a large group of 258 species (element 3/8) whose distributions are largely centred in the KwaZulu-Natal Midlands and the Mpumalanga escarpment (Figs. 62 & 63).

TWINSPAN goes on to subdivide the species groups into 16 elements at the 4th level of division, 30 elements at the 5th level, and 50 elements at the 6th and last level of division (Fig. 49). Although at least some of the elements delimited at the 4th, 5th and 6th levels are ecologically meaningful, they are not treated here as this study is concerned with broad-scale patterns only. The species groups delimited at the second and third levels of division are formally described as phytogeographic Elements and Subelements, analogous to the Regions and Domains described from the TWINSPAN classifications of grid squares (see Chapter 4).

Discussion

The TWINSPAN classification has successfully distinguished between a group of xerophytic mosses, mainly distributed in the arid and semi-arid, temperate south-western and central parts of the study area (element 1/1 of the TWINSPAN 3+ classification), and a mesophytic group distributed in more stable, subtropical habitats in the northern, eastern and southern parts of southern Africa (element 1/2 of the TWINSPAN 3+

classification). The species classification therefore follows the same pattern as the grid classification where the study area was divided into a semi-arid temperate south-western region (region 1/1 of the TWINSPAN 3+ and 5+ classifications) with a xerophytic moss flora, and a subtropical region in the northern and eastern parts, extending southward along the coast (region 1/2 of the TWINSPAN 3+ and 5+ classifications) with a mesophytic moss flora.

The distribution area of the south-western element (element 1/1) coincides with that of the montane palaeogenic element of Stuckenberg (1962) and the Cape-Afromontane group (of genera) of Goldblatt (1978). The distribution area also coincides with the high altitude areas of an Afrotemperate Track mentioned by Kurzweil *et al.* (1991). It is difficult to compare the bryofloristic elements of southern Africa with the floristic elements of Weimarck (1941) since his elements refer to distribution patterns within the Cape flora only. However, Weimarck's (1941) Cape element is more or less comparable to the south-western element or element 1/1 of the moss classification.

The subtropical element (element 1/2 of the species classification) is probably part of an East African or Afromontane element (Weimarck 1941, Hodgetts *et al.* 1999), also called the African track (Linder *et al.* 1992), distributed throughout the Afromontane areas of Africa. Most phytogeographers do not make a clear distinction between this element and the Afrotemperate element, just as they do not regard the Afroalpine region in southern Africa as distinct from the Afromontane region. The southern part of the Afromontane element, from Malawi down to the Cape, has been described as the South African element by Clayton (1975). Weimarck (1941) distinguished five distribution types in the Afromontane element but none of these is recognisable in the TWINSPAN classification.

The distribution area of element 1/2 more or less coincides with the 'North-eastern distribution of tropical and subtropical (grass) species' plotted by Acocks (1971) and the distribution area of mixed evergreen forests in southern Africa (Geldenhuys 1994: 972).

The main distribution areas of element 1/1 and element 1/2 overlap at several points along the eastern escarpment of southern Africa. Element 1/1, is more or less evenly distributed in the two main floristic regions (regions 1/1 and 1/2) of the TWINSPAN 3+ classification of grid squares while the widespread, Afromontane element (element 1/2) is mainly distributed in the subtropical region or region 1/2 of the TWINSPAN 3+ grid classification (Fig. 65).

C. Classification of the Bryofloristic Elements of Southern Africa

I. Introduction

The classification of bryogeographic elements within the FSA region is based exclusively on the results of the TWINSPAN 3+ analysis. The classification is hierarchical (see *Classification of the Bryogeographic Regions of Southern Africa*, Chapter 4) and restricted to the 2nd and 3rd levels of division of the TWINSPAN 3+ species classification (Fig. 64). Endemism in the bryofloristic Elements and Subelements is summarised in Table 37.

The names assigned to the Elements and Subelements are provisional because of the regional nature of this study.

Hierarchical classification of the bryogeographic elements of southern Africa

1. Eastern Highlands Element

1.1 Mont Aux Sources Subelement

1.2 Widespread Subelement

2. Cape Element

2.1 West Coast Subelement

2.2 Boland Subelement

3. Afromontane Grassland Element

3.1 Disjunct Cape Peninsula Subelement

3.2 Drakensberg Subelement

4. Afromontane Forest Element

4.1 Widespread Afromontane Subelement

4.2 Tropical Afromontane Subelement

II. Descriptions of Elements and Subelements

1. Eastern Highlands Element

Taxa

The Eastern Highlands Element consists of 47 species in 29 genera and 13 families (Appendix III,3). Most are from the acrocarpous Orders of Dicranales (three families), Pottiales (three families), Funariales (two families), Bryales (two families), as well as the Orthotrichales (two families), and Thuidiales with a single species. Only 13 families are represented in this element of which Pottiaceae is the largest with 13 species, followed by Funariaceae with seven and Bryaceae with six species.

A total of 10 species/infraspecific taxa is southern African endemics. This constitutes 21% of species in this element or 9% of all southern African endemics. None of the genera restricted to this element is a southern African endemic but *Quathlamba* of the Afromontane Forest Element (see note there) may actually belong here. One species of the southern African endemic genus *Ptychomitriopsis* (*P. aloinoides*) is a part of this element.

Geographic distribution

This element is mainly distributed on the high altitude plateau of Lesotho and adjacent areas (Fig. 52), extending as far south as the Sneeuberge near Graaff Reinet (grid 3224 B). The distribution ranges of up to 13 species extend eastwards into the KwaZulu-Natal Midlands. This element is centred in the Drakensberg and Maloti mountains of northern Lesotho and more precisely in the Mont Aux Sources-Oxbow area (grid 2828 D) where 29 of the 47 species occur. Other areas

where up to 12 species occur are the Mpumalanga escarpment, the Magaliesberg, the Amathole Mountains near King William's Town and the Cape Fold mountains of the south-western Cape.

The distribution ranges of the species vary from those that are nearly restricted to the centre (e.g. *Anomobryum drakensbergense*, *Ptychomitrium diexaratum*, *Orthotrichum oreophilum*) to more widespread species reaching the northern provinces and the Cape (e.g. *Funaria rottleri*, *Bartramia hampeana*, *Ptychomitrium cucullatifolium*). The wide distribution of this element is only achieved through the inclusion of a few very widespread species, viz. *Funaria hygrometrica*, *Bryum argenteum*, *B. pycnophyllum* and *Trichostomum brachydontium*.

Discussion

This element is named after the Eastern Highlands Centre of Stuckenberg (1962). It has also been described as the Drakensberg endemic centre by Kurzweil *et al.* (1991). Most of the species favour microhabitats in, or the harsh climate of the high altitude, summer rainfall grassland areas, while the few widespread species of this element have wide ecological amplitudes.

The Eastern Highlands Element is mainly distributed in the Highlands and Afromontane Regions (Fig. 65) although the Afromontane distribution is probably exaggerated as a result of grid squares spanning the Lesotho/KwaZulu-Natal escarpment.

The numbers of Eastern Highlands species occurring in each of the Biomes (Rutherford & Westfall (1986) are listed in Table 25. Given the distribution of this element it is not surprising to find that:

- Most species (92%) occur in the Grassland Biome (Table 25).

- A large percentage of Eastern Highlands species (72%) are found in the Nama-Karoo Biome, especially the north-eastern Lesotho ‘island’ which coincides with the centre of distribution.
- Relatively few species (30%) are found in forest areas.

1.1 Mont Aux Sources Subelement

Taxa

This group is the largest of the Eastern Highlands divisions and contains 35 species in 23 genera and 12 families (Appendix III,7). *Funaria* (Funariaceae) with five species, and *Didymodon* (Pottiaceae) and *Bryum* (Bryaceae) with four species each, are the largest genera in this group.

The southern African species of Encalyptaceae (a family of montane and arctic mosses fide Horton, 1982), are restricted to the Mont Aux Sources Subelement. *Funaria*, a large and widespread genus, and *Didymodon*, which is known as “...a cosmopolitan genus widely diversified in temperate and montane regions” (Zander 1993), are largely restricted to this subelement in southern Africa.

There are nine southern African endemics in this subelement:

Anomobryum drakensbergense, *Didymodon jackvancei*, *Funaria bergiana*, *Microbryum davallianum* var. *conicum*, *Orthotrichum oreophilum*, *Physcomitrium spathulatum* var. *sessile*, *Ptychomitriopsis aloinoides*, *Ptychomitrium diexaratum* and *Weissia dieterleniae*. This constitutes 26% of the element.

Geographic distribution

This element is largely restricted to the mountains of north-eastern Lesotho and is named after Mont Aux Sources, one of the the highest mountain peaks in grid 2828 D and the centre of distribution (Fig. 56). The

number of species per grid drops rapidly outside the main distribution area and the relatively wide distribution is only achieved through species such as *Fissidens curvatus*, *Didymodon ceratodonteus*, *Funaria rottleri*, *Bryum alpinum* and *Bartramia hampeana*. The endemics *Didymodon jackvancei*, *Weissia dieterleniae*, *Anomobryum drakensbergense*, *Ptychomitrium diexaratum* and *Orthotrichum oreophilum* are largely restricted to the main distribution area of the subelement.

Discussion

The Mont Aux Sources Subelement is congruent with the Basutoland–Drakensberg Highlands and Eastern Plateau Slopes subcentre of Stuckenberg (1962). It is mainly distributed in the Drakensberg Alpine Domain with a secondary peak in the Cape Domain (Fig. 65). As in the Eastern Highlands Element, most of the species in this subelement occur in the Grassland (89%) and Nama-Karoo (71%) Biomes (Table 29).

1.2 Widespread Subelement

Taxa

The Widespread Subelement is a group of 12 species (Appendix III,8) in the families Fissidentaceae (2), Archidiaceae (1), Dicranaceae (1), Pottiaceae (2), Grimmiaceae (1), Funariaceae (2) and Bryaceae (3). Some of the most frequently collected and widespread species, in southern Africa as well as the world, have been classified here. They are: *Trichostomum brachydontium* (Pottiaceae), *Schistidium apocarpum* (Grimmiaceae), *Funaria hygrometrica* (Funariaceae) and *Bryum argenteum* (Bryaceae), all with (sub)cosmopolitan distributions, and *Bryum cellulare* which is pantropical in distribution.

Funaria rhomboidea (Funariaceae) is the only endemic in this group.

Geographic distribution

This element is more or less evenly distributed throughout the study area as a result of the widespread species *Trichostomum brachydontium*, *Schistidium apocarpum*, *Funaria hygrometrica*, *Bryum argenteum*, *B. cellulare* and *B. pycnophyllum* (Fig. 57). The main area of distribution seems to be the KwaZulu-Natal Midlands and Drakensberg foothills, and the mountains of the eastern Free State. The group has its highest diversity around the eastern Free State town of Fickburg (grid 2827 D) where nine species occur.

Other areas of relatively high species diversity are (Fig. 57):

1. The Port St. Johns area on the Eastern Cape Wild Coast (grid 3129D).
2. The Ngome forest area near Vryheid in KwaZulu-Natal (grid 2731 C).
3. The Magaliesberg range between Pretoria and Rustenburg (grids 2527 D & 2528 C).
4. The Sabie/Graskop/Blyderivierspoort area (grids 2430 D & 2530 B) as well as the adjacent Sekhukuneland (grid 2430 C).
5. The Malolotja Nature Reserve in northern Swaziland (grid 2631 A).
- 6) The Houtbosch and other forests east of Pietersburg in the Northern Province (grid 2329 D).

Discussion

The areas of high species diversity within the Widespread Subelement (Fig. 57) include historical and recent collection sites. A few examples are:

- Port St. Johns (3129 D), the largest town on the Wild Coast, has been visited by many plant collectors, including bryologists such as T.R. Sim and H.A. Wager.
- Bryophytes were collected in the Fouriesburg-Lady Brand (grids 2827 D, 2828 C, 2927 A & B) and Zastron-Lady Grey (grids 3027 A & C)

areas of the eastern Free State by J. van Rooy in 1980 and 1986 respectively.

- The Free State city of Bloemfontein is situated in grid square 2926 A, the site of one of the earliest settlements north of the Orange River. Mosses were collected here by botanists passing through and residents such as G. Potts, Professor of Botany, University College of the Orange Free State (Gunn & Codd 1981).
- Grid 2928 D in Lesotho stands out as a result of R.E. Magill's collecting there in 1977.
- The relatively high number of species in grid 2430 C is the result of a collecting trip to Sekhukuneland by R.E. Magill in 1977.
- The Malolotja Nature Reserve in north-western Swaziland (grid 2631 A) was the focus of attention of K. Braun, L. Smook and others who worked or visited there in the early nineties.

The concentration of Widespread taxa along the Mpumalanga escarpment has been described as the Eastern Transvaal Subcentre by Stuckenberg (1962).

The Widespread subelement has its main centre of distribution in the Drakensberg Alpine Domain but it is well represented in most Domains (Fig. 65). The lowest numbers of species occur in the Caprivi and Namaqua Domains.

All 12 species occur in the Grassland as well as the adjacent Savanna Biome, nine (75%) are found in the Nama-Karoo Biome, eight (67%) in the Fynbos Biome, seven (58%) in the Forest Biome, four (33%) in the Succulent Karoo Biome, and only one (8%) in the Desert Biome (Table 30).

2. Cape Element

Taxa

The Cape Element consists of 84 species in 52 genera and 25 families (Appendix III,4). Most moss taxa are xerophytic and adapted to the dry, hot summers of the mediterranean-type climate, as in the case of the vascular plant flora of this region (Goldblatt 1978). For discussions and a list of ephemerals see the *Karoo-Namib Region, Chapter 4*, and element 1/1 under the first TWINSPAN 3+ division (this Chapter). The acrocarpous family Pottiaceae, with 24 species, is the best represented in this element followed by Funariaceae with seven, and Dicranaceae, Grimmiaceae and Bryaceae six species/infraspecific taxa each.

The endemic, monotypic family Wardiaceae has been classified here. *Wardia hygrometrica* is a semi-aquatic moss restricted to streams of the south-western Cape (Fig. 13). Three or 50% of genera endemic to southern Africa form a part of this element. They are: *Microcrossidium* (Pottiaceae), *Cygnicollum* (Funariaceae) and *Wardia* (Wardiaceae). This represents 6% of genera in the Cape Element or 2% of genera in southern Africa. All three are monotypic and restricted to the main distribution area which may indicate a possible origin in the Pliocene as a result of the inception of a mediterranean type climate in the Cape (Deacon *et al.* 1992). However, Frey (1990) is of the opinion that a mediterranean-type distribution pattern, which he described as the Xerothermic Pangaeen genoelement, is an ancient one, supposedly of pre-angiosperm origin. A total of 30 species (36% of species in this element) are FSA endemics.

Geographic distribution

The main distribution is in the winter rainfall area of the western Cape and more specific along the north-south axis of the western zone of the Cape Fold Mountains, from the Cape Peninsula right up to Namaqualand and northwards to the Richtersveld (Fig. 53). The number of species per grid drops rapidly outside

the main distribution area and very few species reach the eastern Cape coast, KwaZulu-Natal, Swaziland, and the northern provinces.

The main centre of distribution is in the mountains of the south-western Cape, in particular Table mountain (grid 3318 C) with 64 species, the mountains at Stellenbosch (3318 D) with 54 species, and the mountains of the Boland (3319 C) with 51 species (Fig. 53). A secondary centre, which probably is an extension of the main centre, is situated in the Clanwilliam – Vanrhynsdorp area, in particular the Clanwilliam grid (3218 B) with 47 species. Other areas showing concentrations of species are the western escarpment around Springbok (2917 D), the mountains of the Richtersveld, in particular grid 2927 A, the Outeniqua Mountains between George and Oudsthoorn (3322 A & C), and the southern KwaZulu-Natal drakensberg (grids 2929 A & C).

Some species such as *Bruchia brevipes*, *Tetrapterum tetragonum*, *Ptychomitrium crassinervium*, *Zygodon runcinatus* and *Orthotrichum incurvomarginatum* are restricted to the main distribution area while others like *Fissidens rufescens*, *Tortula atrovirens*, *Pseudocrossidium crinitum*, *Syntrichia ruralis*, *Grimmia pulvinata* and *Bryum canariense* give this element it's wide distribution.

Weimarck (1941) classified species of the Cape Element with a wide distribution in the Cape area as The Cape Ubiquists.

Discussion

This element is named after the Cape Centre of Stuckenberg (1962). The Cape Element is distributed in more or less the same area as Weimarck's (1941) 'Species endemic in the Cape Proper', the 'Cape Species' of Nordenstam (1969), the 'western type of distribution' of Acocks (1971), and the combined Karoo-margin species and Cape Floristic Centre of Kurzweil *et al.* (1991). It must be remembered, however, that those elements were subjectively determined, with reference to the Cape flora in the case of Weimarck (1941) and specific vascular plant taxa in the case of Nordenstam (1969), Acocks (1971) and Kurzweil *et al.*

(1991). Unlike the vascular plant elements, up to 15 species or 18% of the mosses in the Cape Element occur to the east of the Cape area. The main distribution area of the Cape Element might also be compared to that of Weimarck's (1941) Cape Ubiquists with a Knysna Interval.

The Cape Element has its main distribution in the southern part of the Afromontane Region or the Cape Domain but this may be exaggerated as a result of the grid resolution (the coarse grain) and the phytogeographic heterogeneity of the area. As expected the Cape Element is well represented in the Karoo-Namib Region (Fig. 65).

The main distribution area of the Cape Element coincides with the western part of the Fynbos Biome (83% of species) while more than half of the species (55%) ranges northwards into the Succulent Karoo Biome (Table 26). The main distribution area of this element doesn't include many forest areas and this is reflected in the low percentage of Cape species found in the Forest Biome (19%).

2.1 West Coast Subelement

Taxa

The xerophytic West Coast Subelement is the largest of the two Cape subelements and consists of 57 species in 25 genera and 17 families (Appendix III,9). By far the largest family is the Pottiaceae with 23 species. Most of the ephemerals in the study area (see *element 1/1* under *1. First level of division*, this Chapter) are found in this group.

A large percentage (40%) of taxa in this subelement are southern African endemics. Two of the six endemic genera (*Cygnicollum* and *Microcrossidium*), or 33% of genera endemic to southern Africa belong to this subelement.

The monotypic *Bryobartramia* (Bryobartramiaceae) is shared with western and southern Australia where mediterranean type climates similar to that of the western Cape are found. In fact, a great number of non-endemics (40%) occurs in other mediterranean and temperate to hot, semi-arid to arid areas of the world (see map in Gess, 1992). Together with endemics in the West Coast Subelement, these taxa represent 80% of the element. Frey (1990) described this mediterranean-type distribution pattern as the Xerothermic Pangaeon genoelement, supposedly of pre-angiosperm origin. He found that many mosses with the Xeropottioid life syndrome display this kind of distribution pattern (see *Floristic composition of the Karoo-Namib Region, Chapter 4*).

Species of the West Coast Subelement which are also found in other mediterranean and temperate to hot, semi-arid to arid areas of the world

Acaulon leucochaete	Fissidens rufescens
Aloina bifrons	Gigaspermum repens
Bartramia compacta var. compacta	Grimmia laevigata
Bruchia brevipes	Grimmia pulvinata
Bruchia queenslandica	Ischyrodon lepturus
Bryobartramia novaevalesiae	Orthotrichum diaphanum
Bryum canariense	Pleuridium nervosum
Bryum radiculosum	Pseudocrossidium hornschuchianum
Bryum torquescens	Syntrichia chisosa
Didymodon australasiae	Syntrichia princeps
Fissidens pygmaeus	Syntrichia ruralis
	Tortula atrovirens

Some of these species are restricted to areas with mediterranean type climates, e.g. *Fissidens pygmaeus*, *Acaulon leucochaete*, *Bruchia brevipes*,

Bryobartramia novaevalesiae, *Gigaspermum repens*, *Bartramia compacta* var. *compacta* and *Ischyrodon lepturus* while others are widespread and also occur in other climatic regions e.g. *Didymodon australasiae*, *Pseudocrossidium crinitum*, *Syntrichia princeps*, *Tortula atrovirens*, *Bryum canariense*, *Bryum radiculosum*, *Bryum torquescens* and *Orthotrichum diaphanum*.

Geographic distribution

The geographic distribution of the West Coast Subelement is more or less the same as that of the Cape Element. The main distribution area runs parallel to the West Coast, from the Cape Peninsula in the south to the Richtersveld in the north (Fig. 58). The highest numbers of species are found in the Clanwilliam (3218 B) and Cape Town (3318 C) areas with pockets of relatively high species diversity in the Kamiesberge (3018 A) and the northern part of the Richtersveld (2817 A). A number of species also ranges eastward to the Langeberg mountains near Montagu (3320 C) and the Outeniekwa Mountains near George (3322 C). The distribution ranges of some species include the high altitude interior plateau but few occur to the north and east of Lesotho.

Discussion

Both subdivisions of the Cape Element have main centres of distribution in the Cape Peninsula and therefore overlap in the south-western Cape area. The West Coast Subelement is comparable to the 'Western' phytogeographic groups of Weimarck (1941), Dahlgren (1963) and Nordenstam (1969), and the 'Nearly (Cape) ubiquitous species Concentrated in the West' of Dahlgren (1963).

One of the main centres of distribution, The Cape Town or Table Mountain centre (Fig. 58), coincides with the Cape Peninsula Subcentre (South Western Centre) of Weimarck (1941) while the Clanwilliam centre

more or less coincides with the Cedarberg Subcentre (North -Western Centre). The distribution centre in Namakwaland overlaps with the Kamiesberg Subcentre (North -Western Centre) of Weimarck (1941). The concentration of species in the Richtersveld has been described as the Gariiep Centre by Croizat (1965) and Nordenstam (1969). It should be noted, however, that the name 'Gariiep Centre' has more recently been applied to a chorological subdivision of the Western Cape Domain or the Succulent Karoo (Hilton-Taylor 1987, 1994, 1996; Cowling *et al.* 1999) and to a centre of plant endemism (Van Wyk & Van Wyk 1997).

The West Coast Subelement has its main distribution in the Cape and Western Cape Domains (Fig. 65) with a minor peak in the Drakensberg Alpine Domain. It is completely absent from the Caprivi Domain.

The two main centres of distribution fall into the Fynbos Biome (75% of species) but the main distribution area extends into the Succulent Karoo Biome (72% of species). More or less the same numbers of species occur in the Grassland (42%), Nama-Karoo (40%) and Savanna (42%) Biomes (Table 31).

2.2 Boland Subelement

Taxa

The Boland Subelement consists of 27 species in 19 genera and 16 families (Appendix III,10). The families Aulacomniaceae and Wardiaceae are restricted to this subelement in southern Africa. The only representative of the Aulacomniaceae, *Leptotheca gaudichaudii*, is also distributed in the southern temperate areas of southern South America, the Falkland Islands, Juan Fernandez, South Georgia, the Auckland and Campbell islands, southern and eastern Australia, Tasmania, and New

Zealand. The genera *Archidium* (Archidiaceae) and *Racomitrium* (Grimmiaceae) with three species each are the best represented in this group.

Seven of the 27 species (26%) are FSA endemics. This includes the monotypic family Wardiaceae.

Geographic distribution

This element is largely restricted to the south-western corner of the study area (Fig. 59). The centre of distribution is Table Mountain (grid 3318 C with 21 species) and the Cape Fold mountains of the Boland (grids 3318 D with 18 species and 3319 C with 19 species). The number of species per grid drops rapidly outside the main distribution area and very few make it to the northern provinces of South Africa. Up to eight species range as far as the Cedarberge near Clanwilliam, the Groot Swartberge and Outeniekwaberger mountain ranges of the Klein Karoo, and the Sani Pass–Sehlabathebe area in the KwaZulu-Natal Drakensberg.

Species more or less restricted to the centre of distribution include *Andreaea subulata*, *Archidium rehmannii*, *Racomitrium lanuginosum*, *Pyrrhobryum vallisgratae*, *Leptotheca gaudichaudii*, *Zygodon runcinatus* and *Wardia hygrometrica*, all restricted to Gondwana fragments except *Racomitrium lanuginosum* with a widespread bipolar distribution. This subelement is only present in the northern provinces through the inclusion of *Archidium ohioense*, *Fissidens fasciculatus*, *Leucoloma spengelium* and *Rhacocarpus purpurascens*.

Discussion

The main distribution area of the Boland Subelement coincides with that of Weimarck's (1941) Western Group or the South-Western Centre. The centre of distribution (Table Mountain) coincides with Weimarck's (1941)

Cape Peninsula Subcentre. The concentrations of species in grids 3318 D and 3319 C have been described as the Hottentotsholland and French Hoek Subcentres by Weimarck's (1941).

The Boland Subelement is largely confined to the Cape Domain (Fig. 65) and all of the species occur in the Fynbos Biome (Table 32).

3. Afromontane Grassland Element

Taxa

The smallest of the widespread, subtropical elements, the Afromontane Grassland Element consists of 63 species in 40 genera and 21 families (Appendix III,5). The family Pottiaceae is the best represented with 15 species, followed by the Bryaceae with nine and the Dicranaceae with eight species/infraspecific taxa. The pleurocarpous orders of Isobryales, Hookeriales, Thuidiales and Hypnobryales are poorly represented, and the Andreales and Polytrichales completely absent from the Afromontane Grassland Element.

There are 10 southern African endemics (16% of species in this element or 9% of all southern African endemics) in this element of which three belong to the family Pottiaceae.

Geographic distribution

The Afromontane Grassland Element is characterised by three widespread centres of distribution which include Table Mountain (grid 3318 C) in the Western Cape (Fig. 54). The other two centres are situated in the KwaZulu-Natal Midlands (2930 C) and Drakensberg (2828 D, 2929 A & C) area, and the Graskop – Blyderivierspoort area (grid 2430 D) in Mpumalanga. Other areas of relatively high species concentrations include the grids adjacent to the main centres of distribution, the King William's Town area (3227 C), the Lady Grey area in the Eastern Cape (3027 C), the north-eastern Free State including the Maseru grid

(2927 B), and the Magaliesberg Mountains between Pretoria and Rustenburg (grids 2527 C & D, 2528 C). Compared to the Afromontane Forest Element, the number of Afromontane Grassland elements in the George – Knysna area of the southern Cape, the Eshowe – Empangeni area in KwaZulu-Natal, and the northern and southern parts of the ‘eastern Transvaal’ escarpment, is relatively low.

Some species are more or less restricted to the Cape centre of distribution (*Trematodon pillansii*, *Sphagnum pycnocladulum*, *Calypstrochaeta asplenioides*), others only occur in the KwaZulu-Natal centre (*Distichium capillaceum*, *Aongstroemia julacea*, *Barbula microcalycina*, *Bryum caespiticium*, *Pohlia cruda*), but none is restricted to the northern or Mpumalanga centre. A number of species occurs in all three centres, of which *Fissidens bryoides*, *Syntrichia fragilis*, *Mielichhoferia bryoides*, *Philonotis dregeana*, *Ptychomitrium crispatum*, *Fabronia pilifera*, *Pseudoleskeopsis claviramea*, *Leptodon smithii*, and *Hypnum cupressiforme* are the most widespread.

Discussion

The Afromontane Grassland Element is mainly distributed in the Afromontane Region with minor peaks in the Zambezian and Highlands Regions (Fig. 65).

Great numbers of species occur in the Grassland Biome (94%) and its southern Afromontane replacement, the Fynbos Biome (64%), as well as the Savanna Biome (76%). This element is further characterised by the relatively great numbers of species present in the semi-arid Succulent Karoo (22%) and Nama-Karoo (56%) Biomes compared to only 0.16% and 11% of the Afromontane Forest Element. The southern centre of distribution is evident in the relatively high percentage of species (64%) present in the Fynbos Biome compared to the 45% of the Afromontane Forest Element (Table 27).

3.1 Disjunct Cape Peninsula Subelement

Taxa

The Disjunct Cape Peninsula Subelement is the smallest of all the subelements with only 11 species in 11 genera and eight families (Appendix III,11).

Of the 11 species in this subelement three or 27% are southern African endemics (*Trematodon pillansii*, *Plagiothecium membranosulum* and *Isopterygium punctulatum*), five are distributed in the African–Arabian–Madagascan region (*Sphagnum truncatum*, *Fissidens plumosus*, *Pseudocrossidium porphyreoneurum*, *Weissia latiuscula*, *Fabronia pilifera*) and three are widespread or subcosmopolitan (*Syntrichia pagorum*, *Bryum capillare*, *Pohlia elongata*).

Geographic distribution

This subelement (Fig. 60) is centred in the Cape Peninsula (grids 3318 C and 3418 A) with disjunct occurrences in the KwaZulu-Natal Midlands at Pietermaritzburg (grid 2930 C), the Graskop–Blyderivierspoort area on the Mpumalanga escarpment (2430 D), and the Magaliesberg mountains between Pretoria and Rustenburg (grids 2527 C & D, 2528 C). It is largely absent from the high altitude plateau and mountains of the Free State and Lesotho as well as large parts of the southern and Eastern Cape and KwaZulu-Natal (Fig. 60).

The Cape endemic *Trematodon pillansii* (Dicranaceae) is the only species more or less restricted to the main centre of distribution while *Weissia latiuscula* (Pottiaceae) and *Bryum capillare* (Bryaceae) are only found in the northern regions. The wide geographic distribution of this subelement is attained through species such as *Sphagnum truncatum*,

Pseudocrossidium porphyreoneurum, *Syntrichia pagorum* *Bryum capillare*, and *Fabronia pilifera*.

Discussion

The Disjunct Cape Peninsula Subelement is most abundant in the Cape Domain with secondary occurrences in the Drakensberg, Bushveld and Caprivi Domains (Fig. 65).

Eighty two percent of species occur in each of the Grassland, Savanna and Fynbos Biomes where the disjunct centres of distribution are located (Table 33). Although Afromontane forests are present in all three centres, only 27% of species in this element were recorded from this Biome.

3.2 Drakensberg Subelement

Taxa

The 52 species in this element are mostly acrocarpous, distributed in the drier areas of the Afromontane region and beyond. They belong to 35 genera and 20 families (Appendix III,12). The Pottiaceae is the best represented with 11 species followed by the Dicranaceae and Bryaceae with seven species each. *Bryum* is the largest genus in this subelement with four species, followed by *Campylopus*, *Philonotis* and *Ptychomitrium* with three species each. Seven (14%) of the species are FSA endemics.

Geographic distribution

The main distribution area is in the Midlands and Drakensberg region of Kwazulu-Natal, and the eastern Free State down to the Zastron-Lady Grey area (Fig. 61). Significant numbers of species are also present along the escarpment in northern Swaziland and Mpumalanga, the Magaliesberg mountains west of Pretoria, and the mountains of the Cape Peninsula and Boland. The main centre of distribution is situated in the KwaZulu-Natal

Drakensberg (grids 2828 D, 2929 A & C) with secondary centres in the Graskop-Blyderivierspoort area of Mpumalanga (grid 2430 D) and Table Mountain in the Western Cape (grid 3318 C).

Species more or less restricted to the main Drakensberg centre of distribution are: *Distichium capillaceum*, *Aongstroemia julacea*, *Barbula microcalycina*, *Bryum caespiticium* and *Pohlia cruda*. Widespread species include: *Fissidens bryoides*, *Hypodontium dregei*, *Syntrichia fragilis*, *Campylopus introflexus*, *Brachymenium acuminatum*, *Philonotis dregeana*, *Philonotis falcata*, *Ptychomitrium crispatum* and *Hypnum cupressiforme*.

Discussion

The subelement is most abundant in the Cape and Drakensberg Domains and a significant number of species is present in the Drakensberg Alpine Domain (Fig. 65).

Almost all of the species (96%) occur in the Grassland Biome and great numbers are also present in the Savanna (75%), Forest (62%), Nama-Karoo (62%), and Fynbos (60%) Biomes (Table 34). The relatively great number of species distributed in the Nama-Karoo Biome (62%) is only as a result of this biome's presence in the north-eastern part of Lesotho (Fig. 2).

4. Afromontane Forest Element

Taxa

By far the largest of the bryogeographic elements, the Afromontane Forest Element consists of 307 species (61% of all the mosses in southern Africa) in 157 genera and 46 families (Appendix III,6). Most species belong to the Dicranaceae (33), Orthotrichaceae (23), Bryaceae (20) and Pottiaceae (18) while *Fissidens*

(Fissidentaceae) with 19 species, *Campylopus* (Dicranaceae) with 15 species, and *Fabronia* (Fabroniaceae), *Brachythecium* (Brachytheciaceae) and *Sematophyllum* (Sematophyllaceae) with seven species each, are the largest genera.

In southern Africa most of the (sub)tropical forest species, many who belong to the pleurocarpous Orders of Isobryales, Hookeriales, Thuidiales, and Hypnobryales, figure in this element. However, a number of xerophytic taxa such as species of *Archidium* (Archidiaceae) and *Ephemerum* (Ephemeraceae) shares a similar distribution pattern.

Of the 307 species in this element 62 (or 20%) are southern African endemics. This represents 54% of all FSA endemics, the highest figure for all the elements. Two of the six, or 33% of genera endemic to southern Africa, are restricted to this element. They are: *Physcomitrellopsis* (Funariaceae) and *Quathlamba* (Bartramiaceae). The monotypic *Quathlamba* grows high up on the Drakensberg escarpment at Sani Pass (Magill 1987) and may actually belong to the Eastern Highlands Element, but as a result of the predominantly Afromontane grid square (2929 C) in which it occurs, it has been classified here. *Physcomitrellopsis*, the other southern African endemic, grows on the edge of a forest area in the Eastern Cape Province. One species of the southern African endemic genus *Ptychomitriopsis* (*P. africana*) belongs to this element, the other (*P. aloinoides*) is part of the Eastern Highlands Element.

Geographic distribution

The Afromontane Forest Element is mainly distributed in the KwaZulu-Natal Midlands and Drakensberg area, and along the escarpment of the northern provinces (Fig. 55). The two main centres of distribution are Pietermaritzburg (grid 2930 C) with 117 species and Blyderivierspoort (grid 2430 D) with 129 species.

Other areas of relatively high species diversity are (Fig. 55):

- Table Mountain in the Western Cape (grid 3318 C) with 86 species.
- The southern Cape forests in the George (grid 3322 C with 64 species) and Knysna (grid 3423 A with 53 species) area.
- Forests in the Amathole Mountains near King William's Town (grid 3227 C with 66 species).
- The Zululand forests in the Empangeni (grid 2831 D with 54 species) – Eshowe (grid 2831 C with 77 species) area.
- The forests on the slopes of the Soutpansberg in the Northern Province (grid 2230 C) with 54 species.

Compared to the Afromontane Grassland Element, the numbers of species distributed in the mountains of the Cape Peninsula and Boland, Lady Grey and eastern Free State, and the Magaliesberg, are relatively low in this element. The numbers of species distributed in the semi-arid and arid central and western parts of the study area are very low (Fig. 55).

The distribution ranges of the species vary from those restricted to one of the main distribution centres, to species present in both main centres, to widespread species found throughout the distribution area of the element.

The following species are restricted to the northern centre of distribution situated in the Graskop-Blyderivierspoort region:

Campylopus fragilis

Campylopus jamesonii

Platyhypnidium macowanianum

Rhacopilopsis transvaaliensis

Rigodium toxarion

Syrrhopodon asper

Trachypodopsis serrulata

Species more or less restricted to the KwaZulu-Natal centre of distribution include:

Drepanocladus aduncus

Fissidens enervis

Oligotrichum afrolaevigatum

Plagiobryum Zierii

Pterobryopsis rehmannii

Stoneobryum mirum

The following species are widespread and occur in forest areas from Table Mountain in the Cape to the Soutpansberg in the Northern Province:

Aerobryopsis capensis

Brachymenium pulchrum

Fissidens glaucescens

Hypopterygium laricinum

Macrocoma tenue subsp tenue

Neckera valentiniana

Polytrichum commune

Porotrichum madagassum

Pyrrhobryum spiniforme

Sematophyllum dregei

Discussion

The distribution area of the Afromontane Forest Element overlaps with that of the Afromontane Grassland Element except in Namakwaland and southern Namibia where it is absent. The Afromontane Forest Element is largely restricted to the Afromontane Region (Fig. 65).

As with the Afromontane Grassland Element, the greatest numbers of species occur in the Grassland (76%) and Savanna (59%) Biomes (Table 28). However, the numbers of species found in the semi-arid Succulent Karoo (0,16%) and Nama-Karoo (11%) Biomes are much lower than in the Afromontane Grassland Element and only 45% of species occur in the Fynbos Biome compared to 64% of the Afromontane Grassland Element.

4.1 Widespread Afromontane Subelement

Taxa

This subelement consists of 49 species in 38 genera and 21 families (Appendix III,13). The genus *Campylopus* (Dicranaceae) with four species is the best represented followed by *Fissidens* (Fissidentaceae) and *Sematophyllum* (Sematophyllaceae) with three species each.

The family Catagoniaceae with its single, endemic representative *Catagonium nitens* ssp. *maritimum* is restricted to this subelement. Six or 12% of species in the Widespread Afromontane Subelement are southern African endemics.

Geographic distribution

Species in this group are widespread throughout the southern African part of the Afromontane Region (see *Chapter 4*) or the Drakensberg regional mountain system (Domain) of White (1978) and Denys (1980). The main distribution areas are (Fig. 62):

- The escarpment forests of the northern provinces, from the Soutpansberg in the north to Swaziland in the south.
- The Magaliesberg kloof forests between Pretoria and Rustenburg.
- Forests of the KwaZulu-Natal Midlands and Drakensberg.

- Forests of the Eastern Cape Province (represented by grids 3129 B and 3227 C), still very much under-collected.
- The southern Cape forests in the George-Knysna region.
- Forest patches on Table Mountain and the Somerset West-Betty's Bay area of the Western Cape.

The main centres of distribution are (Fig. 62):

- The Graskop-Blyderivierspoort area (grid 2430D) on the Mpumalanga escarpment.
- The forests around Pietermaritzburg (grid 2930 C) in the KwaZulu-Natal Midlands.

Only a few species are more or less restricted to the northern centres of distribution (*Archidium acanthophyllum*, *Campylopus perpusillus*, *Leptodictyum riparium*) or reach their southern limit in the Eastern Cape (*Anomobryum filiforme*, *Hedwigia ciliata*, *Lindbergia viridis*, *Thuidium matarumense*). Most species in this subelement occur in the south as well as the north of the distribution area and the following are among the most widespread: *Spagnum capense*, *Fissidens glaucescens*, *Campylopus pyriformis*, *Campylopus robillardaei*, *Macrocoma tenue* subsp. *tenue*, *Brachythecium implicatum*, *Sematophyllum brachycarpum*, *Sematophyllum dregei* and *Polytrichum commune*. Species which range into the arid western parts of the study area include: *Erpodium coronatum* subsp. *transvaaliense*, *Philonotis hastata* and *Physcomitrium spathulatum* var. *spathulatum*.

Discussion

Surprisingly this subelement is most abundant in the Cape Domain and not the Drakensberg Domain where the main centres of distribution are situated (Fig. 65). It is absent from the arid Namaqua Domain.

The species are abundant in each of the Biomes found along the Afromontane region, i.e. the Grassland (94%), Savanna (92%), Forest (76%) and Fynbos (80%) Biomes (Table 35). The widespread nature of this subelement is evident in the relatively high percentage (63%) of species that occur in all of these Biomes (Grassland, Forest, Savanna as well as the Fynbos Biome) compared to only 16% of species in the Tropical Afromontane Subelement.

4.2 Tropical Afromontane Subelement

Taxa

By far the largest of the bryogeographic subelements, the Tropical Afromontane Subelement consists of 258 species in 140 genera and 44 families (Appendix III,14). Particularly well represented are the largely pleurocarpous orders Orthotrichales, Isobryales, Hookeriales, Thuidiales and Hypnobryales. Dicranaceae (26 species) is the largest family as far as the number of species is concerned, followed by Orthotrichaceae (19), Bryaceae (17) and Fissidentaceae (16). *Fissidens* (Fissidentaceae) is by far the largest of the genera with 16 species, followed by *Campylopus* (Dicranaceae) with 11 and *Brachythecium* (Brachytheciaceae) with six species.

Two (33%) of the six genera endemic to the FSA region, *Physcomitrellopsis* (Funariaceae) and *Quathlamba* (Bartramiaceae), both monotypic, belong to this subelement. One species of the southern African endemic genus *Ptychomitriopsis* (*P. africana*) is part of this subelement, the other species (*P. aloinoides*) belongs to the Mont Aux Sources Subelement. FSA endemics constitute 22% of species in this subelement, most of which are found in the Orthotrichaceae (9), Brachytheciaceae (7), Fabroniaceae (5) and Polytrichaceae (5).

Geographic distribution

Although widely distributed in the eastern and southern parts of the study area, the Tropical Afromontane Subelement is concentrated in a few areas of the Afromontane region (Fig. 63). The two main distribution areas are:

- The KwaZulu-Natal Midlands and Drakensberg.
- The Mpumalanga Drakensberg escarpment.

The group has its highest diversity in the Graskop-Blyderivierspoort area (grid 2430 D), where 91 of the species are found, and around Pietermaritzburg (grid 2930 C) where 81 species occur (Fig. 63). Other areas of relatively high species concentrations are:

- The montane forests in the Tzaneen-Haenertzburg area of the Northern Province.
- The Zululand forests around Empangeni and Eshowe.
- The forests of the Amathole Mountains north of King William's Town in the Eastern Cape Province.
- The Outeniekwa Mountains near George in the Western Cape Province.
- The Afromontane forest on the slopes of Table Mountain, Cape Town.

The following species are more or less restricted to the two main distribution areas in the north-east of the study area: *Brachymenium leptophyllum*, *Brachymenium nepalense*, *Calymperes rabenhorstii*, *Campylopus fragilis*, *Campylopus jamesonii*, *Floribundaria floribunda*, *Leptodontium longicaule*, *Leucoloma chrysobasilare*, *Levierella perserrata*, *Pogonatum oligodus*, *Porotrichum elongatum* and *Rhabdoweisia fugax*.

Mosses restricted to the Mpumalanga centre of distribution include:

Platyhypnidium macowanianum, *Rhacopilopsis transvaaliensis*, *Rigodium toxarion*, *Syrrhopodon asper* and *Trachypodopsis serrulata*.

The following are examples of mosses more or less restricted to the

KwaZulu-Natal centre of distribution: *Drepanocladus aduncus*, *Fissidens enervis*, *Oligotrichum afrolaevigatum*, *Plagiobryum zierii*, *Stoneobryum*

mirum. Taxa restricted to the top of the Lesotho escarpment, (e.g.

Quathlamba debilicostata and *Orthotrichum armatum*) might also be

included in this group but, as explained earlier under the *Afromontane*

Forest Element, it is most likely that they have been classified here as a

result of the grid resolution and probably belong to the Mont Aux Sources

Subelement of the Eastern Highlands element.

Widespread species include: *Aerobryopsis capensis*, *Atrichum*

androgynum, *Brachymenium pulchrum*, *Ditrichum brachypodum*,

Hypopterygium laricinum, *Neckera valentiniana*, *Porothamnium*

stipitatum, *Porotrichum madagassum*, *Pyrrhobryum spiniforme*,

Racopilum capense and *Sematophyllum subpinnatum*. Species responsible

for this subelement's distribution in the semi-arid central and northern

parts are : *Brachymenium systylium*, *Erpodium beccarii*, *Erpodium*

grossirete, *Fissidens capriviensis*, *Fissidens erosulus*, *Fissidens*

submarginatus, *Fissidens subobtusatus*, *Hyophila baginsensis* and

Vesicularia galerulata.

Discussion

This subelement has strong (sub)tropical affinities. The majority of

species (38%) display a tropical African-Madagascan distribution pattern,

23% has wider tropical distribution patterns (pantropical, palaeotropical

etc.), 9% of species is widespread or bipolar in distribution, 5% is

southern temperate species, and 3% belongs to other distribution patterns.

Together with the southern African endemics, which constitute 22% of species in this subelement, 83% of species has (sub)tropical distribution patterns.

The Tropical Afromontane Subelement is most abundant in the Drakensberg and Cape Domains and absent from the Namaqua Domain (Fig. 65).

This subelement is most abundant in the Grassland Biome (73%) while only about half of the species occur in each of the Forest (51%) and Savanna (52%) Biomes (Table 36). The northern bias of this group is illustrated by the relatively low percentage of species (39%) present in the Fynbos Biome compared to 80% in the Widespread Afromontane Subelement. The restricted nature of this subelement is evident in the relatively low percentage (16%) of species that occur in the Grassland, Forest, Savanna as well as the Fynbos Biomes compared to the 63% of species in the Widespread Afromontane Subelement.

D. World Distribution Elements

It is beyond the scope of this study to present a detailed analysis of the total or world distribution ranges of southern African mosses. However, the distribution data in the MOSS database (see Table 2) makes it possible to present a preliminary, broad-scale classification of world distribution elements in the moss flora of southern Africa. The classification is subjective and heavily influenced by other schemes.

The basic area used to plot the distributions is the political country, or occasionally a region within a country. The group or element with the most restricted geographic distribution is therefore the mosses endemic to the FSA area or the endemic element.

World distribution elements in the moss flora of southern Africa

Cosmopolitan/widespread/bipolar element	86 (17%)
Tropical element	241 (48%)
African subelement	168 (33%)
Pantropical subelement	37 (7%)
Palaeotropical subelement	15 (3%)
African–neotropical subelement	21 (4%)
Mediterranean/semi-arid element	24 (5%)
Southern Hemisphere element	35 (7%)
Endemic element	114 (23%)
Other elements	3 (1%)

The largest world distributional element in the moss flora is the Tropical element which consists of 241 species or 48% of all the mosses in southern Africa. This element can be divided into a number of subelements of which the African subelement with 168 species (33% of the total) is the largest. This subelement consists of mosses largely restricted to the African region of Hollis & Brummitt (1992) which includes Macaronesia and the west Indian Ocean islands. I therefore agree with Schofield (1992) that the “Affinities of the South African flora are predominantly with continental Africa....”.

E. DCA Ordination of Species

The eigenvalues of the first four DCA ordination axes, which are relative measures of the variation accounted for by each axis, are listed in Table 24. The positions of TWINSpan 3+ species on DCA ordination axes 1 and 2, the two axes with the highest eigenvalues, are shown in Fig. 66. In this scattergram each species is also classified according to the TWINSpan Element it belongs to.

1. TWINSPAN Elements

Although there is considerable overlap among the Elements, especially towards the centre of the DCA scattergram (Fig. 66), the species are roughly grouped into TWINSPAN 3+ floristic elements. Afromontane Forest species form a large group on the left hand side of the scattergram while Cape Element species are grouped towards the right. The Afromontane Grassland and Eastern Highlands species do not form coherent groups but are more or less grouped to the left and to the right of centre respectively.

2. Distributional gradients

Axis 1

There is a clear gradient along axis 1 from Afromontane Forest species with negative or low values at the one end, to Eastern Highlands and Afromontane Grassland species with higher values along the middle of the axis, to Cape species with the highest values at the other end (Fig. 66). Therefore a gradient from species distributed in the northern and eastern part of the study area, to species with an 'eastern highlands' distribution, to species distributed throughout the drier, inland regions of the Afromontane region, to species with a south-western distribution pattern. The distributional gradient therefore runs from the north-east, more or less longitudinally, to the south-west.

The species with extreme negative values along axis 1 (*Fissidens capriviensis*, *Erpodium grossirete*, *Orthostichopsis pinnatella*, *Ptychomitrium exaratifolium*, *Physcomitrellopsis africanum*, *Rhynchostegiella sublaevipes*, *Leskeella zuluensis*) are distributed in the north-eastern corner of the study area (Okavango swamps in Botswana, Northern Province of South Africa, eastern Mpumalanga, and northern KwaZulu-Natal). Species at the extreme positive end of the axis (*Crossidium spiralifolium*, *Leucoperichaetium eremophilum*, *Pterygoneurum macleanum*, *Pottia namaquensis*, *Acaulon leucochaete*, *Tortula splachnoides*, *Cygnicollum immersum*) are distributed in the arid west (Richtersveld, Namaqualand) and interior of the Northern Province (Fig. 67). These two species groups represent the poles of the axis,

a wet eastern pole and a dry western pole, with the rest of the species distributed in between.

Axis 2

Along the second axis most species fall into a narrow range of species scores (mostly between 50 and 150 SD units) indicating little change in geographic distribution (Fig. 66). However, this axis does separate a few species with extreme north-eastern distributions in northern KwaZulu-Natal and eastern Mpumalanga (*Calymperes tenerum*, *C. rabenhorstii*, *Leptodictyum riparium*, *Bryum erythrocaulon*, *B. canariense*), most which belong to the Afromontane Forest Element, from species with extreme northern and western distributions in the Caprivi (*Fissidens capriviensis*, *Erpodium grossirete*) and Namibia (*Bruchia queenslandica*, *Archidium dinteri*, *A. microthecium*, *Ptychomitriopsis aloinoides*, *Funaria rhomboidea*).

The species with extreme negative values along axis 2, i.e. those with northern and western distributions, are clearly separated along axis 1 (Fig. 66). From Afromontane Forest species with negative values (*Fissidens capriviensis*, *Erpodium grossirete*), distributed in the north of South Africa and north-eastern Namibia (Caprivi), to Eastern Highlands species mainly distributed in central Namibia (*Funaria rhomboidea*, *Ptychomitriopsis aloinoides*), to Cape species restricted to Namibia (*Archidium dinteri*, *Bruchia queenslandica*).

Axis 3

There is a more gradual change in species scores along the 3rd and 4th DCA axes which indicates a better distributional gradient. However, the lower eigenvalues (Table 24) indicate that each axis only captures about half of the distributional information accounted for by DCA axis 1.

Axis 3 contrasts species distributed in the Highlands of Lesotho and other high altitude areas on the interior plateau (Fig. 68), i.e. those species with extreme positive values (*Didymodon trivialis*, *D. jackvancei*, *Syntrichia austroafricana*, *Weissia*

a wet eastern pole and a dry western pole, with the rest of the species distributed in between.

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Axis 3 contrasts species distributed in the Highlands of Lesotho and other high altitude areas on the interior plateau (Fig. 68), i.e. those species with extreme positive values (*Didymodon trivialis*, *D. jackvancei*, *Syntrichia austroafricana*, *Weissia*

dieterlenii, *Campylopus julaceus* subsp. *arbogastii*, *Encalypta vulgaris*, *E. ciliata*, *Bryum caespiticium*, *B. turbinatum*, *Ptychomitrium cucullatifolium*, *Bryoerythrophyllum recurvirostrum*), with species mainly distributed in the southern and south-western Cape (*Pogonatum borgenii*, *Calymperes levyanum*, *Microcrossidium apiculatum*, *Breutelia elliptica*, *Philonotis vagans*, *Cheilothela chilensis*, *Andreaea nitida*, *Leucobryum rehmannii*, *Fontinalis antipyretica* var. *gracilis*, *Dicranella rigida*, *Dicranoloma billardieri*). Most of the species with extreme positive scores belong to the Mont Aux Sources Subelement of the Eastern Highlands Element, while most species with extreme negative scores belong to the Afromontane Forest Element. The south-western and southern Cape species with extreme negative values are mainly concentrated in the Vanrhynsdorp area (grid 3118 D), the Cape fold mountains of Stellenbosch and the Boland (grids 3318 D, 3418 B and 3319 C), and the Knysna -Tsitsikamma area (grids 3323 C & D).

The gradient along DCA axis 3 supports the TWINSpan classification gradient, with eastern Highlands species at the one end and Afromontane species at the other. The DCA gradient runs from low altitudes in the south and south-west to high altitudes on the central plateau, geographically exactly the same as the compositional gradient along axis 3 of the TWINSpan 3+ grid ordination (see Fig. 43).

Axis 4

Species with extreme positive scores along axis 4 (*Crossidium spiralifolium*, *Leucoperichaetium eremophilum*, *Weissia latiuscula*, *Barbula eubryum*, *Erpodium coronatum* subsp. *transvaaliense*, *Campylopus catarractilis*, *C. perpusillus*, *Didymodon tophaceopsis*, *Ptychomitrium exaratifolium*, *Archidium acanthophyllum*, *Bryum capillare*) are distributed throughout the bushveld or savanna vegetation types of the Savanna Biome (Low & Rebelo 1996) in the northern and central parts of southern Africa (Fig. 69). Most of these species belong to the Afromontane Forest element. Species with extreme negative scores (*Pterygoneurum macleanum*, *Tortula splachnoides*, *Bruchia queenslandica*, *Archidium dinteri*, *Physcomitrium spathulatum* var. *sessile*, *Microbryum davallianum* var. *conicum*, *Acaulon leucochaete*, *Pottia*

namaquensis, *Rhabdoweisia crispata*, *Quathlamba debilicostata*, *Leptoterigynandrum austro-alpinum*) are distributed in the arid and semi-arid Succulent and Nama Karoo Biomes (Low & Rebelo 1996). Most of these species belong to the West Coast Subelement of the Cape Element.

Geographically this gradient is more or less the same as the DCA gradient of TWINSPAN 3+ grids (see Fig. 44), contrasting southern temperate areas, and other high altitude areas along the Great Escarpment, with bushveld areas in the central and northern parts of southern Africa.

Discussion

The first and most important DCA axis of the species ordination represents an east-west distributional gradient in South Africa, similar to the east-west compositional gradient described by the 1st axis of the grid ordination. Through indirect analysis of the compositional gradient (see *D. Indirect Gradient Analysis*, Chapter 4) it has been established that this gradient can be related to moisture parameters, in particular the mean annual precipitation (see map in Schultze 1997a).

The east-west distributional gradient displayed by species with extreme northern and north-western distributions in southern Africa coincides with the east-west climatic gradient in these parts (Barnard 1998). Moisture parameters, in particular the mean annual precipitation and mean water deficit (Barnard 1998), seem to describe this gradient the best. This confirms the importance of moisture (rainfall) in determining the distribution of floristic elements, also in the undercollected, (semi-) arid parts of the study area.

The distributional gradients along axes 3 & 4 are geographically the same as the compositional gradients along axes 3 & 4 of the TWINSPAN 3+ grid ordination. I have suggested (see *Correlation with environmental variables*, Chapter 4) that these gradients, running altitudinally as well as latitudinally, are related to several temperature parameters and indices.