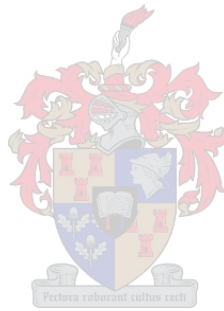


# PHYTOGEOGRAPHIC STUDY OF THE KAOKOVELD

## CENTRE OF ENDEMISM

by

**PATRICIA CRAVEN**



*Dissertation presented for the degree of Doctor of Philosophy*

*at*

*Stellenbosch University*

Department of Botany and Zoology

Faculty of Science

Promoter: Prof. L.L. Dreyer  
Co-Promoter: Prof. A.E. Van Wyk

Date: March 2009

## **Declaration**

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: 9 February 2009

Copyright © 2009 Stellenbosch University

All rights reserved

## Abstract

An intriguing biogeographic area that lies in northwestern Namibia and southwest Angola is known for having numerous endemic taxa. It had, however remained vaguely defined because of the complex flora, the arid environment and confusing and inconsistent use of biogeographic terminology. This thesis redefined the area as a centre of endemism based on recurrent patterns of plant distributions by shared species. The end result is a well-defined entity with regard to, not only geographic boundaries and floristic elements, but also to its history and floristic relationships.

A vast amount of information on the plants of the area, their affinities and their distributions is required for a study of this nature and this was undertaken through literature surveys and field work. All the relevant information on Namibia and the southwestern Angolan flora, i.e. the region and the study area, were incorporated into a database which formed the bases for numerical analysis and GIS studies. The database also brought together a wide range of information from literature sources that included facts and theories about the past and present physical environment. The structure of the database permitted querying this electronic data in many different ways.

To accommodate the wide variety of subjects in a logical way, the thesis was divided into two sections. Section A concentrated on the region and provided background information and context. The theory, terminology and phytogeographic studies in the region were evaluated as a first step. A large amount and variety of palaeo-environmental and palaeo-ecological information, pertinent to the region was incorporated. Secondly the flora was assessed. Besides the diversity, distribution patterns of the plants within and outside the region, including disjunct distributions, phylogenies were assessment. Finally taxa with similar geographic ranges were grouped. These entities were mapped and both the taxa and their environments were evaluated

Section B focused on the core area, namely the Kaokoveld Centre of Endemism, which was delimited by numerical techniques, and then investigated further with regard to its floristic components, relationships and origins. The flora and endemic components are described in detail. The result is a well-defined centre of endemism which comprises one endemic family, 10 endemic genera and nearly 300 endemic species. The flora of the Centre includes about 1600 species in nearly 550 genera in 130 families. Three floristic Groups, identified in section A, that have a remarkable number of endemics are found in the Centre. Historical explanations for the distribution patterns were suggested and the Group that includes *Welwitschia mirabilis* Hook.f., has been shown to be linked to the Arid Corridor.

The demand for accurate knowledge about biodiversity has been highlighted by the Convention of Biological Diversity and there are a remarkable number of users with different requirements today. This study provides a much needed alternate look at the plants of the region, as well as a summation of the principle phytogeographic elements of the Namibian flora. It also includes a new phytogeographic classification and map of the floristic Groups of Namibia, which will contribute to defining floristic areas in the region.

# Opsomming

'n Interessante biogeografiese area in noordwes Namibië en suidwes Angola is bekend daarvoor dat dit baie endemiese taksa bevat. Dit het egter vaag gedefinieer gebly as gevolg van die kompleksiteit van die flora, die droë omgewing en die verwarrende en inkonsekwente gebruik van biogeografiese terminologie. Hierdie tesis herdefinieer die area as 'n sentrum van endemisme gebaseer op herhalende patrone van plantverspeiding wat deur spesies gedeel word. Die resultaat is 'n goed gedefinieerde entiteit in terme van nie slegs geografiese grense en floristiese elemente nie, maar ook in terme van geskiedenis en floristiese verwantskappe.

Groot hoeveelhede informasie oor die plante van die area, hulle verwantskappe en hulle verspreidings word benodig vir 'n studie van hierdie aard, en dit is onderneem deur literatuur studies en veldwerk. Al die relevante informasie oor Namibiese en suidwes Angolese flora, met ander woorde die streek en die studie area, is in 'n databasis geïnkorporeer wat die basis gevorm het van numeriese analyses en GIS studies. Die databasis het ook 'n wye reeks informasie vanuit literatuurbronne bymekaar gebring, wat feite en teorieë oor die vroeëre en huidige fisiese omgewing insluit. Die struktuur van die databasis het toegelaat dat hierdie elektroniese data op baie verskillende maniere ontleed kon word.

Om die wye verskeidenheid van onderwerpe logies te kon akkommodeer is die tesis in twee seksies verdeel: Seksie A het gekonsentreer op die streek en het agtergrondinformasie en konteks aan die studie verskaf. Die teorie, terminologie en fitogeografiese studies in die streek is as eerste stap geëvalueer. Die groot hoeveelheid en diversiteit van paleo-omgewings en paleo-ekologiese inligting wat op die streek betrekking het is as eerste stap geëvalueer. Tweedens is die flora geëvalueer. Benewens die diversiteit is verspreidingspatrone van die plante binne en buite die streek, insluitend disjunkte verspreidings en filogenetiese herkonstruksies ook ondersoek. Ten slotte is taksa met eenderse geografiese strekkings gegroepeer. Hierdie groepe is gekarteer, en beide die taksa en hul omgewings is geëvalueer.

Seksie B het op die hoof area, naamlik die Kaokoveld Sentrum van Endemisme, gekonsentreer wat deur numeriese tegnieke afgebaken is. Dit is toe verder ondersoek in terme van die ingeslote floristiese komponente, verwantskappe en oorspronge, en die flora en die endemiese komponente is in detail bespreek. Die resultaat was 'n goed gedefinieerde sentrum van endemisme wat een

endemiese familie, 10 endemiese genera en byna 300 endemiese spesies insluit. Die flora van die Sentrum sluit ongeveer 1600 spesies in byna 550 genera binne 130 families in. Drie floristiese Groepe met 'n merkwaardige aantal endemiese taksa kom binne die Sentrum voor. Historiese verduidelikings vir die verspreidingspatrone is voorgestel en daar is gewys dat die Groep wat *Welwitschia mirabilis* Hook.f. insluit gekoppel is met die Ariede Korridor.

Die behoefte vir akkurate kennis oor biodiversiteit is beklemtoon deur die Konvensie van Biologiese Diversiteit en daar is vandag 'n indrukwekkende aantal gebruikers met verskillende behoeftes. Hierdie studie verskaf 'n baie nodige alternatiewe beskouing van die plante van die streek, asook 'n opsomming van die hoof fitogeografiese elemente van die Namibiese flora. Dit sluit ook 'n nuwe fitogeografiese klassifikase en kaart van die floristiese Groepe van Namibië in.

## Acknowledgements

I would like to express my sincere thanks to the following people:

My promoters, Professor L.L. **Dreyer** and Professor B.E. **Van Wyk** who not only guided me, but believed I had something to say about Namibia and especially the Kaokoveld.

My colleague, field companion and outstanding botanist, **Herta Kolberg** for all the encouragement, discussions and stimulating conversations, and Tyronne for making the tea.

My family, **Daniel, Vera, Myra** and **Dan** who did not moan much about botanizing on holidays and made this study possible.

This project would not have been possible without the encouragement, help and enthusiasm of the late Mr Willy Giess and Dr Mike Muller, the first curators of the National Herbarium of Namibia (WIND), who started me on this road of discovery.

# Table of Contents

Declaration .....	1
Abstract .....	2
Opsomming .....	4
Acknowledgements.....	6
List of Figures .....	8
List of Tables .....	9
Chapter 1: Introduction .....	11
Chapter 2: Procedures and approach .....	14
<b>Section A</b>	
Chapter 3: Plant geography in Namibia.....	27
Chapter 4: Phytogeographical aspects of the flora of Namibia.....	58
Chapter 5: Natural floristic Groups of Namibia.....	87
<b>Section B</b>	
Chapter 6: Demarcating the Kaokoveld Centre of Endemism: A numerical approach.....	122
Chapter 7: Floristic and environmental analysis of the Kaokoveld Centre of Endemism.....	134
Chapter 8: Flora of the Kaokoveld Centre of Endemism.....	152
Chapter 9: Endemic seed plants of the Kaokoveld Centre of Endemism .....	170
Appendix I: List of species endemic to the Kaokoveld Centre of Endemism.....	191
Appendix II: An overview of the newly defined Kaokoveld Centre of Endemism.....	197
Chapter 10: Conclusions .....	205
Chapter 11: References .....	209



## List of Figures

- Figure 2. The region in which the study area falls and the Centres and Transition zones identified by White (1983)
- Figure 5.3.1. Welwitschia-desert Group
- Figure 5.3.2. Kaoko Group
- Figure 5.3.3. Highland Group
- Figure 5.3.4. Namib-dune Group
- Figure 5.3.5. Southern Namib succulent desert Group
- Figure 5.3.6. Huns-Orange Group
- Figure 5.3.7. Gordonia Group
- Figure 5.3.8. Kalahari-sand Group
- Figure 5.3.9. The nine floristic Groups identified within the Namibian flora based on distributions of species
- Figure 6.1. The number of species per relevé used in the numerical analysis
- Figure 6.2. Five divisions resulting from the TWINSpan classification
- Figure 6.3. North and south concentrations of the Kaoko division after TWINSpan analysis
- Figure 6.4. North and south concentrations of the Welwitschia division after TWINSpan analysis

## List of Tables

- Table 3.1. Summary of subdisciplines of ecological phytogeography indicating their main foci and results following Van Wyk & Smith (2001)
- Table 3.2. Summary of selected studies providing evidence for the history of parts of Namibia
- Table 4.1. Summary of the 26 largest families in Namibia, ranked according to the number of included species. Global, Namibian and endemic species and genus numbers are supplied for each family
- Table 4.2. Genera with their main distribution within Namibia and/or partially in neighbouring countries
- Table 7.1. Comparison of biotic and abiotic features of the Welwitschia-desert and Kaoko Groups proposed by Craven (2009, Chapter 5) with additional information for species that occur in Angola
- Table 7.2. Similarities and differences between the Divisions and the Groups in the KCE
- Table 8.1. Number of taxa (families, genera and species) present in the KCE, with reference to the representation of the main seed plant groups
- Table 8.2. Genera in the KCE with the most species, along with the number of species present in the Region
- Table 9.1. Families present in the KCE with high numbers of endemic species and the total number of species in the KCE and in the Region
- Table 9.2. Genera with high numbers of species endemic to the KCE, along with the number of species in both the Centre and in the Region
- Table 9.3. Estimates of the number of endemic taxa (families, genera, species and infraspecific taxa in the KCE divided between each of the main seed plant groups
- Table 9.4. Families and genera with the most endemic species in the KCE (the number of endemics in other genera of the same family given in brackets)
- Table 9.5. Distribution of *Commiphora* species within the two floristic Groups of the KCE
- Table 9.6. Species of *Euphorbia* arranged according to their main ranges within the KCE
- Table 9.7. List of species restricted to the Brandberg Mountain
- Table 9.8. List of species occurring on the Brandberg Mountain that are also restricted to disjunct mountains or areas mainly in central or southern Namibia



*Petalidium* species (Acanthaceae) in the Kaokoveld Centre of Endemism



# Chapter 1

## Introduction

Northwestern Namibia and bordering southwestern Angola comprise a well-known species rich and floristically diverse area with a rich endemic flora (Volk 1966; Maggs 1998; Craven & Vorster 2006) and fauna (Shortridge 1934). It is also frequently cited as one of Africa's most species- and endemic-rich areas by the World Conservation Union (IUCN) (Beentje 1994, Hilton-Taylor 1994) and a Centre of Endemism (Van Wyk & Smith 2001). Despite all the recognition, this intriguing biogeographic area has remained vaguely defined.

The aim of this study is to address the following key questions:

- What is the Kaokoveld centre of plant endemism?
- Why is the Kaokoveld considered a centre of plant endemism?

These two simple questions belie their complexity. Not only must a broad range of aspects be considered when looking for answers, but the scope of the study and the terminology used must be clearly defined. Biogeographic areas can be demarcated using diverse criteria and words like centre, region, area, etc. may denote specific entities. The first step is therefore a comprehension review of the theory of phytogeographic delimitations, followed by a study of a broad range of aspects for the core area, as well as the region.

Phytogeography is the study of geographical distributions of plants. The branch that deals with taxa (families, genera and species) with similar geographic distributions and historical processes that led to the formation of these patterns, is historical plant geography (van Wyk & Smith 2001). Very little is known about this branch in general, and this is particularly true in this study area. This contrasts with what is known about the other branch (ecological phytogeography), that looks at the relationships between the plants and their environment. Vegetation types and biomes are well-documented for Namibia and broad vegetation units are recognised for southwestern Angola. Ecological entities (vegetation) and those of the flora (taxa) do not necessarily converge for a number of reasons, and floristic elements may range over numerous vegetation communities.

The focus of this study is historical phytogeography. The outline of the centre will be based on the distribution patterns of the floristic composition only. Once the floristic elements are identified,

different dimensions will be considered so that the centre can be defined with regard to its other features like the geographic boundaries, history and floristic relationships.

Components to be evaluated are:

- The diversity: What plants occur in the area?; What are the floristic elements?; What other floristic elements are represented?; Can endemic areas be identified?; Do these plants show any taxonomic patterns?
- The flora: How does the total flora of the area differs in composition, diversity and distribution patterns from other areas of the world and what areas would have close relatives?
- The history: What past events could have contributed to the present distribution patterns. Can the existence of the Kaokoveld as a centre be explained by factors like geology, past climatic and/or geological events, or dispersal.

Listing all required tasks to be undertaken for phytogeographic analysis methodically is complicated because of the overlapping details. Information is scattered in numerous literature sources and much of it can also be obtained from manipulating electronic databases. The first task is therefore to bring together all the information relevant to any of the associated fields and formatting these data into source material. These data and the theory of phytogeography are covered in the first three papers which makes up Section A. The focus of Section B is the core area, namely the Kaokoveld Centre of Endemism

Section A introduces the theory of phytogeography relevant to an assessment of a centre of endemism and in the context of the region. Secondly, it reviews systematically the phytogeographic characteristics of Namibia and analyses the overall distributions of indigenous families, genera and species. Lastly it presents and discusses floristic groups that are based exclusively on distribution patterns of species. Although the emphasis in section A appears to be predominantly from a Namibian perspective, this should not negatively influence the outcomes. The wedge-shaped section of southwestern Angola covered by this study falls within the Karoo-Namib Regional Centre of Endemism of White (1983) and is clearly demarcated from the Angolan flora by the steep escarpment inland. In other words, southwestern Angola is floristically much closer related to Namibia than to the rest of Angola.

Section B consists of a numerical analysis of the plant species recorded in northwestern Namibia and southwestern Angola to evaluate the floristic support for a centre of endemism in the area. The

resulting outline was investigated further with regard to its floristic components, relationships and origins. Finally the flora and endemic components are described in detail.

The two sections are placed between an introductory chapter, which provides background to the study, and a concluding chapter which defines the Kaokoveld Centre of endemism in terms of its floristic and environmental boundaries.

## References

Beentje, H.J. 1994. Regional overview: Africa. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 101–116. Oxford University Press, Oxford.

Craven, P. & Vorster, P.V. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.

Hilton-Taylor, C. 1994. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.

Maggs, G.L. 1998. Plant diversity in Namibia. In: Barnard, P. (ed.). *Biological diversity in Namibia: A country study*. Pp. 116–122. The Namibian National Biodiversity Task Force, Windhoek.

Shortridge, G.C. 1934. *The mammals of South West Africa*. Heineman, London.

Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.

Volk, O. H. 1966. Die Florengebiere von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.

White, F. 1983. The vegetation of Africa: A Descriptive Memoir to accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa. United Nations Educational Scientific Cultural Organization, Paris.

## Chapter 2

### Procedures and approach

#### The study area

The study area stretches from *ca.* 14° S in Angola to 24° S in Namibia. The stoneless plains covered with Kalahari sand, known as the Karstveld, more or less forms the eastern border around the 16° E. It includes the province of Namibe in Angola and the politically demarcated Kunene and Erongo political regions of Namibia. It covers the area described as a biogeographic region by various authors, for example Shortridge (1934); Volk (1964, 1966); Hilliard (1974); Nordenstam (1974); Werger (1978), Hilton-Taylor (1994); Van Wyk & Smith (2001); Craven (2002, 2005) and Steenkamp *et al.* (2005); It also includes the area outlined by the distributions of defining elements such as *Welwitschia*.

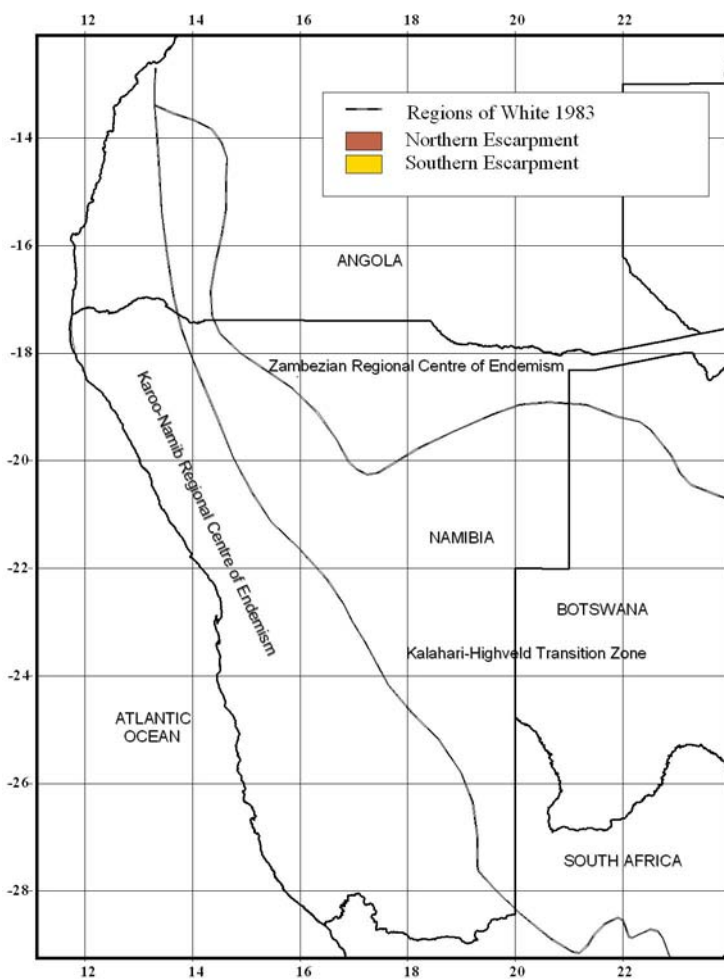


Figure 2. The region in which the study area falls and the Centres and Transition zones identified by White (1983)

## **The physical features**

The study area shows considerable variation in topography, climate and soil type, and this is regarded as one of the reasons for the relatively high plant diversity. The physical features of most of the area are described by Van Wyk & Smith (2001) and Craven (2005), while Huntley (1974) gives an overview of the wedge-shaped part in Angola. Shape files for use with the geographic information systems of the environmental parameters were obtained from the Atlas for Southern Africa (2002) and Atlas of Namibia Project (2002). ArcView (ESRI 2000) and DIVA GIS (2007) systems were used for overlaying shape files of both taxa and physical features for evaluation.

## **The flora**

Over 1600 seed plant species have been recorded from the study area. Data compilation has been ongoing since the first preliminary checklist of Kaokoveld plant species was compiled (Craven & Maggs 1993, unpub.; Craven 2001, unpub.). These lists were based on *Prodromus einer Flora von Südwestafrika*, (Merxmüller 1966–1972), *Flora of southern Africa* (various editorial teams; 1963–ongoing) and *Conspectus Florae Angolensis* (various editorial teams; 1937–1970), as well as numerous other sources referred to in the database of Craven & Kolberg (on-going) and by van Wyk & Smith (2001). This study included indigenous spermatophytes only. Accepted, code-compliant taxon names, generally follow Germishuizen & Meyer (2003), except for species not included in this checklist or where more current and preferred alternate systematic concepts are followed. Those of doubtful status were included if their exclusive distribution lay within this area. Individual judgements were made in order to standardise species concepts in Angola with those in Namibia based on available literature or expert opinion. Besides a grass checklist for Angola (Costa *et al.* 2004), information on legume endemics (Soares *et al.*, 2007), the Rubiaceae family (Figueiredo 2008), a few isolated publications (Bruyns 2005) and Lebrun & Stork (2003, 2006), information on the plants in Angola is very limited. There are also no updated national plant lists. Information was, however, obtained from herbarium specimens in K, M, PRE, NBG, BOL and personal collections of the main author and the collecting lists of De Winter & Leistner (pers. comm.).

Selection of endemic taxa was based on overall distribution according to the definition of Major (1988). The list of Kaokoveld endemics in Craven (2005) and those from Angola, listed by van Wyk & Smith (2001), were updated from literature sources and collections. Finally a list of over 350 species and infraspecific taxa was used as the basis for the numerical analyses. A list of



endemic taxa is supplied in Appendix 1. Because a study of endemism is as sensitive to species names as to collection sites, steps were taken to ensure precise taxonomic and distributional data. This was not always possible for the Angolan taxa and distributions. A number of taxa require further taxonomic scrutiny, but this could not be carried out in the time period of this study, however numerous taxonomic problems were highlighted or clarified. Problems included lack of updated or comprehensive botanical revisions, the diversity of taxa involved which would require extensive expertise, and the problems related to obtaining Angolan material. Fortunately, the Angolan section is small compared to the Namibian section and the problems should not affect the overall picture presented here. Numbers are expected to change as a result of further collecting and study.

Targeted collecting as well as wide-ranging field work by Craven and Kolberg (pers. comm.) has resulted in many new plant records in Namibia. Many species previously known only from type collections or not collected for many years have been found again. Recent field work by Craven in this centre in Angola contributed much needed first hand information on many aspects of the centre. Soares *et al.* (2007) found that recent collections were rare in Angola and difficult to access, thus their analysis of legumes refers mostly to the period up to 1975, after which collection activities practically ceased due to the war in that country. The most productive period for collections in Angola was between 1960 and 1973, and an absence of specimens from the period is believed to reflect rarity (Soares *et al.* 2007). This assumption is not necessarily correct for the centre covered by this paper, as it is extremely arid and longer periods of collecting are required to cover the flora that is present when conditions allow. Soares *et al.* (2007) identified 32 endemic legumes from the area covered in this centre, although since locality information is limited, this number may also include taxa from the Sera de Chela. A further problem is that petaloid monocotyledons (which may flower for a very brief period only) and annuals are under-collected due to the aridity of the area and the difficulty of being in the area when the plants are visible. The high number of succulent species recorded in Angola is undoubtedly due to specialist collecting, as living plants of these groups are mostly taken and cultivated elsewhere. Selection of species according to the limited information for Angola made the job difficult and time consuming. The list is not exhaustive for this reason as many could not be traced.

### **The database**

All the information required for the analysis and evaluation of the KCE was stored in the database of Craven & Kolberg (on-going). This database has been on-going for a few decades and besides

the index of all taxa in the Region, it consists of diverse fields containing information on for example, both local and world-wide present day distribution, voucher specimens, life forms, uses, local names and endemic status. It is constantly updated from literature sources, study of herbarium specimens and through own field collections. A personally compiled list of over 1600 species and infraspecific taxa, recorded for the area and *ca.* 350 range restricted species were used as the basis for the investigation.

### **Herbarium specimens**

Georeferencing herbarium specimens, following the grid-reference system of Edwards & Leistner (1971), is standard practice in southern Africa, and is widely used for mapping purposes. This distribution data, in quarter degree squares, was added to the database for each species. The data were used for mapping and for the numerical analysis. Datasets based on herbarium records and published material, reflect historical ranges and collecting biases are noticeable. Some grids are totally uncollected and areas like the Skeleton Coast Park are botanically poorly known. Locality data from Angola is also limited. Recent field trips, tracing of collections in herbaria (including K, M, PRE, NBG, BOL) did contribute, but the information is still not comparable to that known for the area south of the Kunene River and may result in anomalous biases. Data from web-based maps like the African Flowering Plants Database (<http://www.ville-ge.ch/cjb/bd/africa/index.php>) and those in Lebrun & Stork (2003) were added to distribution data as well as personal collections of the author and of Kolberg (pers.comm.). Underlying specimens were not checked.

### **Numerical analysis**

Distribution data in quarter degree squares for each species was entered via Turboveg 1.97 (International Single User Version, Stephen Hennekens) and Megatab 2.2 (Elsware) into the computer program TWINSpan (two-way indicator species analysis) (Hill 1979) for numerical analysis. TWINSpan was chosen because it is the best method with which to analyse a “complex, noisy, large or unfamiliar” dataset (Steenkamp *et al.* 2005). Other reasons included its “proven combination of effectiveness, robustness, relative objectivity, availability and speed” (Gauch & Whittaker 1981, Moreno Saiz *et al.* 1998, Van Rooy 2000). TWINSpan is a divisive hierarchical classification technique that detects overall patterns of differences in biological data (Van Rooy 2000). Default settings were used for all TWINSpan parameters.

## Methodology

After an extensive review of literature and compilation of source material, the species and specimens information was entered or updated on the database. This was followed by the numerical and floristic analyses. Finally detailed accounts of the flora and endemics were prepared.

## Terminology and definitions

A broad-spanning phytogeographic study such as the one presented here, requires the use of diverse and often confusing and or conflicting terminology. Our interpretations of these definitions are summarised below, but for convenience a few terms are discussed first. These words are used consistently throughout the thesis.

The word *Region* is used here for the wedge-shaped southwestern part of the Angola, south of Benguela and west of the escarpment, Namibia and marginally into neighbouring countries in the south and southwest. This more or less corresponds to the Karoo-Namib Regional centre of endemism and Kalahari-Highveld Regional transition zone of White (1983) in area, but not definition. This contrasts with the use of *region* and *area*, which denote any undefined locality. An *Area of Endemism* is used according to the definition given below.

The *floristic groups* identified in this study are based on broad distributions in the tradition of Weimarck (1941), Nordenstam (1969) and Hilliard (1994) who recognised such groups after taxonomic study. These authors generally also identified concentration of species, many of which are endemic, within these groups, as phytogeographic *centres*. These *floristic groups* are not called phytochoria, as the latter are phytogeographic (floristic) regions of any rank that are hierarchically arranged with ranks such as Domain, Region, Kingdom (Van Wyk & Smith 2001). The term *group*, when used alone indicates any undefined cluster of taxa and differs from a *floristic group* according to the definition given below.

**Area of endemism:** a natural floristic region with the same biogeographic relationships (Linder 2001).

**Centre of endemism:** an area with a high concentration of endemics, the elements of which may not necessarily have similar evolutionary developments (Van Wyk & Smith 2001).

**Endemic taxon:** a taxon confined to a particular area due to historical, ecological or physiological reasons (Major 1988).

**Floristic group:** a group of taxa with similar geographic distributions.

**Floristic element:** a distinctive complement of species with congruent distribution patterns (Van Wyk & Smith 2001). The species do not necessarily show identical geographic ranges, but the patterns are more-or-less coincident (McLaughlin 1989).

**Habitat specialists:** endemic species confined to a small area because of the restricted range or isolated location (Richardson 1978).

**Historical plant geography:** a study that classifies and maps areas based on their floristic composition and generates and test hypotheses about the origin, development and maintenance of the observed plant distribution patterns (van Wyk & Smith 2001).

**Holoendemics:** extremely restricted endemics that are usually associated with isolated habitats in which special climatic conditions prevail, such as on mountain peaks surrounded by hot, arid lowlands (Richardson 1978).

**Near-endemic:** a taxon marginally present elsewhere, sometimes as distant satellite populations (Matthews *et al.* 1993).

**Neo-endemics:** new or evolutionary young species (Richardson 1978).

**Palaeoendemic:** remnants of a species that formerly had a wider distribution (Richardson 1978).

**Phylogeny:** hypothesis of evolutionary relationships.

**Phytogeography:** the study of the geographical distribution of plants.

**Track:** the distribution of a taxon (Linder *et al.* 1992).

## Abbreviations

GIS Geographic Information system

KCE Kaokoveld Centre of Endemism

### Herbarium acronyms

K Kew

M Munich

PRE Pretoria

NBG National Botanical Garden, Kirstenbosch

BOL Bolus Herbarium, University of Cape Town

## References

African Flowering Plants Database. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, "Retrieved 2007/2008", from <<http://www.ville-ge.ch/cjb/bd/africa/index.php>>.

Atlas for Southern Africa. 2002. Dynamic Atlas Resource CD. FAO-GTOS and SKE Inc.

Atlas of Namibia Project. 2002. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek. <http://www.dea.met.gov.na/>.

Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.

Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar* 1 & II. Umdaus Press, Hatfield.

*Conspectus Florae Angolense* (various editorial teams). 1937–1970. Centro de Botânica, Instituto de Investigação Científica Tropical, Lisboa.

Costa, E., Martins, T. & Monteiro, F. 2004. A checklist of Angola grasses – Checklist das Poaceae de Angola. *Southern African Botanical Diversity Network Report* 28. SABONET, Pretoria.

Craven, P. 2001. *Checklist: Kaokoveld*. Unpublished. National Herbarium of Namibia, National Botanical Research Institute, Windhoek.

Craven, P. 2002. Plant species diversity in the Kaokoveld, Namibia. In: Bollig, M., Brunotte, E. & Becker, T. (eds), *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 75–80. *Kölner Geographische Arbeiten* 77, Köln.

Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET news* 9: 24–44.

Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.

Craven, P. & Maggs, G.L 1993. *Checklist: Kaokoveld*. Unpublished. National Botanical Research Institute, Windhoek.

DIVA GIS 2007. A Geographical Information System for the Analysis of Biodiversity data. International Potato Center (CIP), [www.cipotato.ORG](http://www.cipotato.ORG)

Edwards, D. & Leistner, O.A. 1971. A degree reference system for citing biological records in South Africa. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 501–509.

ESRI. 2000. *ArcView 3.2a Software*. Environmental Systems Research Institute, Redlands, USA.

Figueiredo, E. 2008. The Rubiaceae of Angola. *Botanical Journal of the Linnean Society* 156: 537–638.

*Flora of southern Africa* (various editorial teams). 1963–ongoing. National Botanical Institute, Pretoria.

Gauch, H.G. & Whittaker, R.H. 1981. Hierarchical classification of community data. *Journal of Ecology* 69: 537–557.

Germishuizen, G. & Meyer, N.L. (eds). 2003. *Plants of southern Africa: an annotated checklist*. *Strelitzia* 14. National Botanical Institute, Pretoria.

- Hill, M.O. 1979. TWINSPAN - A FORTRAN program for arranging data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*. Cornell University. Ithaca, New York.
- Hilliard, O.M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Hilton-Taylor, C. 1994. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.
- Huntley, B.J. 1974. Outlines of Wildlife Conservation in Angola. *Journal of South African Wildlife Management Association* 4: 157–166.
- Lebrun, J.-P. & Stork, A.L. 2003. *Tropical African flowering plants. Ecology and distribution 1, Annonaceae – Balanitaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.
- Lebrun, J.-P. & Stork, A.L. 2006. *Tropical African Flowering plants. Ecology and distribution 2, Euphorbiaceae – Dichapetalaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.
- Linder, H.P., Meadows, M.E. & Cowling, R.M. 1992. History of the Cape flora. In: Cowling, R.M. (ed.). *The ecology of fynbos. Nutrients, fire and diversity*. 5: 113–134. Oxford University Press, Oxford.
- Major, J. 1988. Endemism: A botanical perspective. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 117–146. Chapman & Hall, London.
- Matthews, W.S., Van Wyk, A.E. & Bredenkamp, G.J. 1993. Endemic flora of the north-eastern Transvaal escarpment, South Africa. *Biological Conservation* 63: 83-94.

- McLaughlin, S.P. 1989. Natural floristic areas of the western United States. *Journal of Biogeography* 16: 239–248.
- Merxmüller, H. (ed.). 1966–1972. *Prodromus eine Flora von Südwestafrika*. Cramer Verlag, Lehre.
- Moreno Saiz, J.C., Castro Parga, J. & Sainz Ollero, H. 1998. Numerical analysis of distributions of Iberian and Balearic endemic monocotyledons. *Journal of Biogeography* 25: 179–194.
- Nordenstam, B. 1969. Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica* 23: 7–75.
- Nordenstam, B. 1974. The flora of the Brandberg. *Dinteria* 11: 3–67.
- Richardson, I.B.K. 1978. Endemic taxa and the taxonomist. In: Street, H.E. (ed.). *Essays in plant taxonomy*. Pp. 245–262. Academic Press, London.
- Shortridge, G.C. 1934. *The mammals of South West Africa*. Heineman, London.
- Soares, M., Abreu, J., Nunes, H., Silveira, P., Schrire, B. & Figueiredo, E. 2007. The Leguminosae of Angola: Diversity and endemism. *Systematics and geography of plants* 77: 141–212.
- Steenkamp, Y., van Wyk, A.E., Smith, G.F. & Steyn, H. 2005. Floristic endemism in southern Africa: A numerical classification at generic level. *Biologiske skrifter* 55: 253–271.
- Van Rooy, J. 2000. Diversity and phytogeography of the moss flora of southern Africa. PhD thesis University of Pretoria, Pretoria.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Volk, O.H. 1964. Die afro-meridionale-occidentale Floren-Region in Südwestafrika. *Beiträge zur Phytologie zu Ehren Prof. H. Walters 65 Geburtstages*. Ulmer, Stuttgart.
- Volk, O. H. 1966. Die Florengebiete von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.



Weimarck, H. 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Acta University Lund* 3: 5–143.

Werger, M.J.A. (ed.). 1978. *Biogeography and ecology of southern Africa*. Junk, The Hague.

White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.



*Welwitschia mirabilis*

## **SECTION A**

## Chapter 3

### Plant geography in Namibia

#### Abstract

3.1	Introduction.....	28
3.2	Ecological phytogeography.....	31
3.3	Historical phytogeography.....	32
3.4	Approaches which are neither ecological nor historical.....	35
3.5	The history of the Namibian flora.....	36
3.6	The history of the Namibian flora from palaeo-palynology.....	38
3.7	Discussion.....	40
3.8	Conclusions.....	42
3.9	References.....	43

# Plant geography in Namibia

## Abstract

The plants of Namibia have been mapped in several ways using different criteria. This paper categorises these maps according to different approaches to phytogeography. A summary and analysis of these diverse methods, their scientific merit and usefulness of each in terms of defining the geographic patterns of plants in Namibia is given. In addition, abiotic aspects, e.g. the palaeo-environment, and pollen studies relevant to historical phytogeography, are discussed.

## 3.1 Introduction

During an analysis of the Kaokoveld Centre of Endemism (KCE) (Craven 2009, Chapter 6), it became apparent that defining terms like Kaoko and endemism have been used for various phytogeographic concepts. Moreover, no specific criteria were used for these definitions. Historical phytogeography in particular was found to be largely unknown in Namibia, resulting in misapplication of the concepts or misunderstanding of the few studies in this field. In addition the importance of historical biogeography for research and conservation is underestimated.

Phytogeography is the study of geographical distributions of plants. The world flora may be mapped in different ways depending on the botanical criteria used for defining mapping units. Globally the mapping of vegetation types or biomes have received considerable attention, and Namibia is no exception. This is in sharp contrast to spatial data based on historical biogeography, where various areas have different species, even when the areas are ecologically similar (Buffon's law, Poynton 1986). The Atlas of Namibia (Mendelsohn *et al.* 2002) maps types of vegetation, vegetation structure and production, and patterns of diversity and endemism. Shape files of Namibia, for use with GIS software, are also freely available on the internet. What is absent for Namibia are representations of the phytogeographic patterns of taxa. Although Namibia's position within floristic regions at the mega-regional scale is well documented, attempts have only recently been made to identify more local floristic regions inside Namibia (Craven 2009, Chapter 5).

The plant diversity of an area is made up of the genes, species and communities of plants within that particular area. Reasons for the presence of particular plant species in a given area include past and present climatic-ecological conditions, the biology of the plants and anthropogenic activity and movement. For a full understanding of this diversity, it is therefore imperative that both the

ecological and historical phytogeography is reviewed, taking into account the differences between the two. When spatial data are used without considering the precise criteria used to define such data, results may be confusing. Differences in approach may be so complete that it is largely impossible to make biogeographical comparisons between groups (mapping units) demarcated by different authors. Poynton (1986), for example, argues that the avifauna and herpetofauna chapters in Werger (1978) cannot be compared because of the two different approaches followed to compile these data. Two research traditions in biogeography are generally recognized, namely ecological and historical biogeography (Rosen 1988), however there are approaches that fit neither of these traditions.

Ecological phytogeography is based on growth form of plants regardless of their taxonomic identity, e.g. biomes; or based on growth form and/or floristic composition, regardless of distribution ranges of taxa. Time scale is contemporary and the scale of resolution is micro-regional to macro-regional. Van Wyk and Smith (2001) divided this approach into autecological, synecological and phytosociological subdisciplines and clarify the specific focus and resulting outcome of such research (Table 3.1).

Table 3.1. Summary of subdisciplines of ecological phytogeography indicating their main foci and results following Van Wyk & Smith (2001)

<b>Approach</b>	<b>Subdiscipline</b>	<b>Focus</b>	<b>Outcome</b>
patterns in vegetation & species ranges as determined by climatic, soil ( <b>edaphic</b> ) & biotic factors.	autecological ( <i>individuals</i> )	relationship between <i>individual</i> organisms & their environment	habitat suitability, species tolerances, competition, herbivory & disturbance regimes
	synecological ( <i>groups or communities</i> )	the <b>ecosystem</b> approach	communities & especially their structure & environmental relations
		phytosociological (or community ecology)	the description & classification of vegetation; why certain combinations of plant species, but not others, co-occur in a given habitat

Examples of ecological phytogeographic categories include:

**Biomes:** a group of similar types of communities characterized by the distinctiveness of the life-forms of the principle climax species they contain, and by their responses to that environment. (Little & Jones 1980).

**Vegetation:** the general effect produced by the growth of some or all of these taxa in combination.

**Vegetation types:** plants seen in communities that share similar climate, geological and soil requirements.

**Veld types:** units of vegetation whose range of variation is small enough to permit the whole of it to have the same farming potential (Acocks 1953).

Historical phytogeography is based on the total geographical range of taxa, regardless of their growth forms, e.g. the flora (the constituent plant taxa of an area, usually global); or phytogeographic region (an area with its own distinctive complement of species). It is a taxon-centred approach focussed on species, genera and/or families. The ranges of individual taxa are not identical, but included taxa are recognized by more-or-less coincident range patterns that were determined by climatic, geological, migrational or evolutionary events. Particular significance is attached to the taxonomy and presumed evolutionary relationships (phylogeny) of taxa, endemics and taxa with disjunct distributions. Data required following this approach are obtained from taxonomic research. The time scale is historical and the scale of the area depends on individual species or related groups of taxa (Van Wyk & Smith 2001) A major goal of floristic plant geography is the classification of the earth into floristic areas (Good 1974, Takhtajan 1986), for example, Kingdoms, Regions, Provinces, District. Most of these are hierarchical, i.e. smaller areas are nested within successively larger areas, but there has up to now been no uniform terminology. Recently, however, an International Code of Area Nomenclature has been proposed (Ebach *et al.* 2008).

In the Bibliography of South West African Botany (Giess 1989), papers relevant to ecological phytogeography are identified by the keyword “vegetation” and historical phytogeographic papers are listed under “flora”. The terms vegetation and flora are thus consistently used to denote these two different approaches, the former usually resulting from research by plant ecologists, while the latter has mainly been the focus of plant taxonomists or systematists.

### 3.2 Ecological phytogeography

The plant geographical tradition of studying plant communities has dominated the study of Namibian vegetation. Irish (1994) identified four biomes in Namibia, which were viewed as large land communities distinguished on the basis of dominant (plant) life forms and on climatic features. Terms used in this demarcation (e.g. desert, savanna, etc.), are also applied in broad scale studies elsewhere in the world, despite considerable variation in the floristic composition. Vegetation maps presented in the Atlas of Namibia (Mendelsohn *et al.* 2002) cover biomes, broad vegetation types and smaller vegetation units. In total 29 broad vegetation types are defined for Namibia, each confined to a biome. The dominant structure of the vegetation, types of soil and landscapes are tabulated. Numerous other detailed studies of areas, not associated with biomes, have been published for Namibia.

Vegetation projects in Namibia, both published and unpublished, were reviewed in a paper by Burke & Strohbach (2000). They aimed to summarise vegetation surveys and to identify priorities for future research. They differentiated between phytosociological studies, vegetation in relation to environmental parameters and surveys based on remote sensing, based on communities of plants. Unfortunately there is little consistency in assigning the recorded studies to these particular categories. Burke & Strohbach (2000) do not clearly define their approach, and lumped surveys based on very different criteria and aims. In the general vegetation surveys (GVS) section, incongruent data resulting from numerous checklists and the historical phytogeographic evaluation by Volk (1966) are erroneously lumped together. This review thus perpetuated the already confusing demarcation of vegetation units within Namibia.

The Vegetation Mapping project of the National Botanical Research Institute (Windhoek) is currently ongoing and aims to provide sufficient data for rangeland and resource management. Within this project, vegetation is defined as “the combination of species in a certain area, depending on a particular habitat” (Strohbach & Strohbach 2004). Braun-Blanquet Sampling procedures are recommended in conjunction with detailed soil analyses. A limited number of surveys have been done since publication of the review under the auspices of the Vegetation mapping unit and BIOTA. All of these follow an ecological phytogeographic approach because they are plant community-based and environmental parameters are considered. Species diversity (floristic) lists generated from the relevés using TurboVeg are useful byproducts of community studies, provided these are backed by voucher specimens in herbaria that can be subjected to taxonomic verification if



necessary. These lists are, however, not necessarily complete for an area as they reflect what has been found in relevés, not the total flora.

Although the review of Burke & Strohbach (2000) provides a useful bibliography of research in Namibia up to 2000, misunderstanding the different branches of phytogeography has resulted in rather generalized proposals and statements. For example, they state that many plant surveys did not attempt to explain the vegetation in relation to their environment. This indicates the neglect of historical phytogeography and other methodologies. Another example is the proposal that a detailed vegetation survey could resolve the delimitation of vegetation units in the southern Namib and the work of Giess (1971), Werger (1978), Jürgens (1991) and Irish (1994) is mentioned. Considering that these studies approached the area from different angles, backgrounds, aims and objectives, it is no wonder that proposed boundaries differ, rendering the proposals by Burke & Strohbach (2000) untenable.

### **3.3 Historical phytogeography**

Historical biogeography asks the question: what lives where and *why*? The reason why a taxon lives in a specific area may be due to it having evolved there or having moved into the area. This was already recognised by Buffon (1766) and Sclater (1858) according to Ebach (2004). Historical biogeography emphasises areas rather than ecosystems, as distribution patterns are repetitive and areas identified by the plant taxa within them (i.e. autonomous of abiotic factors) is possible. The basic principle is that the world and its biota evolved together (Parenti & Humphries 2004). Reconstructing past biogeographic events is possible by considering the distribution of individual groups (taxon biogeography) or areas of endemism (area biogeography). The focus may be on local large-scale (microregional) distribution patterns, or on global patterns of taxa and is concerned with evolutionary processes over millions of years.

Approaches to historical phytogeography include, for example, the establishment of centres of origin and dispersal, panbiogeography, phylogenetic and cladistic biogeography. Although the best approach is debatable, each one is said to contribute to a different type of biogeographical question. It has also benefited from the recent development of analytical and numerical methods. Unfortunately very few of the many approaches and techniques relating to historical biogeography summarised by Crisci (2001) have been applied to Namibian taxa or areas. Unlike the work of Volk (1964, 1966) and the new floristic divisions proposed by Craven (2009, Chapter 5), most studies of historical phytogeography in Namibia are limited to studies carried out on the southern African

region as a whole. Historical biogeography has thus largely lagged behind, especially because much of the methodology relies on availability of good systematic studies. It requires the identification of taxa, their systematic classification and knowledge of their overall geographic distribution, i.e. as many as possible of the indigenous seed plants both in Namibia and their distributions elsewhere. Mistakes and defects in taxonomic work can, and have, led to fundamentally wrong conclusions. Such errors in ecologically-centred work do not necessarily have such bad consequences (Poynton 1962). Floristic databanks, when made available for evaluation, allow a quick and efficient retrieval of a great number of phytogeographic data otherwise scattered in the literature or herbarium. They can also generate computerised distribution maps. Unfortunately data errors are legion and data cleaning requires much patience and effort. Another problem is the availability of this information for people without the necessary taxonomic background to analyse or evaluate it according to standard phytogeographic methods, e.g. the divisions of the Namib by Jürgens (1991, 1992). Another problem is the tendency to use this computerized information without supplementation by proper field and herbarium studies.

Friis (1986) traces the historical development of phytogeography in Africa. Maps produced by Schouw (1823), Engler (1882), Lebrun (1947), Robyns (1948), Monod (1957), Troupin (1966), White (1971, 1976) and Wickens (1976) are included. Werger (1978) did the same for southern Africa. These proposals formed the basis of the divisions by Volk (1964, 1966), who was the first to use certain species distributions to verify and comment on this phytogeographical subdivision for Namibia. Besides outlining the Karoo-Namib Region, Volk (1964, 1966) divided the tropical floristic elements, with their main distributions in tropical areas of Africa, into Sudan-Sambesi, Sambezi and Kalahari elements. Volk (1966) also recognizes four endemic regions in Namibia: (1) Lüderitz Centre, from the Orange River to Maltahöhe; (2) Namib Centre; (3) Kaokoveld Centre from Swakopmund to Angola and (4) Gordonia Centre which includes the sandy parts of the southwest Kalahari. Despite its significance, the work of Volk (1964, 1966) is little known, as it was published in German in a rather obscure book and local journal, without a visual presentation of his proposals.

Following the higher-order phytogeographical subdivisions of Takhtajan (1986), Namibia lies within the Palaeotropical Floristic Kingdom with the Sudano-Zambesian Region (Zambesian Domain) situated in the northeast of the country and the Karoo-Namib Region making up the rest. The proposal of Jürgens (1991, 1997), on the basis of the analysis of a large set of succulent taxa, to include southwest Namibia to north of Swakopmund, in a Greater Cape Flora, is not supported by Born *et al.* (2007). Like Werger (1978), their boundary for the Cape flora lies south of the Orange

River and does not include the southern Namib Desert of Namibia. A detailed, species distribution-based analysis of the same area undertaken by Craven (2009, Chapter 5) and named the Southern Namib succulent desert Group is supported by Born *et al.* (2007) who describe the flora as being highly specialized and adapted to the dry and extremely windy climate for the same area, i.e. from the Holgat River in South Africa north to Lüderitz in Namibia.

The study of endemism and disjunct distribution patterns is central to historical phytogeography. Craven (2009, Chapter 4) discusses both of these floristic attributes in the Namibian context. Areas of floristic endemism in Namibia have been documented, especially after taxonomic study on specific taxa by Hilliard (1994), Nordenstam (1969) and Van Wyk (1991). Species from Namibia are also linked to southern African taxon-specific floristic groups like those proposed by Weimarck (1941). Examples include The Karroo Ubiquists; The Namaqualand-Cape Group; The Namaqua Group and The Arid Northern Cape-Namibia Group. Although “area of endemism” is generally defined as an area with a high concentration of taxa with limited geographic distributions, it is also used in much broader contexts, making it essential to differentiate between these concepts, as follows:

**1. An Area of Endemism:** a natural floristic region determined by only the endemic component of the flora. According to Linder (2001) “an implicit assumption .... is that its biota has a single history and consequently that the biogeographical relationships of all the elements in the biota should be the same“. Protocols for locating areas of endemism have been neglected. Linder (2001) proposed criteria for the evaluation of such areas. Such areas may also be disjunct, and in some cases they may also cover the same area as a Centre of Endemism.

**2. A Centre of Endemism:** a high concentration of endemics, the elements of which may not necessarily have similar evolutionary development, as defined by van Wyk & Smith (2001).

**3. Regional Centres of Endemism of White (1983)** summarised by Linder *et al.* (2005) as follows:

- a. A non-hierarchical classification.
- b. Delimitation based on species distributions.
- c. Recognizes three regions, namely Regional centres of Endemism, Regional Transition Zones and Regional Mosaics, each with their own specific criteria.
- d. All species are taken into account, although the delimitation is based largely on dominant species.

### 3.4 Approaches which are neither ecological nor historical

White (1965) presented the first version of what he later called the “AETFAT chorological divisions of Africa”. Further maps appeared in White (1971), White (1976) and White (1983). Although White’s emphasis and criteria evolved over time, the distributions of taxa remained the basis for classification throughout his work. He did, however, not distinguish between historical and ecological causes of the distribution patterns, but set out his own rules to delimit his phytochoria based on the criteria summarized by Linder *et al.* (2005) above. In his later work, White (1983) recognised eighteen phytochoria with centres of plant diversity and endemism for Africa. The three areas of importance to Namibia include the Zambezian Regional Centre of Endemism with a few endemic genera, one of which occurs in Namibia (*Volkiella* (Goldblatt 1978)); the Kalahari-Highveld Transition Zone with the endemic genus *Neuradopsis* and the Karoo-Namib Regional Centre of Endemism. The one family endemic to this centre occurs in Namibia, namely Welwitschiaceae.

Although the phytogeographic subdivision of the Namib Region of Jürgens (1991) and Jürgens (1997) were largely based on Werger (1978) and White (1983), they were developed from distributional data supplemented with “general ecological gradients and specific qualities of the taxa” (Jürgens 1992). Despite the disparity, Jürgens (1991, 1997) places his classification of regions within Floristic Kingdoms and subordinate units that are based on the component plants only. He also uses a combination of terms from biomes and endemic centres. For example, the Karoo-Namib becomes Nama-Karoo. Unfortunately these differences went unnoticed, and the areas outlined by Jürgens (1991, 1997) have subsequently been referred to merely as floristic zones, e.g. by Bruyns (2005) and Cowling *et al.* (1998).

Terrestrial Ecosystems of the world (WWF & National Geographic 2001, Burgess *et al.* 2004, Kier *et al.* 2005) or Ecoregions (Olson & Dinerstein 2002) are defined as geographical areas that share the majority of their species (plants and/or animals) and ecological processes, and represent first attempts to set conservation priorities at the continental scale. These mapping units are considered to be of global biological importance due to their concentration of endemic species. Despite this definition, the Ecosystems defined by this initiative in Namibia do not take plant species distributions into consideration. The Kaokoveld Desert (AT1310) for example, which besides the confusion caused by its name (i.e. it lies outside the “hilly” region know as Kaoko), only partially covers the distributions of the species discussed as representative for this unit, e.g. *Welwitschia mirabilis*. The Namib Desert (AT1315), which stretches from the Uniab River to Lüderitz, contains

the southern part of the Kaokoveld Desert species distributions, but also includes an area with a totally different species composition. Outlining congruent distribution patterns (Craven 2009, Chapter 5) will hopefully contribute to a better understanding of ecosystems and their threats.

Centres of Plant Diversity are species-rich, and/or known to contain a large number of endemic species (WWF/IUCN (1994), Beentje 1996). Two well-known centres listed for Namibia are the Gariiep and the Kaokoveld centres (Hilton-Taylor 1994a, b; van Wyk & Smith 2001; Craven 2002, 2005; Craven and Vorster 2006).

The concept of biological hotspots was first developed by Myers (1988) and adopted by Conservation International in 1989 and updated in 1996 (Mittermeier *et al.* 1998; Mittermeier & Mittermeier 2001; Mittermeier *et al.* 2004). Among the most important additions to biological hotspots were quantitative criteria with endemism being the most important. Hotspots are defined as exceptional concentrations of species with high levels of endemism (i.e. 1500), that face exceptional threats of destruction (already lost 75% or more of the original vegetation). Currently a total of 34 hotspots are recognized worldwide, with the Succulent Karoo Biome representing one of these. The southwestern part of Namibia therefore falls within the broader Succulent Karoo Hotspot. Unfortunately the term Hotspot has been used out of this context in Namibian publications, especially in Environmental Impact Assessments and requires definition when being used.

Centres of diversity are areas with a high concentration of taxa within the area, and these were mapped for plants by Craven (2002) in the Namibian Atlas (Mendelsohn *et al.* 2002). These centres were inferred from a simple grid-diversity count and the identities of the species within the areas were not taken into consideration.

### **3.5 The history of the Namibian flora**

Plant distributions may also be considered the result of past events (Lawrence 1971) and thus phylogenies (hypotheses of evolutionary relationships) of taxa and theories used to describe the history of the earth must be taken into account. A large amount and variety of palaeo-environmental and palaeo-ecological information, pertinent to Namibia, is available. Making use of these data is, however, not without its difficulties. Some data are so specialized/or and speculative that it is difficult for any individual specialist to comprehend and relate to floristic patterns. Facts are often difficult to reconcile with some of the conclusions drawn from them. In this regard Nimis *et al.*

(1998) warn that the interpretation of patterns in terms of palaeohistory should be used with great caution.

Aspects such as pollen deposits, fluvial deposits, lacustrine deposits, marine cores, soils, caves and speleothem have been studied to reconstruct the geological and biological history of Namibia (Table 3.2). Analyses of these data for the purpose of this paper showed that, despite many attempts to find new or synthesise existing data, the environmental history of Namibia remains complex and poorly resolved. In its present form these data cannot significantly contribute to an improved understanding of the history of the Namibian flora.

Table 3.2. Summary of selected studies providing evidence for the history of parts of Namibia

<b>Subject</b>	<b>Reference</b>
Archaeobotany; archaeology	Knoll 1983; Albrecht <i>et al.</i> 2001; Vogelsang <i>et al.</i> 2002; Eichhorn 2004
Atlantic sea surface temperatures	Dupont <i>et al.</i> 2004
Climate	Vogel 1989; Heine 1992, 1998, 2005; Lancaster 2002; Segalen <i>et al.</i> 2004
Dune sand and fine-grained silty deposits	Besler 1977; Eitel <i>et al.</i> 2001; Eitel <i>et al.</i> 2002
Fauna	Poynton 1962, 1995; Coetzee 1969, 1983; Endrödy-Younga 1982; Haacke 1982; Holm & Scholtz 1983; Avery 1993; Coe & Skinner 1993; Holm 1990; Irish 1990; Pickford 2000; Sole <i>et al.</i> 2005
Fluvial deposits, river clay, river silt terraces	Vogel & Rust 1987; Rust & Vogel 1988; Eitel <i>et al.</i> 1998; Rust 1999; Bourke <i>et al.</i> 2003; Srivastava <i>et al.</i> 2004; Srivastava <i>et al.</i> 2005; Eitel <i>et al.</i> 2005; Brook <i>et al.</i> 2006
General	Torquato 1970; Walter 1983; Ward & Corbett 1990; Besler 1991
Geology; geomorphology	Rust 1984, 1987; Heine & Walter 1996; Atlas of Namibia Project 2002
Lake-level changes	Brook <i>et al.</i> 2007
Ocean core	Siesser 1978, 1980; Marlow <i>et al.</i> 2000
Palaeo-environments; palaeo-hydrology	Lancaster 1984; Heine & Heine 2002

Palaeo-palynology	Van Zinderen Bakker 1984a, b, c; Van Zinderen Bakker & Müller 1987; Scott <i>et al.</i> 1991; Scott 1996; Shi & Dupont 1997; Shi <i>et al.</i> 1998; Carrión <i>et al.</i> 2000; Shi <i>et al.</i> 2000; Shi <i>et al.</i> 2001; Dupont & Wyputta 2003; Scott <i>et al.</i> 2004; Dupont <i>et al.</i> 2005; Dupont 2006; Dupont & Behling 2006; Gil-Romera <i>et al.</i> 2006; Dupont <i>et al.</i> 2007; Gil-Romera <i>et al.</i> 2007
Radiocarbon dates	Rust <i>et al.</i> 1984; Carr <i>et al.</i> 1976
Sedimentological and pedological	Teller <i>et al.</i> 1990; Brunotte <i>et al.</i> 2002
Silt, soil and sediments, landslides	Eitel & Zöller 1996; Eitel <i>et al.</i> 1999; Brunotte & Sander 2000; Stengel 2000; Stengel & Leser 2004; Srivastava <i>et al.</i> 2005; Srivastava <i>et al.</i> 2006
Speleotherm, tufa and sand dune; tufas	Brook <i>et al.</i> 1996; Brook <i>et al.</i> 1999
Vegetation	Van Zinderen Bakker 1975; Eichhorn & Jürgens 2003; Jacobson & Lester 2003; Vogel 2003

### 3.6 The history of the Namibian flora from palaeo-palynology

Pollen research in deserts is known to be problematic, because conventional pollen-bearing deposits are rare in hyper-arid regions (Van Zinderen Bakker 1983). Hyrax middens, however, may serve as an archive for a range of palaeoenvironmental proxies, including palynological information, but hitherto this potential source still remains largely unexplored in Namibia (Gil-Romera *et al.* 2006, 2007). Despite this, studies of fossil pollen have received considerable attention in Namibia (Table 3.2), but the interpretation of these results presented more questions than answers.

Problems associated with palaeopalynological data analysis are summarized as follows:

**Scientific practice:** Often authors are unaware of the significance of research results in specialist fields other than their own. Many researchers also often fail to really understand the present flora. This is unfortunate, as the absence of a particular species may be as important as its presence (Deacon and Lancaster 1988). This is particularly important in the evaluation of key species such as *Welwitschia*. Knowledge of the flora in the region requires extensive field collections covering all spectra of life forms and cannot be reliably attained from popular field guides only. Field guides, by their very nature, are often limited in coverage to selected groups of plants or the more conspicuous plant species, and are often not taxonomically correct or up to date. *Cadaba aphylla* (Thunb.) Wild in the Capparaceae cited by Gil-Romera *et al.* (2006), for example, is mistaken for *Calicorema capitata* (Moq.) Hook.f. of the Amaranthaceae, a species found further south, based on an erroneous

record (Curtis & Mannheimer 2005). Another example is the frequent recording of *Combretum* pollen in areas far from living plants. This may be a consequence of mistaking *Phaeoptilum spinosum* Radlk. for a member of the *Combretum* genus. Both have similarly winged fruit and are often confused. In other instances pollen data could certainly contribute more information than what is currently retrieved. Palynological data of the Acanthaceae, for example, is informative at the generic level, and yet, Acanthaceae pollen is often simply lumped at the family level. *Dodonaea viscosa* Jacq, is another interesting example. It is considered to be a non-indigenous plant in Gil-Romera *et al.* (2006) based on Curtis and Mannheimer (2005). It is, however, an intriguing disjunct occurring in southern Namibia and the eastern Cape of South Africa (Craven 2009, Chapter 5).

**Complexities of pollen analysis:** Although pollen data are potentially very informative, the limitations should not be overlooked. Pollen cores are thought to generally reflect the present local flora (Dupont & Behling 2006). To this end it is important to remember that a species may be lacking in the pollen record simply because its pollen type preserves poorly, and not because this species was not present in a region. Furthermore pollen influx via rivers and wind from distant regions may complicate environmental interpretations. This is particularly important when the river arises in a floristically poorly known area such as the Angolan highlands. Pollen, for example in ocean cores, tends to yield general information on vegetation history of the whole region, rather than supplying information at a more local scale.

**Inference of vegetation units and life form:** Categorizing taxa identified through pollen analysis only into biomes or vegetation units is tenuous and dangerous. Similarly the reliance on life form spectra instead of comprehensive analyses of species composition misrepresents natural floristic units. A good example is presented by *Passerina* pollen recovered from the Brandberg (Scott *et al.* 2004). As *Passerina* is a fynbos genus, it was described as a Cape element. In reality, however, this pollen may represent that of the species *P. montana* Thoday, which today has a relictual occurrence near Windhoek in Namibia and is also associated with the Angolan highlands and the eastern Great Escarpment of southern Africa (Bredenkamp & Van Wyk 2006, Craven 2009, Chapter 5). More comprehensive palaeo-palynological studies would be valuable, but as mentioned by Hedberg (1954) the task can certainly not be accomplished without a good working knowledge of the flora.

The thorough evaluation of the literature discussed in the present paper has resulted in important findings:

1. There is no palaeopalynological evidence to suggest that the winter rainfall region ever reached as far north as the Brandberg (Linder 2003). Neither is there convincing evidence



that Cape floral communities reached the tropics along the western escarpment, despite such pollen being present in marine cores along the west coast (Scott *et al.* 2004).

2. Studies of fossil pollen (Scott *et al.* 1991) indicate a moist and warm phase of climate between c. 7000 and 6000 yr BP near Windhoek that conforms to reconstructions based on other southern African pollen sequence data. This contrasts to the indications that dry conditions prevailed in the Namib Desert during this same time period (Rust & Vogel 1988; Vogel 1989; Heine 1998). This evidence may confirm the closer relationship of the flora of the Windhoek highlands with the Highveld of South Africa as shown by Craven (2009, Chapter 5).

### **3.7 Discussion**

Namibia's biodiversity assessment (Barnard 1998) states that "existing classification schemes for biomes, vegetation types .... were felt to summarise Namibia's terrestrial ... variety adequately". Management plans, gap analysis, future goals, etc., identified in this study therefore lacked one important aspect of plant life, namely the contribution of floristic zones. Deductions and conclusions drawn by palaeo-botanists and other researchers may also be different or enhanced when historical phytogeography is considered. An example is the study of fossil pollen in the northwestern Namib Desert by Gil-Romera *et al.* (2007), where the pollen is said to occur in the Nama-Karoo Biome. The species listed for the area, however, are better matched with the Kaoko floristic Group (Craven 2009, Chapter 5).

Historical phytogeography helps define the taxonomic limits of closely related species. It aids predicting where a primitive sister group may be found. It is also fundamental to optimal planning and sustainable development, and can assist in defining priorities for action. Its role in identifying Important Plant Areas (Radford 2004; Smith 2004), which will assure the protection of 50% of the most important areas of plant diversity, which is Target 5 of the Global Strategy for Plant Conservation (UNEP 2003), is invaluable. It is also critically important to the current studies on climate change. It is further necessary for the interpretation and understanding of biotic distribution patterns of biological and abiotic phenomena by workers in different fields. Zoologist and palaeo-scientists have used vegetation maps when discussing their findings due to the lack of a floristic map. As Croizat (1994) states: "it is unthinkable that the dispersal of plants can conflict with that of animals" and centres of endemism, e.g. the Kaokoveld, have been recognized for both fauna and flora (Shortridge 1934, Craven 2005). It is therefore common sense that any study on the diversity

and geography of taxa other than plants should use a floristic map as well as, or rather than, a vegetation map, as was done in Namibia's Biodiversity country study (Barnard 1998).

Climate change studies should take both historical and ecological phytogeography into account. *Aloe dichotoma* Masson has been the focus of attempts at modeling potential climate change and Midgley *et al.* (2005) state that "An early warning sign of climate change is indicated by the response of populations of *A. dichotoma* to apparent trends in recent climate, which indicate warming and drying trends in Namibia and northern South Africa". Midgley *et al.* (2005) further report that "*A. dichotoma* revealed extensive ongoing mortality in populations near their thermal and/or water balance limits in the northern Cape and Namibia". Although this statement may be valid for the Northern Cape, it is refuted for Namibia. It is clear when overlaying the distribution of *A. dichotoma* in Namibia onto GIS shape files of environmental, vegetation and floristic regions for Namibia (Agro-Ecological Zoning Programme, 1996-ongoing; Atlas of Namibia 2002; Craven 2009, Chapter 5) that its distribution does not fit any that could be explained by numerous other species having the same evolutionary or ecological requirements. Both temperature and moisture vary over its range on a broad scale, in addition to the microclimates caused by the increases in moisture and decreases in temperature made by proximity to the sea's cooling breezes. The lack of juveniles during the study period could be attributed to the fact that an episodic event is necessary for germination and this may only occur in a few decades per century. Besides, numerous areas actually do have plenty of young plants.

Historical phytogeography also requires sound taxonomy, and that of *Aloe dichotoma* is not secure. Specimens seen between Lüderitz and the area further inland, show possible transitions with *A. ramosissima* (Kolberg pers. comm.). In addition both Eggli (2001) and the Flora of South Africa (various editorial teams, 1963-ongoing) differ concerning its concept of species and infra-specific taxa. Another noteworthy statement of Midgley *et al.* (2005) is "The dominant vegetation type simulated in Namibia under current climate conditions, which we term Grassy Savanna, is projected to lose its spatial dominance to Desert and Arid Shrubland vegetation types". This ignores the fact that the "desert" in Namibia is highly influenced by moisture from the cold Benguela current. Species growing in the desert are therefore highly unlikely to be able to move further inland because of climate change. The different species occurring in the Namib-dune Group compared to the *Gordonia* or Kalahari-sand Group (Craven 2009, Chapter 5) is a case in point. Namibia's desert species are accustomed to lower solar radiation levels, cloudiness, humidity and occur at lower altitudes.

The need for employing both vegetation and flora specialists has become even more apparent through the work of Burke (2005). In a study of vegetation types of mountain tops in Damaraland, Burke (2005) stated that “complete botanical surveys, rather than surveys of general descriptors — as in many environmental assessments in Namibia — should thus be undertaken for management purposes”. Burke (2005) stressed the importance of rare species and that “no single environmental driver can explain the vegetation on the investigated mountain tops”. The study of floristic regions by Craven (2006, Chapter 5) could help alleviate this problem. Understanding the past could answer why “high mountain tops in Damaraland are relatively species rich and are prone to harbour species at their limit of distribution” (Burke 2005). This knowledge is also vital in understanding the value of seed banks and therefore their potential for rehabilitation of areas, especially overgrazed plains. Burke (2003) showed that plant communities on tops of inselbergs differ from those on the plains below, with intermingling occurring on the slopes. In addition, the higher the elevation, the more pronounced the differences. This fact is important when considering, for example, rehabilitation practices and the potential future effect of climate change.

Walter (2004) believed that the ideal biogeographer is someone from a “systematics background, is field-orientated and has a good grasp of quantitative techniques and internet databases”. The contribution of plant taxonomy, and its use for evaluating different methodology, is invaluable. Until the difference in specialist training is appreciated, much valuable information will be missed or be of poor quality, as seen in some recent publications from Namibia. It is essential that botanists, especially taxonomists, actively contribute to other research and that it is based on sound principles and botanical vouchers. This is particularly important in Namibia where there are no up-to-date accounts of the flora and new taxa are still found regularly. In addition the goals, procedures and background of phytogeography must be fully defined so that patterns of variation can help explain how they arose and are maintaining themselves so as to predict future patterns and to suggest management strategies.

### **3.8 Conclusions**

To conserve biological resources and develop strategies for conservation, the study of taxonomy, ecology and chorology (i.e. the geographical area occupied by species alone) are essential. Floristic and ecological entities do not necessarily converge for a number of reasons and floristic elements may range over numerous vegetation communities. The role of historical phytogeography in understanding the origin, migration and speciation of plants makes an essential contribution to

characterizing an area. Using different definitions will ensure that conservation problems are properly stated.

### 3.9 References

Acocks, J.P.H. 1953. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa* 28: 1–192.

Agro-Ecological Zoning Programme. 1996-ongoing. Directorate of Agricultural Research and Training, Ministry of Agriculture, Water and Rural Development, Windhoek.

Albrecht, M., Berke, B., Eichhorn, B., Frank, T., Kuper, R., Prill, S., Vogelsang, R. & Wenzel, S. 2001. Oruwanje 95/1: A late Holocene stratigraphy in north western Namibia. *Cimbebasia* 17: 1–22.

Atlas of Namibia Project. 2002. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek. <http://www.dea.met.gov.na/>.

Avery, D.M. 1993. Last interglacial and Holocene altithermal environments in South Africa and Namibia: Micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101: 221–228.

Barnard, P. (ed.) 1998. *Biological diversity in Namibia: A country study*. The Namibian National Biodiversity Task Force, Windhoek.

Beentje, H.J. 1996. Centres of plant diversity in Africa. In: Van der Maesen, L.J.G., van den Burgt, M. & van Medebach de Rooy, J.M. (eds). *The biodiversity of African plants*. Pp. 101–109. Kluwer Academic Publishers, Dordrecht.

Besler, H. 1977. Untersuchungen in der Dünen - Namib (Südwestafrika). *Journal of the SWA Scientific Society* 31: 33–64.

Besler, H. 1991. Der Namib Erg: Älteste Wüste oder älteste Dünen? *Geomethodica* 16: 93–122.

- Born, J., Linder, H.P. & Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147–162.
- Bourke, M.C. Child, A. & Stokes, S. 2003. Optical age estimates for hyperarid fluvial deposits at Homeb, Namibia. *Quaternary Science Reviews* 22: 1099–1103.
- Bredenkamp, C.L. & Van Wyk, A.E. 2006. Phyto geography of *Passerina* (Thymelaeaceae). *Bothalia* 36: 191–199.
- Brook, A., Cowart, J.B. & Marais, E. 1996. Wet and dry periods in the southern African summer rainfall zone during the last 300 kyr from speleothem, tufa and sand dune age data. *Palaeoecology of Africa* 24: 147–158.
- Brook, A., Marais, E. & Cowart, J.B. 1999. Evidence of wetter and drier conditions in Namibia from tufas and submerged speleothems. *Cimbebasia* 15: 29–39.
- Brook, A., Marais, E., Srivastava, P. & Jordan, T. 2007. Timing of lake-level changes in Etosha Pan, Namibia, since the middle Holocene from OSL ages of relict shorelines in the Okondeka region. *Quaternary International* 175: 29–40.
- Brook, A., Srivastava, P. & Marais, E. 2006. Characteristics and OSL minimum ages of relict fluvial deposits near Sossus Vlei, Tsauchab River, Namibia, and a regional climate record for the last 30 ka. *Journal of Quaternary Science* 21: 347–362.
- Brunotte, E. & Sander, H. 2000. Loess accumulation and soil formation in Kaokoland (Northern Namibia) as indicators of Quaternary climatic change. In: S. Kröpelin & N. Petit-Maire (eds). *Global and Planetary Change, Special Volume "Paleomonsoon Variations and Global Change during the Late Quaternary"*. *Global & Planetary Change* 26: 67–75.
- Brunotte, E., Eichhorn, B. & Sander, H. 2002. Quaternary climate change in North Western Namibia: Sedimentologic, pedologic and archaeobotanic evidence. *Palaeoecology of Africa* 39.
- Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar I & II*. Umdaus Press, Hatfield.

- Burgess, N.D., D'Amico Hales, J., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. & Newman, K. 2004. *The terrestrial ecoregions of Africa and Madagascar: A conservation assessment*. Island Press, Washington, D.C.
- Burke, A. 2003. How special are Etendeka mesas? Flora and elevation gradients in an arid landscape in north-west Namibia. *Journal of Arid Environments* 55: 747–764.
- Burke, A. 2005. Vegetation types of mountain tops in Damaraland. *Biodiversity and Conservation* 14: 1487–1506.
- Burke, A. & Strohbach, B.J. 2000. Review: Vegetation studies in Namibia. *Dinteria* 26: 1–24.
- Carr, M.J., Carr, A.C., Jacobsen, L. & Vogel, U. 1976. Radiocarbon dates from the Zerrissene Mountain open station settlement complex. *South African Journal of Science* 72: 251–252.
- Carrión, J.S., Scott, L. & Marais, E. 2006. Environmental implications of pollen spectra from bat droppings and potential for paleoenvironmental reconstruction. *Cimbebasia* 14: 175–186.
- Coe, M.J. & Skinner, J.D. 1993. Connections, disjunctions and endemism in the eastern and southern African mammal faunas. *Transactions of the Royal Society of South Africa* 48: 233–255.
- Coetzee, C.G. 1969. The distribution of mammals in the Namib Desert and adjacent inland escarpment. *Scientific Papers of the Namib Desert Research Station* 40: 23–36.
- Coetzee, C.G. 1983. An analysis of the distribution patterns of the Namibian terrestrial mammals (bats excluded). *Annalen van de Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen* 237: 63–73.
- Cowling, R.M., Rundel, P.W., Desmet, P.G. & Esler, K.J. 1998. Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons. *Diversity and Distributions* 4: 27–36.
- Craven, P. 2002. Phylogeography of the Namibian flora: A taxon approach. Unpublished. MSc thesis, University of Stellenbosch, Stellenbosch.

- Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET News* 9: 24–44.
- Craven, P. 2009. Chapter 4, this volume. Phytogeographical aspects of the flora of Namibia.
- Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.
- Craven, P. 2009. Chapter 6, this volume. Demarcating the Kaokoveld Centre of Endemism: A numerical approach.
- Craven, P. 2009. Chapter 7, this volume. Floristic and environmental analysis of the Kaokoveld Centre of Endemism.
- Craven, P. & Vorster, P.V. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.
- Crisci, J.V. 2001. The voice of historical biogeography. *Journal of Biogeography* 28: 157–168.
- Croizat, L. 1994. Pacific basin biogeography. Marginal notes to a symposium. *Kirkia* 15: 157–246.
- Curtis, B.A. & Mannheimer, C.A. 2005. *Tree Atlas of Namibia*. National Botanical Research Institute, Windhoek.
- Deacon, J. & Lancaster, N. 1988. *Late Quarternary Palaeoenvironments of Southern Africa*. Clarendon Press, Oxford.
- Dupont, L. M. 2006. Late Pliocene vegetation and climate in Namibia (southern Africa) derived from palynology of ODP Site 1082. *Geochemistry, Geophysics, Geosystems* 7: 1–15.
- Dupont, L.M. & Behling, H. 2006. Land-sea linkages during deglaciation: High resolution records from the eastern Atlantic off the coast of Namibia and Angola (ODP Site 1078). *Quaternary International* 148: 19–28
- Dupont, L.M. & Wyputta, U. 2003. Reconstructing pathways of Aeolian pollen transport to the marine sediments along the coastline of South West Africa. *Quaternary Science Review* 22: 157–174.

- Dupont, L.M., Behling, H., Jahns, S., Marret, F. & Kim, J-H. 2007. Variability in glacial and Holocene marine pollen records offshore from west southern Africa. *Vegetation History and Archaeobotany* 16: 87–100.
- Dupont, L.M., Donner, B., Vidal, L., Pérez, E.M. & Wefer, G. 2005. Linking desert evolution and coastal upwelling: Pliocene climate change in Namibia. *Geology* 33: 461–464.
- Dupont, L.M., Kim, J.-H., Schneider, R.R. & Shi, N. 2004. Southwestern African climate independent of Atlantic sea surface temperatures during the Younger Dryas. *Quaternary Research* 61: 318–324.
- Ebach, M.C. 2004. Forum on biogeography: Introduction. *Taxon* 53: 889–891.
- Ebach, M.C., Morrone, J.J., Parenti, L.R. & Vilorio, A.L. 2008. International Code of Area Nomenclature. *Journal of Biogeography* 35: 1153–1157.
- Eggle, U. 2001. *Illustrated Handbook of Succulent Plants: Monocotyledons*. Springer, Berlin.
- Eichhorn, B. 2004. Anthrakologische Untersuchungen zur Vegetationsgeschichte des Kaokolandes, Nordwest-Namibia. PhD dissertation, University of Cologne, Cologne.
- Eichhorn, B. & Jürgens, N. 2003. The contribution of charcoal analysis to the late Pleistocene and Holocene vegetation history of north-western Namibia. In: Neumann, K., Butler, A. & Kahlheber, S. (eds). *Progress in African archaeobotany*. Africa Praehistorica 15: 92–101. Heinrich-Barth-Institut, Cologne.
- Eitel, B. & Zöller, L. 1996. Soils and sediments in the basin of Dieprivier-Uitskot (Khorixas District, Namibia): Age, geomorphic and sedimentological investigation, paleoclimatic interpretation. *Palaeoecology of Africa* 24: 159–201.
- Eitel, B., Blümel, W.D. & Hüser, K. 1998. River silt terraces at the eastern margin of the Namib Desert (NW/Namibia): Genesis and paleoclimatic evidence. *Zeitblät für Geologie und Paläontologie* 1: 243–254.



- Eitel, B., Blümel, W.D. & Hüser, K. 1999. Der Uniab-Lehm: Relikt feuchttropischer Tertiärklimate in der Nördlichen Namib (Skelettküste/Namibia). *Die Erde* 130: 17–27.
- Eitel, B., Blümel, W.D. & Hüser, K. 2002. Environmental transitions between 22 ka and 8 ka in monsoonally influenced Namibia - a preliminary chronology. *Zeitschrift für Geomorphologie* 126: 31–57.
- Eitel, B., Blümel, W.D., Hüser, K. & Mauz, B. 2001. Dust and loessic alluvial deposits in Northwestern Namibia (Damaraland, Kaokoveld): sedimentology and palaeoclimatic evidence based on luminescence data. *Quaternary International* 76/77: 57–65.
- Eitel, B., Kadereit, A., Blümel, W.D., Hüser, K. & Kromer, K. 2005. The Amspoort silts, northern Namib Desert (Namibia): Formation, age and palaeoclimatic evidence of river-end deposits. *Geomorphology* 64: 299–314.
- Endrödy-Younga, S. 1982. The evidence of coleoptera in dating the Namib Desert re-examined. *Palaeoecology of Africa* 15: 217–223.
- Flora of southern Africa* (various editorial teams). 1963–ongoing. National Botanical Institute, Pretoria.
- Friis, I. 1986. Ethiopia in regional phytogeography. *Symbolae Botanicae Upsaliensis* 26: 68–85.
- Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4: 5–114.
- Giess, W. 1989. *Bibliography of South West African Botany*. South West African Scientific Society, Windhoek.
- Gil-Romera, G., Scott, L., Marais, E. & Brook, G.A. 2006. Middle- to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen. *The Holocene* 16: 1073–1084.
- Gil-Romera, G., Scott, L., Marais, E. & Brook, G.A. 2007. Late Holocene environmental change in the northwestern Namib Desert Margin: New fossil pollen evidence from hyrax middens. *Palaeogeography, Paleoclimatology, Palaeoecology* 249: 1–17.

- Goldblatt, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships and origins. *Annals of the Missouri Botanic Garden* 65: 369–436.
- Good, R.D. 1974. *The geography of flowering plants*. Wiley, New York.
- Haacke, W.D. 1982. Distribution patterns of reptiles as indicators of geomorphological events in the Namib Desert. *Palaeoecology of Africa* 15: 225–226.
- Hedberg, O. 1954. A pollen-analytical reconnaissance in Tropical East Africa. *Oikos* 5: 137–166.
- Heine, K. 1992. On the ages of humid Late Quaternary phases in southern African arid areas (Namibia, Botswana). *Palaeoecology of Africa* 23: 149–164.
- Heine, K. 1998. Climate change over the past 135,000 years in the Namib Desert (Namibia) derived from proxy data. *Palaeoecology of Africa* 25: 171–198.
- Heine, K. 2005. Holocene climate of Namibia: A review based on geoarchives. *African Study Monographs, Supplement 30*. 119: 33.
- Heine, K. & Heine, J.T. 2002. A paleohydrologic reinterpretation of Homeb Silts, Kuiseb River, Central Namib Desert (Namibia) and paleoclimatic implications. *Catena* 48: 107–130.
- Heine, K. & Walter, R. 1996. Gypcretes of the central Namib Desert, Namibia. *Palaeoecology in Africa* 24: 173–201.
- Hilliard, O. M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Hilton-Taylor, C. 1994a. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.

- Hilton-Taylor, C. 1994b. Centres of plant diversity: Karoo-Namib region: Western Cape domain (Succulent Karoo). In: Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 204–217. Oxford University Press, Oxford.
- Holm, E. 1990. Notes on faunas bordering on the Namib Desert. In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 55–60. Transvaal Museum Pretoria.
- Holm, E. & Scholtz, C.H. 1983. Zoogeographical delimitation of the Kalahari subregion based on excluded species. *Journal of Arid environments* 8: 165–169.
- Irish, J. 1990. Namib biogeography, as exemplified mainly by Lepismatidae (Thysanura: Insecta). In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 61–66. Transvaal Museum Pretoria.
- Irish, J. 1994. The biomes of Namibia, as determined by objective categorisation. *Research of the National Museum, Bloemfontein* 10: 549–592.
- Jacobson, K.M. & Lester, E. 2003. A first assessment of genetic variation in *Welwitschia mirabilis* Hook. *Journal of Heredity* 94: 212–217.
- Jürgens, N. 1991. A new approach to the Namib region. I. Phytogeographic subdivision. *Vegetatio* 97: 21–38.
- Jürgens, N. 1992. Vegetation der Namib. Ein Beitrag zur ökologische Gliederung, Phytochorologie und Florengeschichte einer afrikanischen Trockengebiet. Unpublished. “Habilitationsschrift” for the University of Hamburg, Hamburg.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495–514.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1–10.
- Knoll, A.H. 1983. Africa and Precambrian biological evolution. *Bothalia* 14: 329–336.

- Lancaster, N. 1984. Paleoenvironments of the Tsondab valley, central Namib Desert. *Paleoecology of Africa* 16: 411–419.
- Lancaster, N. 2002. How dry was dry? Late Pleistocene paleoclimates in the Namib Desert. *Quaternary Science Reviews* 21: 91–107.
- Lawrence, G.H.M. 1971. *Taxonomy of vascular plants*. Macmillan Company, New York.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.
- Linder, H.P. 2003. The radiation of the Cape flora, southern Africa. *Biological Review* 78: 597–638.
- Linder, H.P., Lovett, J.C., Mutke, J., Barthlott, W., Jürgens, N., Rebelo, T. & Küper, W. 2005. A numerical re-evaluation of the sub-Saharan phytochoria. *Biologische Skrifter* 55: 229–252.
- Little, R.J. & Jones, C.E. 1980. *A dictionary of Botany*. Van Nostrand Reinhold, New York.
- Marlow, J.R., Lange, C.B., Wefer, G. & Rosell-Mele, A. 2000. Upwelling intensification as part of the Pliocene-Pleistocene climate transition. *Science* 290: 2288–2291.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, A. 2002. *Atlas of Namibia: A portrait of the land and its people*. David Phillip Publishers, Cape Town.
- Midgley, G., Hughes, G., Thuiller, G., Drew, G. & Foden, W. 2005. Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function. Report for Namibian National Biodiversity Programme.
- Mittermeier, R.A., Myers, N., & Thomsen, J.B. 1998. Biodiversity Hotspots and Major Wilderness Areas: Approaches to setting conservation priorities. *Conservation Biology* 12: 516–520.
- Mittermeier, R & Mittermeier, C. 2001. Hope for Nature's greatest treasures. *Africa Geographic Biodiversity Hotspots* 30–37.

- Mittermeier, R.A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., Lamoreux, J. & Da Fonseca, G.A.B. (eds). 2004. *Hotspots revisited: Earth's biologically richest and most threatened terrestrial ecoregions*. Cemex and Conservation International, Washington.
- Myers, A.A. & Giller, P.S. (eds). 1988. *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Chapman and Hall, London.
- Nimis, P.L., Malyshev, L.I., Bolognini, G. & Friesen, N. 1998. A multivariate phytogeographic analysis of plant diversity in the Putorana Plateau (Northern Siberia). *Opera Botanica* 136: 1–72.
- Nordenstam, B. 1969. Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica* 23: 7–75.
- Olson, D.M. & Dinerstein, E. 2002. The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanic Garden* 89: 199–224.
- Parenti, L. R. & Humphries, C. J. 2004. Historical biogeography, the natural science. *Taxon* 53: 899–903.
- Pickford, M. 2000. Neogene and Quarternary vertebrate biochronology of the Sperrgebiet and Otavi Mountainland, Namibia. *Communications of Geological Survey, Namibia* 12: 359–365.
- Poynton, J.C. 1962. Patterns in the distribution of Southern African amphibia. *Annals of the Cape Provincial Museum* 2: 252–272.
- Poynton, J.C. 1986. Historical biogeography: Theme and south African variations. *Palaeoecology of Africa* 17: 139–153.
- Poynton, J.C. 1995. The arid corridor distribution in Africa: A search for instances among the amphibians. *Madoqua* 19: 45–48.
- Radford, E. 2004. Important plant areas – a practical route to target 5. *Plant Talk* 38: 32–33.

- Rosen, B.R. 1988. Biogeographic patterns: A perceptual overview. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 23–55. Chapman & Hall, London.
- Rust, U. 1984. Geomorphic evidence of Quarternary environmental changes in Etosha, South West Africa/Namibia. In: Vogel, J.C. (ed.). *Late Cainozoic Palaeoclimates of the Southern Hemisphere*. Pp. 279–286. Balkema, Rotterdam.
- Rust, U. 1987. Geomorphologische Forschungen im Südwestafrikanischen Kaokoveld zum Angeblichen Vollariden Quartären Kernraum der Namibwüste. *Erdkunde* 41: 118–133.
- Rust, U. 1999. River-end deposits along the Hoanib River, northern Namib: Archives of Late Holocene climatic variation on a subregional scale. *South African Journal of Science* 95: 205–208.
- Rust, U. & Vogel 1988. Late Quarternary environments in the northern Namib Desert as evidenced by fluvial landforms. *Palaeoecology of Africa* 19: 127–137.
- Rust, U., Schmidt, H.H. & Dietz, K.R. 1984. Palaeoenvironments of the present day arid south western Africa 30 000-5 000 BP: Results and problems. *Palaeoecology of Africa* 16: 142–174.
- Scott, L. 1996. Palynology of Hyrax Middens: 2000 years of palaeoenvironmental history in Namibia. *Quarternary International* 33: 73–79.
- Scott, L., Cooremans, B., De Wet, J.S. & Vogel, U. 1991. Holocene environmental changes in Namibia inferred from pollen analysis of swamp and lake deposits. *The Holocene* 1: 8–13.
- Scott, L., Marais, E. & Brook, G.A. 2004. Fossil hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert. *Journal of Quaternary Science* 19: 1–4.
- Segalen, L., Renard, M., Lee-Thorp, J. A., Senut, B., Pickford, M. 2004. Emergence of the Namib Desert during the Neogene, and correlations with global palaeoclimate changes. *American Geophysical Union, Fall Meeting 2004*, abstract #PP51B-1337.
- Shi, N. & Dupont, L.M. 1997. Vegetation and climatic history of southwest Africa: A marine palynological record of the last 300,000 years. *Vegetation History and Archaeobotany* 6: 117–131.

- Shi, N., Dupont, L.M., Beug, H.-J. & Schneider, R. 1998. Vegetation and climatic changes during the last 21,000 years in south west Africa based on a marine pollen record. *Vegetation History and Archaeobotany* 7: 127–140.
- Shi, N., Dupont, L.M., Beug, H.-J. & Schneider, R. 2000. Correlation between vegetation in southwestern Africa and Oceanic upwelling in the past 21,000 years. *Quaternary Research* 54: 72–80.
- Shi, N., Schneider, R., Beug, H.-J. & Dupont, L.M. 2001. Southeast trade wind variations during the last 135 kyr: Evidence from pollen spectra in eastern South Atlantic sediments. *Earth and Planetary Science Letters* 187: 31–321.
- Shortridge, G.C. 1934. *The mammals of South West Africa*. Heineman, London.
- Siesser, W.G. 1978. Aridification of the Namib Desert: Evidence from oceanic cores. In: Van Zinderen Bakker, E.M. (ed.) *Antarctic glacial history and world palaeoenvironments*. Pp. 105–113. Balkema, Rotterdam.
- Siesser, W.G. 1980. Late Miocene origin of the Benguela upwelling system of northern Namibia. *Science* 208: 283–285.
- Smith, T. 2004. Important plant areas (IPAs) in southern Africa. *SABONET News* 9: 73.
- Sole, C.L., Scholtz, C.H. & Bastos, A.D.S. 2005. Phylogeography of the Namib Desert dung beetles *Scarabaeus* (Pachysoma) MacLeay (Coleoptera: Scarabaeidae). *Journal of Biogeography* 32: 75–84.
- Srivastava, P., Brook, A. & Marais, E. 2004. A record of fluvial aggradation in the Northern Namib Desert during the Late Quaternary. *Zeitschrift für Geomorphologie* 133: 1–18.
- Srivastava, P., Brook, A. & Marais, E. 2005. Depositional environment and luminescence chronology of the Hoarusib River Clay Castles sediments, northern Namib Desert, Namibia. *Catena* 59: 187–204.

- Srivastava, P., Brook, A., Marais, E., Morthekai, P. & Singhvi, A.K. 2006. Depositional environment and single aliquot and single grain OSL chronology of the Homeb silt deposits, Kuiseb River, Namibia. *Quaternary Research* 65: 478–91.
- Steenkamp, Y., van Wyk, A.E., Smith, G.F. & Steyn, H. 2005. Floristic endemism in southern Africa: A numerical classification at generic level. *Biologiske skrifter* 55: 253–271.
- Stengel, I. 2000. Fossil landslides in the Schwarzrand, Huib and Huns escarpment areas – a contribution to the Quaternary morpostratigraphy of southern Namibia. *Palaeoecology of Africa* 27: 221–238.
- Stengel, I. & Leser, H. 2004. Late Quaternary valley-fill terraces and palaeoenvironments of the Huns River, Southern Namibia. *Die Erde* 135: 129–149.
- Strohbach, B.J. & Strohbach, M.M. 2004. An annotated plant species list for Mile 46 LDC and surrounding area in central Kavango, Namibia, with some notes on species diversity. *Dinteria* 29: 55–78.
- Takhtajan, A. 1986. *Floristic regions of the world*. University of California Press, Berkeley.
- Teller, J.T., Rutter, N.W. & Lancaster, N. 1990. Sedimentology and palaeohydrology of late Quaternary lake deposits in the northern Namib Sand Sea, Namibia. *Quaternary Science Reviews* 9: 343–364.
- Torquato, J.R. 1970. Origin and evolution of the Mocamedes Desert (Angola). *Boletim do Instituto de Investigacao Cientifica de Angola* 7: 29–38.
- UNEP. 2003. Global strategy for plant conservation. Target 5: Important Plant Areas. Stakeholder consultation report. UNEP/CBD/GSPC/Target 5. Durban.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Van Wyk, B-E. 1991. A synopsis of the genus *Lotononis* (Fabaceae: Crotalarieae). *Contributions from the Bolus Herbarium* 14: 1–292.



- Van Zinderen Bakker, E.M. 1975. The origin and palaeoenvironment of the Namib Desert biome. *Journal of Biogeography* 2: 65–73.
- Van Zinderen Bakker, E.M. 1984a. Aridity along the Namibian coast. *Palaeoecology of Africa* 16: 149–160.
- Van Zinderen Bakker, E.M. 1984b. A late- and post-glacial pollen record from the Namib Desert. *Palaeoecology of Africa* 16: 421–427.
- Van Zinderen Bakker, E.M. 1984c. Palynological evidence for Late Cenozoic arid conditions along the Namibia coast from Holes 532 and 530A, LEG 75, Deep Sea Drilling Project. Initial Reports of the Deep Sea Drilling Project LXXV, 763–768.
- Van Zinderen Bakker, E.M. Snr. 1983. The late Quaternary history of climate and vegetation in East and Southern Africa. *Bothalia* 14: 369–375.
- Van Zinderen Bakker, E.M. & Müller, M. 1987. Pollen studies in the Namib Desert. *Pollen and Spores* 29: 185–206.
- Vogel, J.C. 1989. Evidence for the past climatic change in the Namib Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70: 355–366.
- Vogel, J.C. 2003. The age of dead trees at Sossus and Tsondab Vleis, Namib Desert, Namibia. *Cimbebasia* 18: 247–251.
- Vogel, J.C. & Rust, U. 1987. Environmental changes in the Kaokoland Namib Desert during the present millennium. *Madoqua* 15: 5–16.
- Vogelsang, R., Eichhorn, B. & Richter, J. 2002. Holocene human occupation and vegetation history in northern Namibia. *Die Erde* 133: 113–132.
- Volk, O.H. 1964. Die afro-meridionale-occidentale Floren-Region in Südwestafrika. *Beiträge zur Phytologie zu Ehren Prof. H. Walters 65 Geburtstages*. Ulmer, Stuttgart.

Volk, O. H. 1966. Die Florengebiete von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.

WWF and IUCN. 1994. Centres of Plant Diversity. *A guide and strategy for their conservation*. Volume 1: Europe, Africa, South West Asia and the Middle East. IUCN Publications Unit, Cambridge, UK.

Walter, H. 1983. The Namib Desert. In: Evenari, M., Noy-Meir, I. & Goodaal, D.W. (eds). *Ecosystems of the world 12B. Hot deserts and arid shrublands*. Pp. 245–282. Elsevier, Amsterdam.

Walter, H. S. 2004. Understanding places and organisms in a changing world. *Taxon* 53: 905–910.

Ward, J.D. & Corbett, I. 1990. Towards the age of the Namib. In: Seely, M.K. (ed.). *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 17–26. Transvaal Museum, Pretoria.

Weimarck, H. 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Acta University Lund* 3: 5–143.

Werger, M.J.A. (ed.). 1978. *Biogeography and ecology of southern Africa*. Junk, The Hague.

White, F. 1965. The savanna woodlands of the Zambezan and Sudanian Domains. An ecological and phytogeographical comparison. *Webbia* 19: 651–681.

White, F. 1971. The taxonomic and ecological basis of chorology. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 91–112.

White, F. 1976. The vegetation of Africa - the history of a completed project. *Boissiera* 24: 659–666.

White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.

World Wildlife <http://www.worldwildlife.org/wildworld/profiles/terrestrial/at/at1310-full.html>

## Chapter 4

### Phytogeographical aspects of the flora of Namibia

#### Abstract

4.1	Introduction.....	59
4.2	Methodology .....	59
4.3	Results.....	60
4.3.1	Families .....	60
4.3.2	Genera .....	64
4.3.3	Species.....	66
4.3.4	Endemics .....	67
4.3.5	Disjuncts.....	67
4.3.6	Disjunctions through substrate preferences.....	75
4.3.7	Origin of the flora and its relationships.....	75
4.4	Discussion and Conclusions .....	78
4.5	References.....	78

# Phytogeographical aspects of the flora of Namibia

## Abstract

The phytogeographic characteristics of Namibia were determined by an analysis of the overall distributions of families, genera and species indigenous to the country. Worldwide distribution patterns provide clues to the floristic relationships and origins of the flora of Namibia. Few taxa have links to South America, but those that do, appear to be amongst the oldest taxa and the most likely explanation for their presence in Namibia is via the Tethys Seaway. The majority of taxa are African with extensions through Arabia to Asia. Disjunct and endemic taxa are re-evaluated with reference to examples and possible reasons for their observed distribution patterns.

## 4.1 Introduction

According to the Atlas of Namibia (Mendelsohn *et al.* 2002), Namibia covers 823,680 km<sup>2</sup>, is 1,320 km long and 1440 km at its widest points. It stretches from 17° S to 29° S and as far as 21° E, except for the long narrow Caprivi Strip in the far north east that reaches 24° E. Despite being considered the second driest area in Africa after the Sahara, both subtropical elements and desert species are present within the country. Although the known number of indigenous species and infra-specific taxa is constantly changing as new species are discovered and revisions published, Namibia is thought to have *ca.* 4 000 higher plant species.

The aim of this paper is the first comprehensive attempt to summarise what is known about the families, genera and species indigenous to Namibia, along with their distributions, relationships and origins. The task was rather overwhelming, because large sections of the flora are still not well-known, data sources are scattered and data are presented in different ways. In addition, no estimates of the age or relationships of the flora have been proposed. This is compounded by the fact that Namibian specimens or species often not being used or referred to in these references. These problems inevitably result in gaps in the information summarized here, but what I present is the best possible summary of information that could reasonably be obtained.

## 4.2 Methodology

The databased index of Namibian plant species (Craven & Kolberg, on-going) provided circumscription of taxa for this review. This database has been developed and expanded over a few decades and includes fields for floristic and biogeographic information. It has been necessary to consult a large number of journals and monographs, emanating from all over the world. The only

Flora dedicated to Namibia, *Prodromus einer Flora von Südwestafrika* (Merxmüller 1966–1972), is now outdated and only available in German. Other regional Floras that cover many taxa also present in Namibia include: *Conspectus Florae Angolensis* (various editorial teams, 1937-1970), which was published in Portuguese, *Flora Zambesiaca* (various editorial teams, 1960–ongoing) and the *Flora of southern Africa* (various editorial teams, 1963–ongoing), but none of these floras have been completed. The Floras of parts of northeast Africa (e.g. Ethiopia and Somalia) have contributed to understanding the taxa with disjunct members present in Namibia.

Definitions used in this paper:

**Cosmopolitan taxa** are taxa with representatives native to all the continents excluding Antarctica. They do not have special distribution centres.

**Subcosmopolitan taxa** represents a subcategory of cosmopolitan taxa and includes species that are absent from one major region or broad type of habitat. Most of these taxa are tropical or subtropical, with few temperate taxa having been recorded.

**Pantropical taxa** includes plants found in all three sectors of the tropical zone (i.e. America, Africa-Madagascar and Asia-Australia), with some extending into temperate regions.

**Disjunct taxa** are taxa that display geographical discontinuities within their geographical ranges.

**Endemic taxa** are taxa confined to a particular area due to historical, ecological or physiological reasons (Major 1988).

**Near endemics** are taxa that are marginally present elsewhere.

## 4.3 Results

### 4.3.1 Families

There are about 164 families of higher plants in Namibia, a few of which, like the Leguminosae and Apocynaceae, include large subfamilies. Of these families, 32 are represented by only one species. In contrast the most diverse families are also those known to be among the largest families worldwide, including the Poaceae, Asteraceae and Leguminosae (Table 9.1). Other cosmopolitan

families, e.g. Convolvaceae, Euphorbiaceae, Malvaceae and Solanaceae are predominantly tropical, while Campanulaceae is mainly temperate (Good 1974). One of the globally largest families in terms of numbers of genera and species, the Apiaceae, has few taxa in Namibia and these occur mainly in the arid west, including two monospecific endemic genera, *Marlothiella* and *Phlyctidocarpa*. Another cosmopolitan family of note in Namibia is the Scrophulariaceae. The genera present in Namibia are mainly confined to Africa and three are endemic to Namibia, namely *Chamaegigas*, *Dintera* and *Manuleopsis*, while *Camptoloma* occurs mainly in the west and is disjunct to northeast Africa. Families in Namibia that are restricted to Africa and South America include the Hydnoraceae, Turneraceae and Velloziaceae.

The centre of diversity for the Ebenaceae is believed to be Africa, while other families occurring predominantly in Africa include the Balanitaceae, Eriospermaceae, Hydrostachyaceae, Kirkiaceae, Melianthaceae, Montiniaceae, Myrothamnaceae, Ptaeroxylaceae, Tecophilaeaceae and Vahliaceae. All of these include only a few taxa. Neuradaceae has a disjunct distribution with India, while Moringaceae and Salvadoraceae occur in Africa and Asia. The Amaryllidaceae and Hyacinthaceae represent monocotyledonous families that include mainly African genera in Namibia.

The predominantly African family Iridaceae shows noteworthy patterns in Namibia. Although most included members occur in what is called the winter rainfall area of Namibia, the three most speciose genera in Namibia also occur in the summer rainfall area. It is significant in an evolutionary and ecological sense that species in *Gladiolus* section *Hebea*, which have radiated largely in the winter rainfall zone elsewhere, will continue to respond to the winter rainfall pattern of their main range, even when found in the summer rainfall region of Namibia (Goldblatt & Manning 1998). *Lapeirousia* is one of a few widespread African Iridaceae genera with centres in the winter rainfall area (of South Africa), tropical Africa and in Namibia. It has its greatest species concentration in the tropical parts (Goldblatt 1990). The distribution of *Moraea* covers most of sub-Saharan Africa to the Western Cape Province (South Africa) and most species of subgenus *Moraea* are found in the winter rainfall area. However, several unusual species, considered ancient relics, are found near the Orange-Fish River confluence in southern Namibia, the ancestors of which must have once thrived here, perhaps when the climate was wetter (Goldblatt 1986).

Despite the predominantly arid climate of Namibia, it includes 14 hydrophytic families: Alismataceae, Aponogetonaceae, Callitrichaceae, Ceratophyllaceae, Droseraceae, Hydrocharitaceae, Lythraceae, Najadaceae, Nymphaeaceae, Podostemaceae, Ruppiaceae,

Sphenocleaceae, Xyridaceae and Zannichelliaceae. At least one family associated with humid forests, the Sapotaceae, is found in northeastern Namibia.

Within some cosmopolitan families, e.g. Apocynaceae (15), Asteraceae (24) and Leguminosae (19) the genera found in Namibia are exclusively African. The centre of diversity of the Mesembryanthemaceae is in the southwestern part of Africa. From here it extends along the coast to southern Angola (Hartmann 1964), but there is a noticeable decrease in numbers from 27° S northwards. The mesemb subfamily Ruschioideae diversified very recently and rapidly and is estimated to be between 3.8 and 8.7 million years old (Klak *et al.* 2004).

Subfamilies and tribes showing geographic ranges of interest include the subfamilies of Poaceae mapped by Gibbs Russell (1986) and subtribe Aervinae of the Amaranthaceae, which is mainly restricted to the drier west and includes smaller genera known only from southern Africa, e.g. the monospecific endemic genus *Arthraerua*.

The overall distributions of endemics in certain families were mapped by Craven (2002) and Craven & Vorster (2006). Although these results show no general pattern in large families like Asteraceae, specific distribution patterns could be observed depending on the underlying data (e.g. families or subfamilies, endemic or overall).

There are no angiosperm families restricted to the political borders of Namibia, but the gymnosperm family Welwitschiaceae occurs only in southwestern Angola and Namibia. Although it is today represented by a single extant species, *Welwitschia mirabilis*, Lower Cretaceous megafossils of various organs have been assigned to the family, and suggests that other extinct members existed in the past. These include *Priscowelwitschia*, erroneously published as *Welwitschiella* (Dilcher *et al.* 2005) from northeastern Brazil. The family Welwitschiaceae is generally considered to be part of the order Gnetales along with *Ephedra* and *Gnetum*, in the Gnetopsida, the most closely related extant seed plants to flowering plants. Recently De-Zhi *et al.* (2004) proposed a new order Welwitschiales. Regardless of the preferred classification used, the split between *Gnetum* and *Welwitschia* is believed to have occurred *ca.* 115 million years ago (Won & Renner, 2003) based on molecular studies and phylogenetic analyses of gymnosperms (Gugerli *et al.* 2001; Rydin *et al.* 2002; Nickerson & Drouin 2004; Won & Renner 2005). Ickert-Bond & Wojciechowski (2004) propose the link between Gnetales and Welwitschiaceae to result from a persistent dry vegetation type that was linked in the Tertiary, from South America, through Central America, Mexico and the Caribbean, along the Tethys Seaway to Africa, Arabia and India.

Table 4.1. Summary of the 26 largest families in Namibia, ranked according to the number of included species. Global, Namibian and endemic species and genus numbers are supplied for each family

	<b>Family</b>	<b>No. of species in Namibia</b>	<b>Species endemic to Namibia</b>	<b>Global species no.</b>	<b>No. of genera in Namibia</b>	<b>Genera endemic to Namibia</b>	<b>Global genera no.</b>
1	Poaceae	410	21	9500	109	1	688
2	Asteraceae	379	73	25000	90	2	1535
3	Leguminosae	355	38	18000	79	0	650
4	Mesembryanthemaceae	189	79	1680	37	3	123
5	Apocynaceae	174	34	4800	48	3	480
6	Acanthaceae	159	43	4350	23	0	350
7	Scrophulariaceae	141	34	4500	29	3	290
8	Cyperaceae	132	1	5000	25	0	104
9	Euphorbiaceae	131	25	5000	23	0	300
10	Hyacinthaceae	87	23	900	7	0	46
11	Crassulaceae	82	12	1500	5	0	33
12	Chenopodiaceae	80	37	1500	9	0	100
13	Lamiaceae	71	6	6700	19	0	252
14	Malvaceae	65	6	2000	11	0	90
15	Rubiaceae	60	4	10200	26	0	630
16	Sterculiaceae	60	10	1500	5	0	72
17	Asphodelaceae	56	22	780	6	0	15
18	Amaryllidaceae	48	10	800	13	0	60
19	Zygophyllaceae	43	8	250	6	1	27
20	Geraniaceae	43	11	800	3	0	11
21	Amaranthaceae	41	5	1000	13	1	69
22	Cucurbitaceae	41	2	735	13	0	120
23	Burseraceae	30	9	500	1	0	16
24	Pedaliaceae	27	4	64	8	1	13
25	Campanulaceae	22	5	700	3	1	35
26	Apiaceae	14	5	3750	9	2	453



### 4.3.2 Genera

Of the 930 indigenous genera in Namibia, less than 200 are cosmopolitan or nearly cosmopolitan, about 350 are pantropical and another *ca.* 370 are essentially African. Of the essentially African genera, *ca.* 170 are confined to southern Africa. Genera with their main distribution within Namibia are summarized in Table 4.2.

Table 4.2. Genera with their main distribution within Namibia and/or partially in neighbouring countries

Geographical region	Genera included
Namibia	<i>Arthraerua, Baynesia, Chamaegigas, Dewinteria, Dintera, Ectadium, Eremothamnus, Jensenobotrya, Kaokochloa, Lavrania, Manuleopsis, Marlothiella, Namacodon, Namibia, Neoluederitzia, Ondetia, Phlyctidocarpa, Ruschianthus</i>
Namibia and marginally into neighbouring parts of the Northern Cape, South Africa	<i>Amphibolia, Anginon, Augea, Chaetobromus, Cheiridopsis, Cladoraphis, Coelanthum, Didelta, Hessea, Jordaaniella, Lyperia, Nymania, Prenia, Septulina, Sisyndite, Stapeliopsis, Suessenguthiella, Xerocladia</i>
Namibia and Angola	<i>Antiphiona, Dauresia, Engleria, Entoplocamia, Eremiolirion, Hiernia, Monelytrum, Welwitschia</i>
Namibia, Cape (South Africa) and Angola	<i>Aizoanthemum, Leucophrys, Leucosphaera, Psilocaulon</i>
South Tropical Africa	<i>Sartidia, Volkiella</i>
South Tropical Africa and southern Africa	<i>Antherothamnus, Marcelliopsis, Melanospermum</i>

Cosmopolitan genera generally include many species, and examples with numerous taxa in Namibia include *Acacia* s.l., *Barleria*, *Cleome*, *Crotalaria*, *Euphorbia*, *Hibiscus*, *Indigofera*, *Ipomoea*, *Polygala*, *Senecio* and *Wahlenbergia*. A number of cosmopolitan genera are aquatics or mesophytics, e.g. *Ceratophyllum*, *Limosella*, *Ludwigia*, *Myriophyllum* and *Nymphaea*. There are a small number of cosmopolitan genera, such as *Atriplex*, *Chenopodium*, *Limonium*, *Salsola*, *Spergularia* and *Suaeda* that inhabit halophytic or desert habitats (Good 1974) and one genus, *Drosera*, is insectivorous. A number of genera in the Cyperaceae and Poaceae are subcosmopolitan and often associated with damp areas: Cyperaceae: *Cyperus*, *Eleocharis*, *Fimbristylis*, *Fuirena*, *Kyllinga*, *Mariscus*, *Pycneus*, *Rhynchospora* and *Scleria*; Poaceae: *Chloris*, *Digitaria*, *Echinochloa*, *Enneapogon*, *Eragrostis*, *Leersia*, *Leptochloa*, *Panicum*, *Pennisetum*, *Setaria* and *Sporobolus*.

The pantropical genera with the most species in Namibia are: *Aristida*, *Brachiaria*, *Combretum*, *Crassula*, *Crinum*, *Hermannia*, *Helichrysum*, *Rhynchosia*, *Searsia* and *Tephrosia*. Genera with pantropical ranges can be subdivided into smaller groups in terms of their occurrence in Namibia and other specific regions of the world. These groups include:

1. **New world taxa:** Cucurbitaceae and Rubiaceae genera that are centred mainly in the New World, but also occur in Namibia include: Cucurbitaceae: *Coccinia*, *Corallocarpus*, *Ctenolepis*, *Cucumis*, *Kedrostis* and *Momordica*; Rubiaceae: *Canthium*, *Gardenia*, *Kohautia*, *Pavetta*, *Psydrax*, *Tarenna* and *Tricalysia*. The Namibian Cucurbitaceae is a genetic source for crop improvement and development. The native centre of origin of the cultivated crop, watermelon, is claimed to be in the Kalahari Desert (Maggs-Kolling 1999).

2. **African, Arabian and Asian taxa:** Namibian genera in the Acanthaceae, Asteraceae, Leguminosae and Poaceae include: Acanthaceae *Blepharis*, *Ecbolium*, *Hygrophila*, *Monechma*, *Peristrophe*, *Petalidium*, *Phaulopsis* and *Rhinacanthus*; Asteraceae: *Anisopappus*, *Baccharoides*, *Dicoma*, *Emilia*, *Grangea*, *Hertia*, *Kleinia*, *Laggera*, *Lasiopogon*, *Psiadia* and *Sphaeranthus*; Leguminosae *Afzelia*, *Dolichos*, *Lablab*, *Lotononis*, *Macrotyloma*, *Mundulea*, *Neonotonia* and *Pericopsis*. The Poaceae also includes numerous genera. The most speciose genera in this group are *Petalidium*, followed by *Commiphora* and *Lotononis*. Some genera, such as *Dyerophytum*, are noteworthy for having only one species in each of Africa, India and Sumatra.

3. **African and Asian taxa:** About 40 genera occur in both of these regions, of which some also extend into Australasia. *Zygophyllum* (also in Arabia) is the largest genus in this group, followed by *Pteronia* and *Pelargonium*.

4. **African and European taxa:** *Lindernia* is probably the only genus occurring only in Africa and Europe, but the following genera also occur in Asia: *Dianthus*, *Erucastrum*, *Ornithogalum*, *Peucedanum*, *Stipagrostis* and *Tamarix*. Besides *Dianthus* and *Ornithogalum*, most of these genera are neither speciose in Namibia nor widespread.

5. **American and African taxa:** Genera in this group that are generally more speciose in America include *Dalechampia*, *Eriocaulon*, *Lantana*, *Lippia*, *Parkinsonia* and *Spermacoce*. *Menodora*, a genus recently found in Namibia, along with *Antheophora*, *Loudetia* and *Rogeria* include more species in Africa than America. A group of disjunct, mainly xeromorphic taxa, occur in arid SW Africa and NW America. These include for example the genera *Thamnosma* and *Turnera*.

**6. African and Arabian taxa:** Almost 30 Namibian genera co-occur in Africa and Arabia. Most of the genera are small, with only four genera including more than 50 species. Most of these genera belong to the Asteraceae and Leguminosae. *Albuca* is the largest of these genera in Namibia, followed by *Ozoroa*, with the latter genus also extending into Madagascar.

Endemic genera: Craven (2002) mapped the overall distribution of genera endemic to Namibia, on quarter degree square scale, and found the area between the northern and southern escarpments to be the richest in endemic genera. This differs from the results of Simmons (1998) and Simmons *et al.* (1998) based on half degree squares. They suggested that most endemics occur on the escarpment. All three studies were based on the same plant data set. The different results are attributed to the use of GIS and finer scale and more accurate assessment of Craven (2002), especially with regard to the limits of the escarpment.

Genera represented in Namibia by few species: A total of 416 genera are represented by one species in Namibia, while 174 include two species, and 96 include three only. That results in only 244 genera in Namibia including more than three species. Genera with more than 50 species are (arranged from large to small): *Euphorbia*, *Eragrostis*, *Salsola*, *Indigofera* and *Crassula*. Genera with 41-49 species include: *Hermannia*, *Ornithogalum* and *Cyperus* and genera with 31-40 species include *Hibiscus*, *Mesembryanthemum*, *Jamesbrittenia*, *Crotalaria*, *Petalidium*, *Stipagrostis*, *Aloe*, *Barleria*, *Zygophyllum*, *Commiphora*, *Acacia* and *Helichrysum*. Most Namibian *Acacia* species occur in the NW of the country, while most of the Angolan *Acacia* species occur in SW Angola, in the area known as the Kaokoveld. Interestingly the two species endemic to Namibia belong to a different subgenus to the two endemics to Angola. The NW Namibia/SW Angola area appears to be one of the more important centres of speciation in *Acacia* in South Tropical Africa (Ross 1981).

### 4.3.3 Species

Distributions of species that show congruent patterns in terms of their distribution ranges outside Namibia, are recorded by Craven (2009, Chapter 5). Species with ranges that are widespread, scattered or show no pattern within Namibia, have been sorted below according to their patterns of distribution outside of Namibia. More data is needed on the overall distributions of many of these before further valid assessments can be made, but certain trends are noticeable:

1. Cosmopolitan species are mainly hydrophytes, especially monocotyledon species such as *Potamogeton* and *Ruppia* and species in the Poaceae.

2. *Dalechampia scandens* L. and *Triumfetta tomentosa* Bojer represent two of very few species that occur in Namibia and America.
3. The majority of these species are found in Africa and their main areas of distribution are:
  - a. southward into the Northern and Western Cape Province, South Africa;
  - b. eastward to the rest of southern Africa;
  - c into the South Tropical Africa including Zimbabwe, Zambia and Angola; and
  - d. north to Arabia and into Asia.

#### 4.3.4 Endemism

The *ca.* 600 species endemic to Namibia occur in over 60 families and in about 230 genera. They are listed in Craven & Vorster (2006) and updated in the databased index of Namibian plant species (Craven & Kolberg, on-going). Outstanding species-concentrations and endemism recorded by Nordenstam (1969) for *Euryops* were also found to be of importance by Hilliard (1994) and Van Wyk (1991). *Lotononis* has a similar geographic distribution to *Androcymbium* (Caujape-Castells *et al.* 2001) with endemic centres in NW Namibia and southern Namibia into Griqualand West, South Africa (Van Wyk 1991).

Endemics known to occur in Centres of endemism, e.g. Kaokoveld and Gariiep, are documented in Craven (2005), while endemics from other centres are summarized in Craven (2002). Species that also occur just over the Namibian border into neighbouring countries, here considered as near endemics, will increase the number of endemics to the region considerably, but to this end a more exact definition of “near” is needed. Generalizations, for example, that the endemics are found on the escarpment, as stated by Thuiller *et al.* (2006) should be avoided. The problem of the period of isolation of relict populations and the time factor in the appearance of endemic species in these populations has not been considered. Statements on such issues are considered premature considering the current state of knowledge of the Namibian flora.

#### 4.3.5 Disjuncts

Disjunct taxa have been recorded in Namibia and some hypotheses suggest explanations for these patterns. No comprehensive study has, however, been carried out and many examples in literature require more precise definition of the area involved and the taxonomic delimitations of the taxa, as well as consideration of new hypotheses. As Stott (1981) points out there is no single explanation for all disjunct patterns and each case must be studied on its own merit. Other factors like altitudinal

position, habitat and dispersal mechanisms must be taken into consideration, but above all, an accurate taxonomic framework is fundamental to describing disjunctions, especially at species level. While researching disjunct patterns in Namibia the need to re-evaluate the present literature sources and much-quoted examples was identified and problems, with examples, are summarized as follows:

1. Identical taxa may have different names in different areas. For example, *Xeroderris stuhlmannii* (Taub.) Mendonça & E.C.Sousa is called by three different names in eastern, central and western Africa, respectively.

2. Misapplied names. For example, the name *Commicarpus squarrosus* (Heimerl) Standl., a species of SW Africa, was erroneously used in NE Africa for the species *C. mistus* Thulin (Edwards *et al.* 2000).

3. Taxonomic revision. *Tribulocarpus dimorphanthus* (Pax) S.Moore in Namibia was considered to be *T. somalensis* Schellenb. in Somalia by Thulin (1994), but has been combined again under *T. dimorphanthus* in the new Flora of Ethiopia (Edwards *et al.* 2000).

4. Inadequate revision. The Acanthaceae, a family of considerable importance in NE-SW disjunctions is a good example of a taxon with inadequate taxonomic revision. While the family has recently been completed for Flora of Ethiopia, the Namibian members of the family are in dire need of an extensive review.

5. Specimen data. *Calliandra redacta* (J.H. Ross) Thulin & Hude is an example of a species cited for Namibia as a disjunct Afro-Arid element (Hilliard 1994), however no specimens could be traced to verify this. Some recent records of its presence in Namibia have been based on erroneous identifications of *Caesalpinia* specimens. Paton *et al.* (1994) map one 1957 collection of *Endostemon tenuiflorus* (Benth.) M.Ashby from Namibia, but this was neither cited nor checked. It is also disjunct to the Transvaal and needs confirmation before being used as an example as in Jürgens (1997). Another example is that of a specimen of *Indigofera cryptantha* which was thought to be *I. amorphoides* and cited as having a disjunct distribution.

6. Distributions at diverse taxonomic levels provide different evidence. For example the genus *Kissenia* has sister species in NE and SW Africa. It is, however, also the only genus of Loasaceae found outside of the New World. The species therefore show NE-SW disjunctions, while the genus

shows Africa-America disjunctions. Another example is that of the genera *Stoebe* and *Passerina*, both of which are Cape elements at generic level, but the species present in Namibia are not Cape elements.

7. Definitions. Different terms and/or concepts, for example the terms aridity and Namib, are not consistently defined, which leads to considerable confusion. Aridity is used for an area having less than 250 mm annual rainfall (Encarta® World English Dictionary ), but arid corridor examples cited by for instance Jürgens (1997) occur in areas with much higher rainfall such as northern South Africa. The distribution area of *Gossypium anomalum* Wawra ex Wawra & Peyr., which stretches from western to eastern areas of North Africa, one such an example.

8. Gondwana, the ancient supercontinent, consisting of India and all present-day continents of the southern hemisphere (Mendelsohn *et al.* 2002), was previously suggested as evidence by many biologists, for linked biota between these continent. Many suggested relationships are now considered differently. It is inadmissible to continue attributing links to this theory, without evaluation of more recent theories, as was done, for example, by Jacobson & Lester (2003).

9. Hypotheses based exclusively on mapped distributions. Hypotheses of disjunction cannot be based on mapped distribution data alone, but must be supplemented by other considerations like dispersal mechanisms. Unfortunately very little dispersal data has been documented or published.

10. Large undefined areas. Evaluation of smaller areas (e.g. the floristic zones proposed by Craven 2009, Chapter 5), may provide better resolution for the true identification of disjunct species.

11. Under collecting. Some disjunct patterns may merely be the result of insufficient collecting. This is particularly important in an arid country like Namibia where some taxa may only be available for collection in a few years per decade or longer. Namibia's National parks are notoriously under-collected and result in gaps in distribution data (Craven 2002). In addition some areas, such as the Angolan Highlands, are very poorly known. Hilliard (1994) pointed out that this certainly affects the confidence with which phylogeographic patterns can be evaluated.

Having highlighted the problems around the identification and validation of disjunct distributions, it is still interesting to evaluate Namibian plants mentioned in taxonomic literature as having disjunct distributions, as well as provide additional examples from own research. These can be summarized as follows:

## 1. The disjunction between arid areas of Northeast and Southwest Africa

The existence of such disjuncts in both plant and animal taxa was recognized as far back as 1921 by Engler (Thulin 1994). Such disjunctions are usually explained through the existence of an “arid corridor” during an arid phase of the Pleistocene. Animal examples include bat-eared foxes, oryx and dik-dik (Meester 1965), amphibians (Poynton 1995) and the scorpion genus *Parabuthus* (Prendini 2001, 2004) which has centres of diversity within Namibia and the north-east Horn of Africa and Arabia.

Disjunctions in plant taxa are common at sister species, section and genus level, with the number of genera being more numerous than the number of species (Thulin 1994). According to Thulin (1994) there are a fair number of taxa with a general north-south disjunction and others with more confined disjunctions in Africa. The former are considered to be Pleistocene relics or the result of long distance dispersal, while the latter may well reflect a more ancient link between the floras, perhaps dating back to the late Tertiary (Thulin & Johansson 1996). Few of the taxa presently proposed as evidence of the arid corridor show specific distribution patterns in Namibia.

In the Acanthaceae, four genera are common to both NE and SW Africa, but only species of *Peristrophe* and *Dicliptera* display the arid corridor pattern. The other two, *Barleria* and *Blepharis*, tend to concentrate in certain geographic regions (Balkwill & Balkwill 1998), but no species are present in both the NE and SW Africa. *Barleria* has two centres of diversity, one in NE Africa and another in South Africa. The three species in *Camptoloma* are interesting, as the one occurs in the Kaokoveld centre of endemism, while the other two occur in the Canary Islands and the Horn of Africa, respectively (Hilliard 1994).

A few genera in the Asteraceae show NE/SW African disjunctions. Nordenstam (1969) considers *Euryops* to have already differentiated in the Tertiary. The Namibian species, which belong to section *Angustifolii*, are the most widespread and considered the most derived. They are disjunct to NE Africa. *Geigeria* species with N-S disjunctions include *G. acaulis* (Sch. Bip) Benth. & Hook.f. ex Oliv. & Hiern. It occurs from Namibia and the Limpopo Province of South Africa to NE Africa. *G. alata* (Hochst. & Steud. ex DC.) Benth. & Hook.f. ex Oliv. & Hiern occurs from the Arabian Peninsula to Somalia in North Africa and in Namibia and Angola in the South. *Pentzia* has 20 species in southern Africa and two in North Africa. The small genus *Leysera* has two southern species (of which one, *L. tenella* DC. occurs in Namibia) and a sister species in North Africa, Spain and SW Asia (Bremer 1978).

In the Boraginaceae, *Trichodesma* species in southern Africa are widespread and occur in various vegetation types, but *T. africanum* (L.) Sm. has a disjunct distribution between Namibia/Northern Cape (South Africa) and North West Africa to Pakistan. *Wellstedia* is known from Socotra, northeastern Somalia, south-eastern Ethiopia, southern Namibia and adjacent parts of the Cape Province (South Africa) (Retief & van Wyk 2008). *W. dinteri* Pilg. is the only species in Namibia and Thulin & Johansson (1996) proposed its link to NE Africa dates back to the late Tertiary.

In the Leguminosae, *Indigofera trigonelloides* Jaub. & Spach is unusual at species level in having a disjunct distribution between the north-east Horn of Africa and Namibia (Schrire *et al.* in press). In the Colchicaceae, *Androcymbium*, a mainly southern African genus, that is viewed as a member of the arid track (Caujape-Castells *et al.* 2001) has some species in arid areas of Namibia. *Ornithoglossum* is believed to have originated in formerly arid regions of tropical Africa, but no links remain today to confirm this (Nordenstam 1982). After a south and southwestward migration, adaptation to different pollinators was an important factor in speciation after migration.

In the Convolvulaceae, *Ipomoea adenioides* Schinz, has one widespread variety unevenly distributed in South Tropical Africa and southern Africa, and a second variety confined to Ethiopia and Somalia. Two species in the Cucurbitaceae show arid track disjunctions, with one, *Cucumella cinerea* (Cogn.) C. Jeffrey also found in Madagascar (Kirkbride 1994). *Dactyliandra welwitschii* Hook.f. is known from NW Namibia and SE Angola and the Thar desert in India. *Kissenia* is the only Loasaceae genus in Africa. *K. arabica* Kiev. is confined to dry regions in the Horn of Africa, while *K. capensis* Endl. is confined to southwestern Africa. The phytogeography of the Pedaliaceae has been comparatively well-researched and *Sesamum rigidum* Peyr., a species from NW Namibia, is considered the most primitive representative of its section, and thus the putative ancestor that later gave rise to species that colonized NE Africa (Ihlenfeldt 1994). *Pterodiscus*, *Rogeria* and *Sesamothamnus* show NE-SW African disjunctions, although they also show either continuously (*Pterodiscus*) or disjunct (*Sesamothamnus*), eastward extensions in southern Africa. An undescribed tree-like species of *Sesamothamnus* from the Kaokoveld (De Winter & Leistner, 5504) is probably the earliest divergent species (Ihlenfeldt pers. comm.).

## **2. Disjunctions between Namibia and South America**

This category includes families such as Amaranthaceae, Tecophilaeaceae, Velloziaceae and Welwitschiaceae. Genera that have been found to be closely related, despite the one being in South America and the other in southwest Africa include: *Welwitschia*, *Gnetum*, *Xerocladia* and *Prosopis*



(Lewis *et al.* 2005; Schrire *et al.* 2005). Karyological information supports the hypothesis that the Velloziaceae originated in South America where it includes six endemic genera, with only one genus, *Xerophyta*, shared between South America and Africa (De Melo *et al.* 1997). The phylogenetic analysis of *Dicoma* (Ortiz 2000) suggests a close relationship between the earliest diverging South American representatives of the tribe Mutisieae to the southern Africa species. *Anisopappus* has a similar distribution and ecology to *Dicoma* (Ortiz 2000).

### **3. Disjunctions between Namibia and Australia**

A much debated disjunction is that of *Nicotiana africana* Merxm. It is the only indigenous *Nicotiana* species in southern Africa and is limited to a few mountains in western-central Namibia. The rest of the genus is known from semi-arid habitats in Australia and South America. Merxmüller & Buttler (1975) believed its taxonomic position to be obscure. It is not a hybrid of the few naturalized or cultivated species in Africa, and it is unlikely to have resulted from a recent long range dispersal of a still unknown species or hybrid. Instead it is considered to be an endemic relict of considerable age. Goodspeed (1954) in Gerstel *et al.* (1979) dated the differentiation of *Nicotiana* in South America to the mid to late Tertiary. Unlike several South American species, *N. africana* is insensitive to tentoxin, a character inherited through the cytoplasm. It also possesses another marker, which occurs in only two species from southern South America and these may be regarded as ancestral (Knapp *et al.* 2004). This species is now considered to be most closely related to a group from Australia and New Caledonia.

### **4. Disjunctions within southern Africa and South Tropical Africa**

#### **A. Angola and montane regions**

For many years the occurrence of *Passerina* on the Auas Mountains was considered to represent a relict of the Cape Floristic Region (CFR) (Rennie 1936). The specimens available were however, sterile. Bredenkamp & van Wyk (2006) verified the identification of these specimens as *P. montana* Thoday, as are specimens from Huila in Angola. This species is assigned to the escarpment zone of southern Africa. It probably originated in the CFR and formed part of a previously wider northern temperate Afromontane grassland-dominated vegetation during the Quaternary, of which relicts remained (Bredenkamp & van Wyk 2006). The disjunctions observed today are thus believed to be due to environmental changes. *Seriphium plumosum* L., previously identified as a *Stoebe* species, was also considered as evidence for the presence of Cape floral elements near Windhoek. In Namibia and Angola it occurs only on mountains (Auas) or plateaus (Huila). Another highlands species is *Selago alopecuroides* Rolfe, from the Huila highlands (1800-2250 m) and then disjuncts to the Waterberg and Regenstein Mountains (Hilliard 1994). In the Lamiaceae, *Aeollanthus*

*buchnerianus* Briq. may also belong in this group, as it has a somewhat disjunct distribution between Angola and the Namibian highlands and the highlands between Tanzania and South Africa. It also extends into the Afromontane Region in several places. *A. rehmannii* Gürke has a similar distribution (Ryding 1986). *Olea europaea* L., in some parts of its range, appears almost strictly afromontane and would appear to be part of the Angola highlands and montane regions, but it cannot be placed in this group because it is so versatile, it also occurs elsewhere (White 1990). In Namibia it occurs in most of the highest parts, except near the Hunsberg. The effect of cooler temperatures at altitude and orographic rainfall must be taken into consideration when researching this group.

B. Namibia and Zambia. *Volkiella disticha* Merxm. & Czech, which is restricted to parts of Namibia and Zambia, is only known from a few collections.

C. Northern Namibia (and maybe Angola) to Mozambique: *Barleria senensis* Klotzsch, *Abutilon austro-africanum* Hochr., *A. englerianum* Ulbr. (Hilliard 1994), *Nuxia oppositifolia* (Hochst.) Benth. (Coates Palgrave 2002) and *Stapelia kwebensis* N.E. Br. (Bruyns 2000) show disjunct distributions between Northern Namibia (Angola) and Mozambique. Hilliard (1994) suggested that this distribution was facilitated by water transport of plant material via the perennial rivers in the north of Namibia that flow in an east-west or west-east direction.

## 5. Disjunctions within southern Africa

A. Highlands of Namibia and eastern South Africa, e.g. Limpopo and Free State: The Namibian species *Cymbopogon dieterlenii* Stapf ex E. Phillips and *Euryops asparagoides* (Licht. ex Less.) DC. are disjunct to the Free State, while *Plectranthus dinteri* Briq. from Otavi has disjunct connections to the Limpopo Province. More widespread species in Namibia with disjunct distributions to the highveld include *Euphorbia guerichiana* Pax, *Kirkia acuminata* Oliv. and *Vernonia cinerascens* Sch.Bip.

B. Eastern Cape Province (South Africa) and watercourses or rocky gorges in southern Namibia: Examples from the Hunsberg area with disjunct connections to the Eastern Cape Province include *Dioscorea elephantipes* (L'Her.) Engl., *Dodonaea viscosa* Jacq. subsp. *angustifolia* (L.f.) Benth. and *Foveolina albidiformis* (Thell.) Källersjö. Those with wider distributions in southern Namibia include *Schotia afra* (L.) Thunb. var. *angustifolia* (E. Mey.) Harv., *Pappea capensis* Eckl. & Zeyh. and *Albizia brevifolia* Schinz (Coates Palgrave 2002). The link between the flora of the Hunsberg area and the eastern Cape is further shown by species that were misidentified for similar vicariant species in the eastern Cape of South Africa (Craven 2009, Chapter 5). *Carissa bispinosa* (L.) Desf.

ex Brenan (previous known as *Carissa haematocarpa* (Eckl.) A. DC. in its southern range), is disjunct to the eastern Cape and the Otavi mountain.

## 6. Disjunctions within Namibia

Various disjunct distributions have been recorded within Namibia (Craven 2002), but most include only one or a few taxa as examples. The most obvious pattern is that of species found on upper reaches of mountains, especially in the central and southern highlands (Craven 2009, Chapter 5). There are also a few species associated with the Brandberg Mountain and surrounds, and southern Namibia, e.g. *Antizoma miersiana* Harv., *Commiphora namaensis* Schinz, *Diospyros acocksii* (De Winter) De Winter, *Leysera tenella* DC. and *Mentha longifolia* (L.) L. subsp. *wissii* (Launert) Codd. Other species on the Brandberg with disjunct distributions elsewhere in Namibia include *Sutherlandia frutescens* (L.) R. Br. and *Tarchonanthus camphoratus* L. A well-defined NW to SE disjunction is shown by the grass *Leucophrys mesocoma* (Nees) Rendle. A few species are confined to the sand dunes scattered along the coast south of the Kunene River, south of the Kuiseb River and around Lüderitz. These include *Acanthosicyos horridus* Welw. ex Hook.f., *Cladoraphis spinosa* (L.f.) S.M. Phillips, *Hexacyrtis dickiana* Dinter and *Stipagrostis schaeferi* (Mez) De Winter. *Mesembryanthemum salicornioides* Pax occurs in places along the coast and a bit further inland in the south, however, it is noticeably less woody and shorter lived in the south compared to specimens in the north. A number of succulent species like *Avonia albissima* (Marloth) G.D. Rowley exhibit disjunct ranges because they prefer quartzitic outcrops. Rather unusual disjunctions are shown by *Hoodia currorii* (Hook.) Decne., *Huernia oculata* Hook.f., *Larryleachia marlothii* (N.E. Br.) Plowes, *Larryleachia tirasmontana* Plowes and *Orbea maculata* (N.E. Br.) L.C. Leach subsp. *rangeana* (Dinter & A.Berger) Bruyns, which occur together in a spot about 30 km from the coast and 150 km south of the Kunene River on the Skeleton Coast, but then also elsewhere like in the Karasberg mountains. Besides the few species that prefer sand dunes along the coast, no disjunct distributions are found between the extreme southwestern Namibia and the rest of the country.

## 7. Disjunction through anthropogenic activity

Transfer of plant material by humans may account for disjunct distribution of some species, for example *Trema orientalis* (L.) Blume. It is found in the Erongo Mountains of Namibia only, but is widespread elsewhere in Africa as well as in tropical Asia. It is a common pioneer of disturbed soil and has been planted for soil reclamation. Distribution patterns of *Searsia leptodictya* (Diels) T.S. Yi, A.J. Mill. & J. Wen and *Aloe buettneri* A. Berger and possibly *Protea gaguedi* J.F. Gmel. (now considered extinct in Namibia) could also have resulted from human transfer, as all of these species

have well-known uses. Vogelsang (2002) mapped the routes by which some of Namibia's first people arrived in this country. Not only do these routes start in areas where these plants are common, but it shows that their present distributions coincide with some of the first inhabited areas. Another odd distribution is that of *Dodonaea viscosa*. In northern Namibia it is considered an escape from cultivation, as it is commonly used as a hedge plant (and therefore not indigenous to the area). In the Hunsberg it occurs with the group that also has disjunct distributions in the Eastern Cape of South Africa and is indigenous (Craven 2009, Chapter 5). Its distribution in the high mountains near Windhoek needs further investigation. Firstly the taxonomy of specimens must be carefully studied, and then an evaluation should be made of the area used by the German troops for their horses during the rinderpest in the early 1900s. The presence of another alien, *Jacaranda mimosifolia*, in the vicinity suggests that this species may be a left-over from the early German settlement.

#### **4.3.6 Disjunctions through substrate preferences**

The discontinuities in the distribution of many species of *Aeollanthus* in South Tropical Africa can probably be explained by the lack of suitable habitat in the intervening areas (Ryding 1986). They prefer well-drained soil and occur on rock outcrops and hill slopes. They usually grow in areas that are dry for a large part of the year, but are often found near small seasonal streams.

#### **4.3.7 Origin of the flora and its relationships**

Interpretations of the origins of the flora of Namibia are complex. The past few years have seen new ideas and concepts emerge and, of the very few suggestions presented in literature, some are no longer considered valid. The main obstacle to deciphering the origin of the Namibian flora is the paucity of systematic and molecular studies. Another problem is the fragmented nature of the fossil record and patchy historical evidence from abiotic sources (Craven 2009, Chapter 3). These data are generally considered on a larger scale than a country, i.e. a biogeographic zone or complete family or genus and thus not directly applicable to Namibia. Knowledge of contemporary floras can contribute to our understanding of the past (White 1990), but to date the information has not been utilised. This is particularly relevant to disjunct populations, but good taxonomies and knowledge of distributions and relationships are essential for this. Some groups, such as most monocotyledons, are also problematic, because they are under-collected, poorly known and very often in need of revision within Namibia.

## 1. Molecular and morphological insights

Phylogenetic relationships based on molecular and morphological characters address questions about the origin of the flora and how it reached its present distribution. Linder (1998) proposed criteria to be met before a phylogeny can be biogeographically informative. At that time, the only study relevant to Namibia that met these criteria was on the genus *Phaulopsis* (Manktelow 1996). To date, this remains the only such study, mainly because all species should be included and because sufficiently detailed distributional information should be available. Few other phylogenetic analyses involving Namibian taxa have been published, and specimens from Namibia have seldom been used. Of the five *Androcymbium* species occurring in Namibia, for example, only one was included in the phylogenetic analysis of Caujape-Castells *et al.* (2001) and then not from a population in Namibia.

Molecular phylogenetic studies in the Zygophyllaceae highlight the conflicting results that can be obtained through restricted species sampling. Only 6 species from southern Africa were included in the phylogenetic analysis of the family by Sheahan & Chase (2000). Beier *et al.* (2003) expanded on their study by adding 2 more southern African taxa. Finally 53 of the 55 southern African species were sequenced by Bellstedt *et al.* (2008), and the generated phylogenies were compared with the morphological character assessments by Van Zyl (2000). The study of Bellstedt *et al.* (2008) showed the opposite direction of migration to that proposed by the former two studies, and further supplies evidence for repeated migrations of *Zygophyllum* species from southern African to the arid areas in the Horn of Africa and Asia. In addition, the *Z. orbiculatum/stapffii* complex which is endemic to NW Namibia and SW Angola, was not included in the earlier studies and it proved to be the earliest diverging elements in the genus.

A very valuable study from a Namibian perspective is that of Schrire *et al.* (2003) and recently a greatly expanded Indigofereae dataset was phylogenetically analysed (Schrire *et al.* in press). Their results showed that all species of *Indigofera* sampled (266) belong to one of four monophyletic subgroups, except the Namibian endemic, *I. nudicaulis* E.Mey. They concluded that *I. nudicaulis* is likely to be sister to any of the four main *Indigofera* clades, although it was argued that it was most likely allied to their Cape clade. This species and the next branching species, *I. merxmulleri* A.Schreib., occur in a group with links to the Eastern Cape of South Africa, particularly the Albany area. The crown age of this clade is given as 20.3 Ma. A species restricted to NW Namibia, *I. anabibensis* A. Schreib., represents another clade, the Tethyan clade. It occurs in arid lowland areas less than 800 m in altitude, represents the second oldest clade and has a crown age of 11.5 Ma. They

concluded that the area of the SW African Arid Corridor region is probably a refugium for some of the oldest lineages of *Indigofera*.

The recent subgeneric classification for *Euphorbia* in southern Africa (Bruyns *et al.* 2006) based on DNA sequence data, included 128 species, representing less than 1% of the total number of species in the genus (1600 overall, 300 in southern Africa). Considering the size of the genus, the criteria suggested by Linder (2001) are therefore not possible to meet. The distribution patterns of *Euphorbia* species within Namibia included in Bruyns *et al.* (2006) revealed no characteristic distribution patterns for the genus.

Molecular systematic study suggests that some stapeliads radiated southwards and eastwards from a region of origin in the NE of Africa REF. Molecular data does, however, also suggest that at least some of the diversity of stapeliads in NE Africa (e.g. *Huernia* and *Orbea*) is the result of northward migration. The stapeliad radiation within southern Africa (Bruyns 2005) is similar to that of *Anacampseros* (Gerbaulet 1992), in that both genera show diversification that proceeded from summer to winter rainfall areas, and from there onwards to more arid parts.

## 2. Fossil record and historical evidence from other sources

A thorough survey of the numerous sources providing evidence for the age of parts of Namibia did not contribute to understanding the history of the Namibian flora (Craven 2009, Chapter 3). Previous studies on other biota, for example Irish (1990), proposed the South American-Africa Trans Atlantic dispersal route along the Walvis ridge, but this does not apply to plants. Gondwana theories as explanations for the origins of many taxa appear in many older studies and the Boreotropical hypothesis, as developed by Wolfe (1975), has been proposed to explain the phylogeny of some taxa, e.g. *Indigofera* (Schrire *et al.* 2003). More recent research, however, favours a narrowly defined Tethys Seaway to explain the distribution of this genus. It differs from the former hypothesis in that the once widespread Tethyan distribution involved seasonally dry tropical vegetation as apposed to the “paratropical” floras of the mid-latitude Northern Hemisphere (Schrire *et al.* 2005).

## 3. Track analysis

A track is the distribution of a taxon (Linder *et al.* 1992). Areas and floras showing previous contact with the Namibia flora, based on the distribution areas or tracks of non-endemic taxa, can be summarized as follows, based on the information outlined above and summarized in Craven (2009, Chapter 5):

1. The Karoo-Namib Region of Angola and Northern Cape (South Africa)
2. The Sudano-Zambesian region, Zambesian Domain to tropical Africa
3. The most northwestern parts of South Africa just south of the Orange River, an extension of the same succulent flora found in the southern Namib.
4. Highveld and Afromontane elements of eastern southern Africa, like the Great escarpment.
5. NE African taxa resulting from the Arid track, which developed after the split of Europe from Africa.
6. South American taxa resulting from the Tethys Seaway (Brown & Lomolino 1998).

#### **4.4 Discussion and Conclusions**

The principal reason for the wealth of species in Namibia is the numerous and various tracks that contribute taxa. Other reasons are similar to those for southern Africa pointed out by Goldblatt (1978). These include: 1. environmental diversity, 2. different rainfall regimes, and 3. recurrent climate fluctuations since early times.

Different taxa in the vicinity of the Hunsberg Mountains suggest that this area may contain an ancient flora (Schrire pers. comm.; Craven 2009, Chapter 5). Further investigations are required to confirm these indications and provide more information on the origin, distribution and diversity of the flora of Namibia. Particular areas worthy of future investigation include establishing accurate disjunct patterns, molecular phylogenetic reconstruction and taxonomic revisions of key groups.

The demand for accurate knowledge about our biodiversity has been highlighted by the Convention of Biological Diversity. A remarkable change in systematics and taxonomy in recent years has been the recognition of different users with different requirements. Unfortunately the number of taxonomists has not kept up with this increased demand. This paper highlights the value of not only the flora, but also of really understanding the flora and the need for professionals to undertake the required taxonomic research.

#### **References**

Balkwill, M.-J. & Balkwill, K. 1998. A preliminary analysis of distribution patterns in a large, pantropical genus, *Barleria* L. (Acanthaceae). *Journal of Biogeography* 25: 95–110.

- Beier, B.-A., Chase, M.W. & Thulin, M.P. 2003. Phylogenetic relationships and taxonomy of subfamily Zygophylloideae (Zygophyllaceae) based on molecular and morphological data. *Plant Systematics and Evolution* 240: 11–39.
- Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.
- Bredenkamp, C.L. & Van Wyk, A.E. 2006. Phytogeography of *Passerina* (Thymelaeaceae). *Bothalia* 36: 191–199.
- Bremer, K. 1978. The genus *Leysera* (Compositae). *Botaniska Notiser* 131: 369–383.
- Brown, J.H. & Lomolino, M.V. 1998. *Biogeography*, 2nd edition. Sinauer Associates, Sunderland.
- Bruyns, P.V. 2000. Phylogeny and biogeography of the Stapeliads 2. Biogeography. *Plant Systematics and Evolution* 221: 227–244.
- Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar* 1 & II. Umdaus Press, Hatfield.
- Bruyns, P.V., Mapaya, R.J. & Hedderson, T. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and psbA-trnH sequence data. *Taxon* 55: 397–420.
- Caujape-Castells, J., Jansen, R.K., Membrives, N., Pedrola-Monfort, J., Montserrat, J.M. & Ardanuy, A. 2001. Historical biogeography of *Androcymbium* Willd. (Colchicaceae) in Africa: Evidence from cpDNA RFLPs. *Botanical Journal of the Linnean Society* 136: 379–392.
- Coates Palgrave, M. 2002. *Keith Coates Palgrave Trees of Southern Africa*. Edition 3. Struik, Cape Town. Edition 3.
- Conspectus Florae Angolense* (various editorial teams). 1937-1970. Centro de Botânica, Instituto de Investigação Científica Tropical, Lisboa.



- Craven, P. 2002. Phytogeography of the Namibian flora: A taxon approach. Unpublished. MSc thesis, University of Stellenbosch, Stellenbosch.
- Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET News* 9: 24–44.
- Craven, P. 2009. Chapter 3, this volume. Plant geography in Namibia.
- Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.
- Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.
- Craven, P. & Vorster, P.V. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.
- De Melo, N.F., Guerra, M., Benko-Iseppon, A.M. & de Menezes, N.L. 1997. Cytogenetics and cytotaxonomy of Velloziaceae. *Plant Systematics and Evolution* 204: 257–273.
- De-Zhi, F., Yong, Y. & Guang-Hua, Z. 2004. A new scheme of classification of living Gymnosperms at family level. *Kew Bulletin* 59: 111–116.
- Dilcher, D.L., Bernardes-de-Oliveira, M.E., Pons, D. & Lott, T.A. 2005. Welwitschiaceae from the Lower Cretaceous of northeastern Brazil. *American Journal of Botany* 92: 1294–1310.
- Edwards, S., Tadesse, M., Demissew, S. & Hedberg, I. (eds). 2000. *Flora of Ethiopia and Eritrea* 2 Addis Ababa, Ethiopia.
- Flora of southern Africa*. (various editorial teams). 1963–ongoing. National Botanical Institute, Pretoria.
- Flora Zambesiaca*. (various editorial teams). 1960–ongoing. Crown Agents for Overseas Development, London.
- Gerbaulet, M. 1992. Die Gattung *Anacampseros* L. (Portulacaceae). 1. Untersuchungen zur Systematik. 2. Untersuchungen zur Biographie. *Botanische Jahrbücher* 113: 477–564, 565–576.

- Gerstel, D.U., Burns, J.A. & Burk, L.G. 1979. Interspecific hybridisations with an African tobacco, *Nicotiana africana* Merxm. *The Journal of Heredity* 70: 342–344.
- Gibbs Russell, G.E. 1986. Significance of different centres of diversity in subfamilies of Poaceae in southern Africa. *Palaeoecology of Africa* 17: 183–191.
- Goldblatt, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships and origins. *Annals of the Missouri Botanic Garden* 65: 369–436.
- Goldblatt, P. 1986. The Moraeas of Southern Africa. *Annals of Kirstenbosch Gardens* 14.
- Goldblatt, P. 1990. Systematics of *Lapeirousia* (Iridaceae-Ixioideae) in tropical Africa. *Annals of the Missouri Botanic Garden* 77: 430–484.
- Goldblatt, P. & Manning, J. 1998. *Gladiolus in southern Africa*. Fernwood Press, Vlaeberg.
- Good, R.D. 1974. *The geography of flowering plants*. Wiley, New York.
- Goodspeed, T.H. 1954. The genus *Nicotiana*. *Chronicles of Botany* 16: 1–536.
- Gugerli, F., Sperisen, C., Büchler, U., Brunner, I., Brodbeck, S., Palmer, J.D. & Qiu, Y.-L. 2001. The evolutionary split of Pinaceae from other conifers: Evidence from an intron loss and a multigene phylogeny. *Molecular Phylogenetics and Evolution* 21: 167–175.
- Hartmann, H.E.K. 1964. On the phytogeography and evolution of Mesembryanthea (Aizoaceae). In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the IIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1165–1189. National Herbarium and Botanic Gardens of Malawi, Zomba.
- Hilliard, O. M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Ickert-Bond, S.M. & Wojciechowski, M.F. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): Evidence from nuclear and chloroplast DNA sequence data. *Systematic Botany* 29: 834–849.

- Ihlenfeldt, H.-D. 1967. Über die Abrensung und die natürliche Gliederung der Pedaliaceae R.Br. *Mitteilungen aus dem Institut für Allgemeine Botanik*, Hamburg 12: 43–28.
- Ihlenfeldt, H.-D. 1994. Phytogeography of Pedaliaceae R.Br. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the IIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1063–1075. National Herbarium and Botanic Gardens of Malawi, Zomba.
- Irish, J. 1990. Namib biogeography, as exemplified mainly by Lepismatidae (Thysanura: Insecta). In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 61–66. Transvaal Museum Pretoria.
- Jacobson, K.M. & Lester, E. 2003. A first assessment of genetic variation in *Welwitschia mirabilis* Hook. *Journal of Heredity* 94: 212–217.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495–514.
- Kirkbride, J.H. 1994. Revision of *Cucumella* (Cucurbitaceae, Cucurbitoideae, Melothrieae, Cucumerinae). *Brittonia* 46: 161–186.
- Klak, C., Reeves, G. & Hedderson, T. 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* 427: 63–65.
- Knapp, S., Chase, M.W. & Clarkson, J.J. 2004. Nomenclatural changes and a new sectional classification in *Nicotiana* (Solanaceae). *Taxon* 53: 73–82.
- Lewis, G., Schrire, B., Mackinder, B. & Lock, M. 2005. *Legumes of the World*. The Royal Botanic Gardens, Kew.
- Linder, H.P. 1998. Numerical analyses of African plant distribution patterns. In: Huxley, C.R., Lock, J.M. & Cutler, D.F. (eds). *Chorology, taxonomy and ecology of the floras of Africa and Madagascar*. Pp. 67–86. Royal Botanic Gardens, Kew.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.

- Linder, H.P., Meadows, M.E. & Cowling, R.M. 1992. History of the Cape flora. In: Cowling, R.M. (ed.). *The ecology of fynbos. Nutrients, fire and diversity* 5. Pp. 113–134. Oxford University Press, Oxford.
- Maggs-Kolling, G.L. 1999. Namibia – a watermelon wonderland. *Spotlight on Agriculture* 16. January 1999.
- Major, J. 1988. Endemism: A botanical perspective. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 117–146. Chapman & Hall, London.
- Manktelow, M. 1996. *Phaulopsis* (Acanthaceae) – a monograph. *Symbolae Botanicae Upsaliensis* 31: 1–184.
- Meester, J. 1965. The origins of the southern African mammal fauna. *Zoologica Africana* 1: 87–93.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, A. 2002. *Atlas of Namibia: A portrait of the land and it's people*. David Phillip Publishers, Cape Town.
- Merxmüller, H. (ed.). 1966–1972. *Prodromus eine Flora von Südwestafrika*. Cramer Verlag, Lehre.
- Merxmüller, H. & Buttler, K.P. 1975. *Nicotiana* in der Afrikanischen Namib – ein pflanzengeographisches Rätsel. *Mitteilungen aus der Botanischen Staatssammlung, München* 12: 91–104.
- Nickerson, J. & Drouin, G. 2004. The sequence of the largest subunit of RNA polymerase II is a useful marker for inferring seed plant phylogeny. *Molecular Phylogenetics and Evolution* 31: 403–415.
- Nordenstam, B. 1969. Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica* 23: 7–75.
- Nordenstam, B. 1982. A monograph of the genus *Ornithoglossum* (Liliaceae). *Opera Botanica* 64: 1–51.

- Ortiz, A. 2000. A phylogenetic analysis of *Dicoma* Cass. and related genera (Asteraceae: Cichorioideae: Mutisieae) based on morphological and anatomic characters. *Annals of Missouri Botanic Garden* 87: 459–481.
- Paton, A.J., Harley, M.M., Harley, R.M. & Weeks, S. 1994. A revision of *Endostemon* (Labiatae). *Kew Bulletin* 49: 673–716.
- Poynton, J.C. 1995. The arid corridor distribution in Africa: A search for instances among the amphibians. *Madoqua* 19: 45–48.
- Prendini, L. 2001. Phylogeny of *Parabuthus* (Scorpiones, Buthidae). *Zoologica Scripta* 30: 13–35.
- Prendini, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109–186.
- Rennie, J.V.L. 1936. On the flora of a high mountain in SWA. *Transactions of the Royal Society of South Africa* 259–263.
- Retief, E. & Van Wyk, A.E. 2008. The genus *Wellstedia* (Boraginaceae: Wellstedioideae) in southern Africa. *Bothalia* 38: 57–63.
- Ross, J.H. 1981. An analysis of the African *Acacia* species: Their distribution, possible origins and relationships. *Bothalia* 13: 389–413.
- Ryding, O. 1986. The genus *Aeollanthus* s. lat. (Labiatae). *Symbolae Botanicae Upsaliensis* 26: 1–152.
- Rydin, C., Källersjö, M. & Friis, E.M. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast dna: Conflicting data, rooting problems, and the monophyly of conifers. *International Journal Plant Science* 163: 197–214.
- Sheahan, M.C. & Chase, M.W. 2000. Phylogenetic relationships within Zygophyllaceae based on DNA sequences of three regions, with special emphasis on Zygophylloideae. *Systematic Botany* 25: 371–384.

Schrire, B.D., Lavin, M., Barker, N.P., Cortes-Burns, H., Von Senger, I. & Kim, J.-H. 2003. Towards a phylogeny of *Indigofera* (Leguminosae-Papilionoideae): Identification of major clades and relative ages. In: Klitgaard, B.B. & Bruneau, A. (eds). *Advances in Legume Systematics 10 Higher Level Systematics*. Pp. 269–302. Royal Botanic Gardens, Kew.

Schrire, B.D., Lavin, M. & Lewis, G.P. 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. *Biologiske skrifter* 55: 375–422.

Schrire, B., Lavin, M., Barker, N.P. & Forest, F. Phylogeny of the tribe Indigofereae (Leguminosae-Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments *American Journal of Botany*. In press.

Simmons, R.E. 1998. Areas of high species endemism. In: Barnard, P. (ed.). *Biological diversity in Namibia: A country study*. Pp. 72–74. The Namibian National Biodiversity Task Force, Windhoek.

Simmons, R.E., Griffen, M., Griffen, R.E., Marais, E. & Kolberg, H. 1998. Endemism in Namibia: Patterns, processes and predictions. *Biodiversity and Conservation* 7: 513–530.

Stott, P. 1981. *Historical plant geography. An introduction*. George Allen & Unwin, London.

Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C. & Woodward, F.I. 2006. Endemic species and ecosystem vulnerability to climate change in Namibia. *Global Change Biology* 12: 759–776.

Thulin, M. 1994. Aspects of disjunct distributions and endemism in the arid parts of the Horn of Africa, particularly Somalia. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the IIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1105–1119. National Herbarium and Botanic Gardens of Malawi, Zomba.

Thulin, M. & Johansson, A.N.B. 1996. Taxonomy and biogeography of the anomalous genus *Wellstedia*. In: Van der Maesen, L.J.G., van den Burgt, M. & van Medebach de Rooy, J.M. (eds). *The Biodiversity of African Plants*. Pp. 73–86. Kluwer Academic Publishers, Dordrecht.

- Van Wyk, B-E. 1991. A synopsis of the genus *Lotononis* (Fabaceae: Crotalariaeae). *Contributions from the Bolus Herbarium* 14: 1–292.
- Van Zyl, L. 2000. A systematic revision of *Zygophyllum* (Zygophyllaceae) in the southern African region. Unpublished. PhD thesis. University of Stellenbosch, Stellenbosch.
- Vogelsang, R. 2002. Migration oder Diffusion? – Frühe Viehhaltung im Kaokoland. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Kaokoland - Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semi-ariden Nordwesten Namibias*. Pp. 137–144. *Kölner Geographische Arbeiten* 77, Köln.
- White, F. 1990. *Ptaeroxylon obliquum* (Ptaeroxylaceae) some other disjuncts and the Quarternary history of African vegetation. *Bulletin du Museum National d'Histoire Naturelle Section B. Adansonia* 2: 139–185.
- Wolfe, J.A. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanic Garden* 62: 264–279.
- Won, H. & Renner, S.S. 2003. Horizontal gene transfer from flowering plants to *Gnetum*. *Proceedings of the National Academy of Science, USA*. 100:10824–10829.
- Won, H. & Renner, S.S. 2005. The chloroplast *trnT-trnF* region in the seed plant lineage Gnetales. *Journal of Molecular Evolution* 61: 425–436.

## Chapter 5

### Natural floristic Groups of Namibia

#### Abstract

5.1	Introduction.....	88
5.2	Materials and methods .....	89
5.3	Results.....	91
5.3.1	Welwitschia-desert Group.....	91
5.3.2	Kaoko Group .....	93
5.3.3	Highland Group .....	96
5.3.4	Namib-dunes Group .....	97
5.3.5	Southern Namib succulent desert Group.....	99
5.3.6	Huns-Orange Group .....	100
5.3.7	Gordonia Group .....	103
5.3.8	Kalahari-sand Group .....	104
5.3.9	Zambesian Domain of White (1971).....	106
5.4	Discussion .....	107
5.5	Conclusions.....	113
5.6	References.....	113



## Natural floristic Groups of Namibia.

### Abstract

Namibia is divided into nine phytogeographic Groups, based exclusively on distribution patterns of plant species. Results are presented in the form of a map based on representative species from each of the nine Groups. The characteristics, floristic composition and relationships of each Group are presented. Possible ecological and historical causes for these divisions are discussed. Evidence from studies of the palaeo-environment proved to be of little use, but (pan-) phytogeographic relationships of the extant flora provided clues, along with climate and topography.

### 5.1 Introduction

An ideal database for determining floristic elements would consist of accurate maps of the ranges of all species occurring in the area under investigation (Takhtajan 1986). Although this ideal is not to be had in Namibia, knowledge of the taxonomy and distribution of Namibia's flora is sufficient to allow provisional assessments of its geographical affinities to be made. Like in all phytogeographic analyses, the following phases were followed here: 1. a descriptive phase, i.e. taxa assigned a range or distribution; 2. analytical and interpretive phases, i.e. distribution patterns of taxa and areas are compared with one another; 3. reasons were sought for past environmental factors that may have been responsible for these relationships or patterns and 4. results were presented as maps showing the geographic distribution of floristic elements.

Although it is clear that “the determination of species distribution patterns is a starting point for all biogeographic analyses.” (Myers & Giller 1988), this knowledge for Namibian plants is limited to large-scale regional patterns and distributions of range-restricted species (Craven 2009, Chapters 3 and 4). The phytogeography of a limited number of Namibian taxa is summarized in Craven (2002). The need for a floristic evaluation for Namibia is therefore obvious, not only for botanists, but for research ranging from the palaeo-environmental assessments to predictions on climate change (Craven 2009, Chapter 3).

There is, however, a confusing number of approaches and techniques to historical biogeography (Crisci 2001). Although no specific method is considered superior, more rigorous research methodology is expected when considering this subject today. In this regard it is critical to remember that biogeographic analyses of areas such as the Cape Floristic Region (CFR) can today

be pursued numerically (Born *et al.* 2007), as ongoing research into the floristics of this flora started many years ago (Adamson 1958; Levyns 1964). These were generally based on individual researchers' knowledge of the flora and the landscape from years of experience and field work. It is also noteworthy that a recent survey of methods used in the *Journal of Biogeography* (Posadas & Donato 2007) showed that a number of papers still did not apply any one particular technique or approach.

This paper is borne out of the belief that a first attempt at dividing Namibia into floristic groups using the traditional or narrative approach has value. Other reasons for this approach were: (1) The smaller the area under study, the greater the need for quality data; (2) The specimen-data at quarter degree square level is data-based for Namibia, but was not available for this study, and even if it were, correcting this database would have been a formidable task. Errors in these data become obvious when mapping at the species level. Previous use of this database did, however, provide necessary experience for this exercise; (3) Many species have narrow ranges resulting in a "busy" dataset, which is more difficult to scrutinize as seen in the numerical analysis of the Kaokoveld centre of endemism (Craven 2009, Chapter 6); (4) 30 years of field work experience in Namibia has contributed greatly to the formulation and review of these proposed groupings. Boundaries between groupings have been verified in the field and field trips to Angola and other neighbouring countries have contributed to a greater understanding of such patterns; (5) by defining these areas, a comparative dataset is made available for future evaluations and studies.

### **Definitions:**

**Floristic regions:** areas of similar floristic composition

**Floristic elements:** groups of taxa that have similar geographical distributions.

## **5.2 Materials and methods**

A modified (updated) version of the database used in earlier evaluations by Craven (2002, 2005, 2009, Chapter 7; Craven & Vorster 2006) formed the basis for this analysis. The arrangement of taxa, accepted concepts, and numbers follow this database (Craven & Kolberg on-going). The numerous data fields include, amongst others, distribution both inside and outside Namibia, endemic status, phylogenetic studies and palaeo-environment evidence. Both for the systematics and phytogeographic data, the most important sources were floras, monographs and web pages such as the African Flowering Plants Database that includes distribution maps of southern African species.

Although extensive datasets were devised, cleaned and evaluated during research for the Succulent Karoo Ecosystem Planning Strategy (SKEP 2002), Sperrgebiet programme (Burke 2002), and for the development of maps for the Namibian Atlas (Mendelsohn *et al.* 2002), they were not available for this study. Views and opinions that germinated during the first author's involvement in these initiatives, and experience gained, provided the background, that has here been substantiated from available sources. The numerical analysis of northwest Namibia (Craven 2009, Chapter 6) also provided impetus for this evaluation, as the results drew attention to areas with congruent patterns of distribution. ArcView (ESRI 2000) and DIVA GIS (2007) systems were used for overlaying shape files of both taxa and physical features for evaluation. Shape files were obtained from the Atlas of Namibia Project (2002).

Not all maps collected over the years were geo-referenced or digitized due to time constraints, so hard copies were manually assessed. This was possible because of extensive background knowledge of Namibia, as well as an understanding of potential problems. Initial general field work throughout the country later became more focused in order to clarify problem areas. The ability to visit areas regularly irrespective of the season allowed for manual adjustment of borders, many of which may appear skewed after abnormally good rain or dry years. Once the floristic areas, defined by recurrent patterns of distribution, were identified, information on the physical environment was obtained from the Atlas of Namibia (Mendelsohn *et al.* 2002) and incorporated. Each district was based on representative example taxa which were subsequently mapped.

Species with ubiquitous or near-ubiquitous distributions, or scattered ranges were excluded, as were taxonomically uncertain species, hydrophytes and parasites. Not all the nearly 4000 species and infraspecific taxa of higher plants indigenous to Namibia were analysed, but a remarkable number portrayed recognizable distribution patterns and could be used in the analysis. Main problems encountered included the lack of specialist studies on large numbers of Namibian taxa, a concentration of work on select groups (often without access or use of Namibian material) and limited representation of Namibian taxa in taxonomic studies because of insufficient floristic exploration.

### 5.3 Results

The following nine floristic Groups were identified within the Namibian Flora:

#### 5.3.1 *Welwitschia*-desert Group

This Group was based on the distribution of *Welwitschia mirabilis*, *Adenia pechuelii* and the *Zygophyllum orbiculatum/stapffii* complex (Figure 5.3.1). The two *Zygophyllum* species occur from southwestern Angola (Namibe to just east of Iona) to the Kuiseb River, like *Welwitschia*. At present one is considered to occur north of the border and the other south of the Kunene River, however they may prove to be the same species (Bellstedt pers. comm.). *Adenia pechuelii* extends from just north of the Kunene River southward as far as the Nubib Mountains, and east of the sand desert [23° S, 15° E]. The area is bordered by the Atlantic Ocean in the west and stretches eastwards to the northern escarpment or the 900 m contour where the escarpment is absent between the Huab and Kuiseb Rivers. The altitude ranges from sea level to 900 m. Numerous western flowing non-perennial rivers cross this area. The 900 m contour is noticeably further inland in the course of the Hoarsib and Ugab Rivers. The terrain varies from coastal sand, gravel plains to hills, rocky outcrops and inselbergs. The climate is influenced by the cold Benguela current that flows northwards along the coast, bringing misty conditions that penetrate 60 km inland (and even further up water courses). The area experiences summer rainfall and strong, hot, dry easterly winds, alternating with cold, moist westerly winds. No higher plants have been shown in this region to take up fog moisture directly, but many plants near the coast derive most of their fresh water from dew or fog that condenses on the plant or substrate and moistens the area below the plant.

The most speciose families include the Acanthaceae, Leguminosae and Poaceae. The distributions of over 200 species correspond with these three examples. Of these, more than 100 species are endemic to Namibia and an additional 55 only co-occur in Angola. One family Welwitschiaceae is endemic. Besides genus *Welwitschia*, there are six endemic genera, namely *Arthraerua*, *Dewinteria*, *Kaokochloa*, *Lavrania*, *Phlyctidocarpa* and *Streptolophus* (in Angola only). The monospecific and very localized genus *Lavrania* is probably part of this Group, as it lies just west of the escarpment. *Eremiolirion* may also be included in this Group. Although it has been collected near the Etosha Pan in good rain years (e.g. 1963 and 1973), it is most commonly collected from south of the Huab River. It has also been collected on the SW coast of Angola. *Petalidium* (Acanthaceae), *Commiphora* (Burseraceae), *Stipagrostis* (Poaceae) and *Salsola* (Chenopodiaceae) are the most species-rich genera within this Group. *Merremia* (Convolvulaceae) includes three endemic species, while the Euphorbiaceae and Asteraceae both include at least 10 endemic species. The Amaranthaceae, usually known for its weedy species, includes 4 endemic species. Two of these are

perennial members of *Marcellioopsis*, with the third species in this genus being an annual found in the Kaoko Group (defined below).

Most species in this Group are confined here or extend only into southwestern Angola. The few species that occur elsewhere, such as *Sterculia quinqueloba* (Garcke) K. Schum., *S. africana* (Lour.) Fiori and *Senna italica* Mill. extend northward into Africa. Species often considered characteristic of this area, e.g. *Acanthosicyos horridus* Welw. ex Hook.f. and *Cladoraphis spinosa* (L.f.) S.M. Phillips, have disjunct ranges between Angola and the Cape (South Africa), because they favour coasted sandy patches. A few species appear to have disjunct distributions with the south, particularly the Hunsberg areas, however, as with *Dauresia alliafolius* (O.Hoffm.) B. Nord. & Pelsner, the southern specimens may be recognized as a different species after revision. *Tribulocarpus dimorphanthus* is one of the few species with disjunct distributions in NE Africa. It also ranges eastwards partially out of the area of this Group. Although some species occur throughout this area, there is a coastal strip populated by species like *Arthraerua leubnitziae* (Kuntze) Schinz, *Brachiaria psammophila* (Welw. ex Rendle) Launert, *Ectadium rotundifolium* (H. Huber) Venter & Kotze, *Mesembryanthemum kuntzei* Schinz, *Stipagrostis hermannii* (Mez) De Winter, and the *Zygophyllum orbiculatum/stapffii* complex. The species composition of the inner drier section tends to differ from those found in the fog zone and a number of species are limited to hills or inselbergs. A significant number of species occur south of the northern escarpment and extend further inland. These include, for example, *Aloe asperifolia* A. Berger, *Barleria solitaria* P.G. Mey., *Blepharis gigantea* Oberm., *Commiphora kraeuseliana* Heine and *Sarcocaulon marlothii* Engl. The eastern extensions of the ranges of some species, such as *Welwitschia mirabilis* near the Petrified forest, as well as in the vicinity of Orupembe, is undoubtedly due to sea mist penetrating further inland up westward flowing river catchments and where the escarpment poses no physical barrier .

Although the Brandberg Mountain lies within the area of this Group, the plants found on the upper parts of this mountain are included in the Highland Group (3) (defined below). Species from the Welwitschia-desert Group are mainly confined to its lower slopes, although a few, such as *Adenia pechuelii*, may occur higher in the west. The northern side (e.g. at Sonsusib) have more species occurring at higher altitudes than the southern side, for example *Hibiscus castroi* Baker f. & Exell.

Life strategies for coping with this environment are varied. Many species are short-lived, non-woody plants that evade harsh conditions by concentrating growth and reproduction in periods after good rains, even if this occurs only a few times during a decade. Almost an equal percentage of

species are dwarf shrubs or shrubs with varying attributes like deciduous succulent leaves (*Zygophyllum orbiculatum/stapffii*) or rodlike stems (*Arthroerua leubnitziae* and *Euphorbia damarana* L.C. Leach). Another adaptation is for the plants to remain leafless under adverse conditions, for example in *Adenolobus pechuelii* (Kuntze) Torre & Hillc., the young stems of which are covered in a blue-green bloom caused by a protective powdery coating. Many genera are dioecious, including *Adenia*, *Commiphora* and *Welwitschia*.

### 5.3.2 Kaoko Group

This Group is based on the distribution of *Sesamothamnus guerichii* (Engl.) E.A. Bruce (Figure 5.3.2), and extends from Benguela in Angola in the north to about 20° S and 15° E in the south. The western limit is the escarpment and the eastern border coincides with the 1500 m contour and the Karstveld. This Group does not go as far south as the Welwitschia-desert Group (1), but some species such as *Cissus nymphaeifolia* (Welw. ex Baker) Planch., *Pachypodium lealii* Welw. and *Stigmatorhynchus hereroensis* Schltr. extend to the 19° E longitude following the 1500 m contour. The altitude ranges between 1200 and 1500 m, except just south of the Kunene, where mountains reach a height of 1800 m (Baynes and Otjihipa Mts). The Kunene River catchment area is in the north, but no other rivers influence the area. Rainfall is in summer, with about 200 mm in the west and up to 350 mm in the east, and there is no frost in winter.

The distributions of more than 150 species are congruent with *Sesamothamnus guerichii*. The most speciose family is the Acanthaceae, followed by Leguminosae, Euphorbiaceae and Asteraceae. There are also at least 6 Lamiaceae species included in this Group. The only member of the Araliaceae (*Cussonia angolensis* (Seem.) Hiern.) present in Namibia is found here. Although *Bayensia* represents the only endemic genus, more than 40 species are endemic to Namibia and a further ca. 60 are also found in southern Angola. Species that also occur outside Namibia and Angola occur in South Tropical Africa and/or further north in Africa. *Lepidagathis scariosa* Nees stretches to India, *Ormocarpum kirkii* S.Moore is found in Africa and *Acacia mellifera* (Vahl) Benth. subsp. *mellifera* extends as far as the Middle East. A number of mainly tree species occur in this area and again in the Caprivi, e.g. *Euphorbia matabelensis* Pax, The taxa *Manilkara mochisia* (Baker) Dubard and *Pterocarpus rotundifolius* (Sond.) Druce subsp. *rotundifolius*. *Elaeodendron transvaalense* (Burt Davy) R.H. Archer and *Acacia ataxacantha* DC. are examples of disjunctions to the Kavango. *Spirostachys africana* Sond. also has a disjunct distribution to the east, but the form in the Kaoko Group is considered different. Other disjunct distributions are found with southern Namibia e.g. *Leucophrys mesocoma* and *Searsia leptodictya* with south tropical Africa and eastern South Africa.

Concentrations of species can be identified within the outlined zone. The Kunene River in this area is home to species like *Ficus capreifolia* Delile, *Hexalobus monopetalus* (A. Rich.) Engl. & Diels and *Salix mucronata* Thunb. subsp. *subserrata* (Willd.) R.H. Archer & Jordaan that are also found in other parts of Africa, and *Rhinacanthus kaokoensis* K. Balkwill & S. Williamson, which is expected to occur more widely, but presently only known from this region. Many range restricted species are found in the mountains in the north. They vary from succulents such as *Baynesia lophophora* Bruyns, *Aloe corallina* I. Verd., *A. kaokoensis* Van Jaarsv., Swanepoel & A.E. van Wyk and *A. omavandae* Van Jaarsv. to tree species such as *Sesamothamnus benguellensis* Welw. and *Maerua kaokoensis* Swanepoel to shrubs like *Hibiscus merxmulleri* Roessler. Most of these range restricted species also occur in Angola or are expected to do so. There are a few species (e.g. *Schrebera alata* (Hochst.) Welw.) that occur more widely in tropical Africa, but they are restricted to mountains.

A number of species extend further east into the Karstveld, for example *Opilia campestris* Engl. and *Kirkia acuminata* Oliv., both of which also occur in other parts of Africa. The distributions of some species overlap with the Welwitschia-desert Group (1), and more habitat details (altitude, aspect, etc) are needed for better placement. These include, for example, *Ceraria longipedunculata* Merxm. & Podlech and *C. kaokoensis* Swanepoel, both of which are currently placed here with *C. carrissoana* Exell & Mendonça, which conforms to the distribution of this Group within Angola. A similar example is *Acacia montis-usti* Merxm. & A.Schreib., named after the Brandberg Mountain, but not included in the Highland Group (3), which contains the Brandberg Mountain, as it is found mainly in the Kaoko Group, especially in Angola and it does not occur on the higher parts of the mountain. The range of this species is thought to correlate with the distribution of granite and also occurs on granite outcrops in the 2014° grid square.

Craven (2009, Chapter 8) discusses the taxonomy and distribution of taxa in Angola included in this Group and the problems associated with the data. More information on, for example, altitude preferences and updated taxonomies of many species is needed before more accurate assessments of this Group can be made. Interestingly, some species occur further west once they have crossed the Kunene River or *vice versa*. Kaoko endemics like *Rhigozum virgatum* Merxm. & A. Schreib. spread eastwards in Angola, while *Megalochlamys marlothii* (Engl.) Lindau and a number of *Commiphora* species extend westwards across this border. The main boundaries between the Kaoko and Welwitschia-desert Groups appear to be altitude and their respective relationships to adjacent floras.

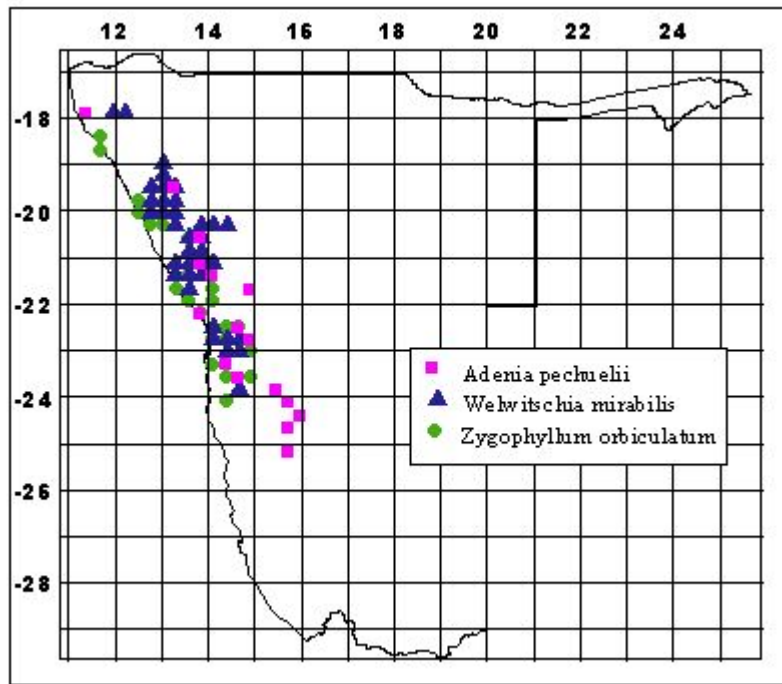


Figure 5.3.1. Welwitschia-desert Group

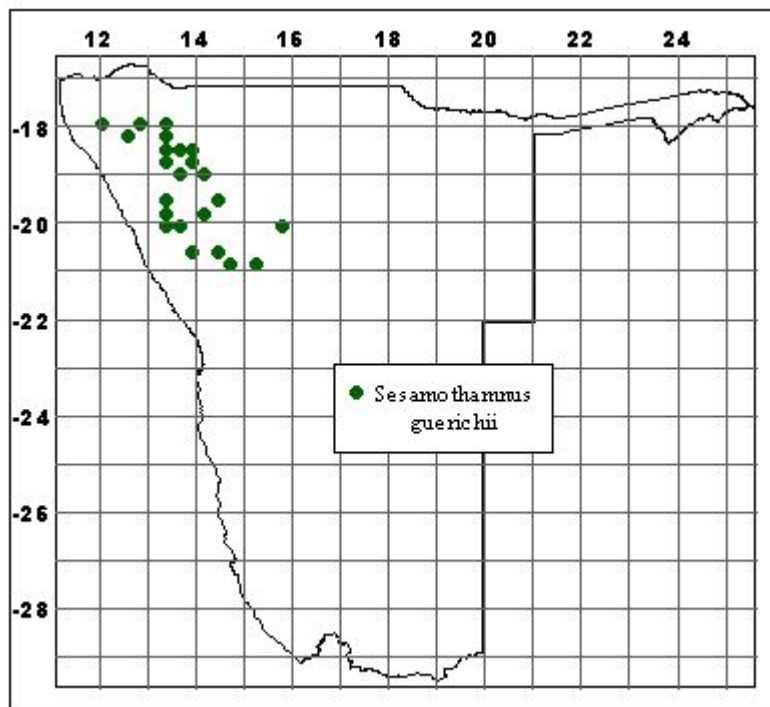


Figure 5.3.2. Kaoko Group



### 5.3.3 Highland Group

The range of this Group is exemplified by *Lightfootia dinteri* Engl. ex Dinter. (Figure 5.3.3), a species that still has to be transferred to the genus *Wahlenbergia*. Publication of the new name, *W. intricata* (Dinter & Markgraf) Craven is in preparation. The distribution pattern of the group is disjointed and irregular, because the Highland Group consists of species confined to upper reaches of mountains or highland areas higher than 1500 m (or perhaps even 1700 m) in altitude. Hilliard (1994) included the Brandberg, Erongo, Khomashochland, Auas, Gamsberg, Naukluft, Tiras and Karasberge in a central and southern highland centre, but further collecting has shown that some species (e.g. *Manuleopsis dinteri* Thell.) are also found on ranges further north, such as in the Kaokoveld and Otavi-Waterberg. In the south, species have also been found at Aus and occasionally on the Hunsberg. They are not found in the Southern Namib succulent desert (5) or the north east (9; Zambezian Domain of White 1983). Over 200 species have been tentatively placed in this Group, but much still needs to be done to define the limits as well as the altitude, habitat requirements, substrate preferences and affinities of the comprising species.

The most speciose family is the Asteraceae, followed by Apocynaceae and Scrophulariaceae. At least 20 grasses are known only from mountain tops, with a few having distribution extensions to north Africa and even India. There are a number of endemic or highly localized Mesembryanthemaceae in the highlands, e.g. *Ebracteola montis-moltkei* (Dinter) Dinter & Schwantes and species of *Lithops*. Endemic genera include *Namacodon*, *Manuleopsis*, *Chamaegigas* and *Dintera*. Most of the highest mountains have their own endemic species, but they are also linked by other range restricted and more widely distributed species. *Aloe viridiflora* Reynolds, for example, occurs on the Brandberg and Gamsberg and *Namacodon schinzianum* (Markgr.) Thulin is known from the Erongo, Gamsberg and Naukluft mountains. *Manulea dubia* (Skan) Overkott ex Roessler is found on the Brandberg, Karasberg, Tiras, Waterberg, Auas areas as well as at Aus.

Numerous species with disjunct distributions in eastern parts of South Africa have been recorded within this Namibian Group. *Chasmatophyllum musculinum* (Haw.) Dinter & Schwantes occurs on the Karasberg and in the Free State. *Cymbopogon dieterlenii* Stapf ex E.Phillips, *Plectranthus dinteri* Briq., *Seriphium plumosum* L. and *Dicliptera eenii* S.Moore are disjunct to the Limpopo and Free State Provinces. *Passerina montana* Thoday is found on the Auas Mountains and Huila in Angola and further east in South Africa. The genus *Cineraria*, an essentially African genus, with its centre of diversity along the eastern highlands of Africa to Ethiopia, is a good example of this

Group. It is known from the mountainous areas of Namibia and southern Angola, and up to much higher altitudes in the mountains of tropical East Africa and the Drakensberg range in South Africa (Cron *et al.* 2008).

Life forms vary, but a surprising number on the highest parts are localized succulents belonging to the Apocynaceae, Crassulaceae and Euphorbiaceae, which if not endemic are likely only to be found further eastward. The Otavi/Waterberg group has more annuals or trees, while the central and southern highlands have more dwarf shrubs.

This Group could be split on the basis of altitude and relationships, with highveld or plateau species having relations with the highveld of eastern South Africa and montane parts that are more closely related to the Angolan highlands and the great Escarpment, as indicated by *Passerine montana*. A cut-off at a specific altitude would, however, be difficult to maintain, because slightly lower elevations occur in some places and also because elements of other Groups, e.g. *Gordonia* (7), occur on the lower parts.

#### **5.3.4 Namib-dunes Group**

This Group follows the distribution of *Hermannia minimifolia* Friedr.-Holzh. (Figure 5.3.4). It consists of a small number of species that grow on sand dunes from the Kuiseb River in the north to the Koichab River (at about the latitude of Lüderitz) in the south, and includes Sossusvlei. It excludes a very narrow coastal strip occupied by species from the Southern Namib succulent desert Group (5). The area is 100 to 150 km broad and has a maximum elevation of 900 m. A few isolated mountains and hills occur in the main Namib sand sea, for example the Hauchab and Uri-Hauchab, with the highest point being 1327 m above sea level. Linear dunes running roughly south to north dominate the inland areas. The reflectivity of the soil is very high, and rain is recorded as being during summer. The eastern border is a narrow section of Namib plains leading up to the southern escarpment. The Tsauchab and Tsondab Rivers extend a part of the Namib plains westwards into the sand sea. These rivers and the Tsaris (also known as the Duwisib) River disappear under the sand and never reach the sea. The most representative family in this Group is the Poaceae, while single species of the Aizoaceae, Geraniaceae and Pedaliaceae are included. Species include *Stipagrostis seelyae* De Winter, *Sesamum abbreviatum* Merxm., *Monsonia ignorata* Merxm. & A. Schreib. and *Trianthema hereroensis* Schinz. The majority of the included species are endemic. The area itself is homogenous and no subdivision of species composition is seen, but a few species (e.g. some legumes and *Hexacyrtis dickiana* Dinter) have disjunct distributions in sandy areas elsewhere.

When these are in the south, the species are likely to be found in the Northern Cape Province of South Africa. All species have perennial life forms, either herbaceous or as dwarf shrubs.

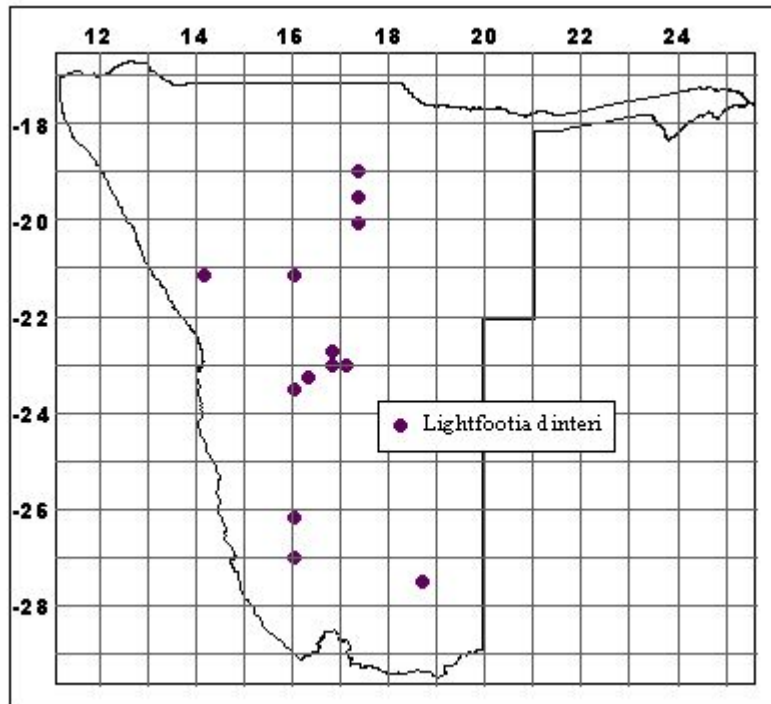


Figure 5.3.3. Highlands Group

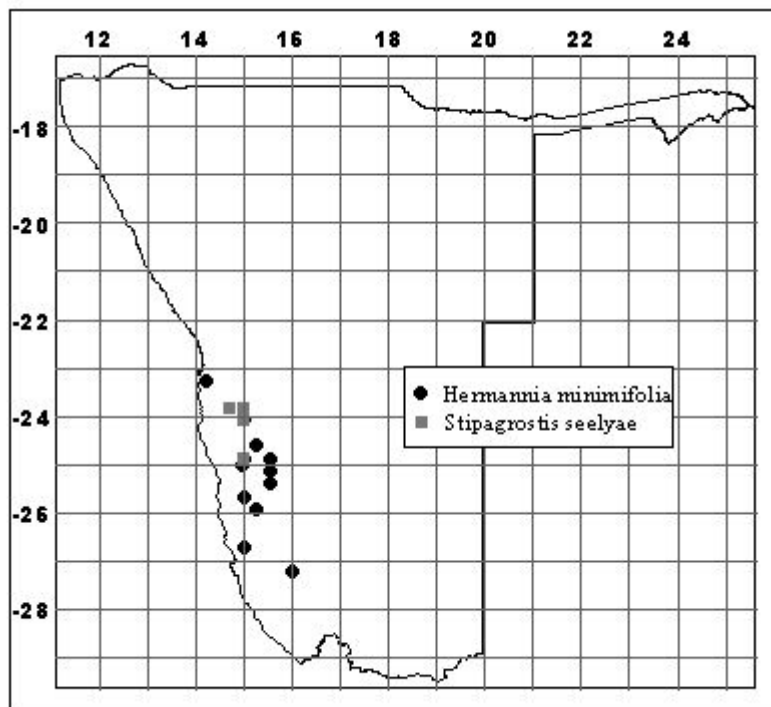


Figure 5.3.4. Namib-dune Group

### 5.3.5 Southern Namib succulent desert Group

The range of this Group is displayed by species such as *Eberlanzia clausa* (Dinter) Schwantes, *Monsonia deserticola* Dinter ex R. Knuth, *Pteronia pomonae* Merxm. and one species, *Limonium dyeri* Lincz., which is confined to the coastal strip (Figure 5.3.5). This Group starts south of the sand sea, i.e. from the Koichab River, extending southwards to the Orange River, with a very narrow extension along the coast almost as far as the Kuiseb River. It stretches eastwards to the base of the southern escarpment. The altitude varies from sea level to 900 m, except for a few mountains such as Klinghardt and Aurus that reach over 1100 m above sea level. No rivers flow through this area. Although what little rain does fall in this area is reported to fall in winter, Mendelsohn *et al.* (2002) used graphs to show that the average rainfall per month are about the same throughout the year. Fog and strong sand storms are common.

This area required detailed re-evaluation, because of several generalizations that have been made in the past. The word Lüderitz, for example, has been used to refer to both a large district, as well as for the town itself. In many studies, taxa were taken to be part of the unusual succulent flora, without assessment of their actual range or relationships outside of Namibia. Many species require further evaluation and these include a number of species restricted to the Aus and Hunsberg Mountains, which were therefore not included in this Group in this study.

The flora can be divided into four subgroups: (1) a coastal group, where most of the endemic genera occur, (2) an inselbergs group, (3) a group of widespread species and (4) those species confined to the parts just west of the escarpment. The latter group includes species at the Numas Mountain and Witputz, but many could not be evaluated with certainty because of lack of information about their exact localities. East facing slopes, devoid of moisture from the coast, have markedly different vegetation to those on the western slopes that can utilize incoming fog. In addition, while species in this Group have extensions southwest of the border, the Aus and Huns-Orange Group (6) is more likely to be associated with the more eastern parts of the Northern Cape, for example in the Kakamas area.

Over 150 species are recorded for the core area and about 15 species occur only along the coast. It is believed that many more will be added to the core area after further investigation. Only about 10 species are shared by the core area and Aus, and the same number with the Hunsberg Mountain. However, this number increases after a succession of good rain years, as was seen recently on the top of the western parts of the Hunsberg. It had succulent species reminiscent of the Southern Namib succulent desert Group, which was in sharp contrast to the dry 1980s when only longer lived

species associated with the more eastern parts (e.g. *Pachypodium namaquanum* (Wyley ex Harv.) Welw.) were found. The highest percentage of species belongs to the family Mesembryanthemaceae, followed by the Asteraceae, Crassulaceae and Iridaceae. Speciose genera include *Pelargonium*, *Salsola* and *Crassula*. The genera *Namibia* and *Jensenobotrya* are endemic to Namibia and *Eberlanzia*, *Hartmanthus*, *Juttadinteria* and *Psammophora* are endemic to both sides of the Orange River. At least 80 species have not yet been found south of the border and a further 120 are shared with the northwestern Cape. A plant found along the Atlantic coastline, *Spartina maritime* (Curtis) Fernald, also occurs here.

The most common life form is succulence such as is found in the Mesembryanthemaceae. There are also many geophytes and dwarf shrubs, often with succulent leaves or stems. *Didelta spinosa* (L.f.) Aiton and *Ozoroa dispar* (C. Presl) R. Fern & A. Fern. are the only tree-like forms.

### 5.3.6 Huns-Orange Group

This Group occurs in the area that consists of the Hunsberg Huib highlands and the arid mountains along the Orange River to the east. The best examples of species included in the Huns-Orange Group include *Jatropha orangeana* Dinter ex P.G. Mey., *Ruellia aspera* (Schinz) E. Phillips and *Bowiea volubilis* Harv. ex Hook.f. subsp. *gariensis* (Van Jaarsv.) Bruyns (Figure 5.3.6). *Haematoxylum dinteri* (Harms) Harms also belongs to this Group, but it is substrate specific and thus extends a bit further northeast than the rest. *Caesalpinia merxmullerana* A. Schreib., is an example of a species that also occurs on the western side of the escarpment, but in an area where fog does not reach and Southern Namib succulent desert Group (5) species do not flourish. *Indigofera merxmulleri* A. Schreib. and *Indigofera nudicaulis* E. Mey are also included here. They have been recorded mainly from the western side of the Hunsberg, but they occur in habitats with other species from this Group. The altitude varies mainly from 900 m to 1500, with a maximum of 1600 m. The Konkiep and Fish Rivers cross the area, cutting deep valleys across the landscape, while the southern boundary is formed by the Orange River. The climate is infrequently affected by coastal fog that may penetrate up valleys with access to the coast. Rainfall is very low and erratic. At least 70 species are endemic to the outlined area. The biggest difference between this Group and the Southern Namib succulent desert Group (5) is the increase in members of the Acanthaceae, especially those with restricted ranges, and the decrease in members of the Mesembryanthemaceae.

Only a few taxa of each of the following families are present: Asteraceae, Burseraceae, Crassulaceae, Euphorbiaceae, Leguminosae, Scrophulariaceae, Zygophyllaceae, and no family is dominant. Species in this Group generally do not occur in the area of the Southern Namib succulent

desert Group (5). The mountains in this area are also not as high as the mountains of the Highland Group (3) and very few taxa are shared between the two Groups. It is the only area in southern Namibia from where terrestrial orchids have been recorded. Very few grasses are limited to the area and although the numbers of Apocynaceae are lower than in other Groups, one of the most well-known and conspicuous species in the family, *Pachypodium namaquanum*, occurs here. The genus *Ruschianthus* and at least 6 species from other genera are endemic to this Group. A further *ca.* 50 species are restricted to this Group and have extensions eastwards into the Northern Cape Province.

The area also includes a number of species with disjunct distributions, such as *Diospyros acocksii* and *Commiphora namaensis* Schinz that are also found near the Brandberg. It also includes *Wellstedtia dinteri* Pilg., a much-cited example of an arid corridor disjunct species. The most interesting disjuncts are those that co-occur in the Eastern Cape Province, an area known to have both winter and summer rainfall, as is often the case here, although in far more limited quantities. These include *Schotia afra* (L.) Thunb. var. *angustifolia* (E. Mey.) Harv., *Foveolina albidiformis* (Thell.) Källersjö and a species each of the genera *Dioscorea* and *Dodonaea*. Species confined to the banks of the Orange River, e.g. *Maerua gilgii* Schinz, are not listed in this Group, as some may also be found further west and grow on the riverbank, rather than on outcrops near the river. The majority of species in this Group are woody, mostly dwarf shrubs to shrubs. Few have succulent leaves, e.g. *Zygophyllum* spp. and *Portulacaria armiana* Van Jaarsv. Geophytes and herbs are in the minority, along with dwarf succulents such as *Euphorbia lavrani* L.C. Leach and *Ruschianthus falcatus* L. Bolus.

More species from the Aus area appear to be associated with this Group than with the Southern Namib succulent desert Group (5). This may, in part, be ascribed to their relationships outside Namibia which occur in the east and not in the west. The affinity of the flora around Aus needs further investigation.

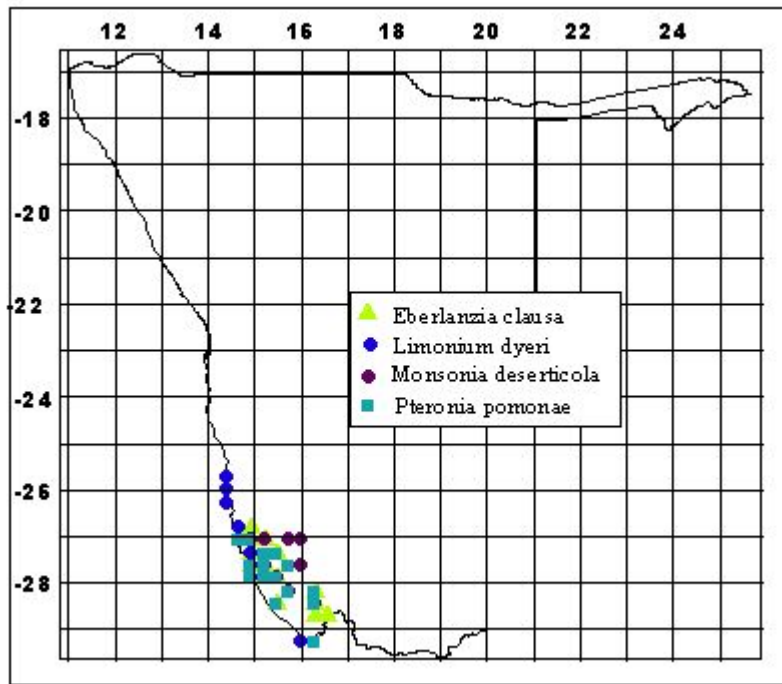


Figure 5.3.5. Southern Namib succulent desert Group

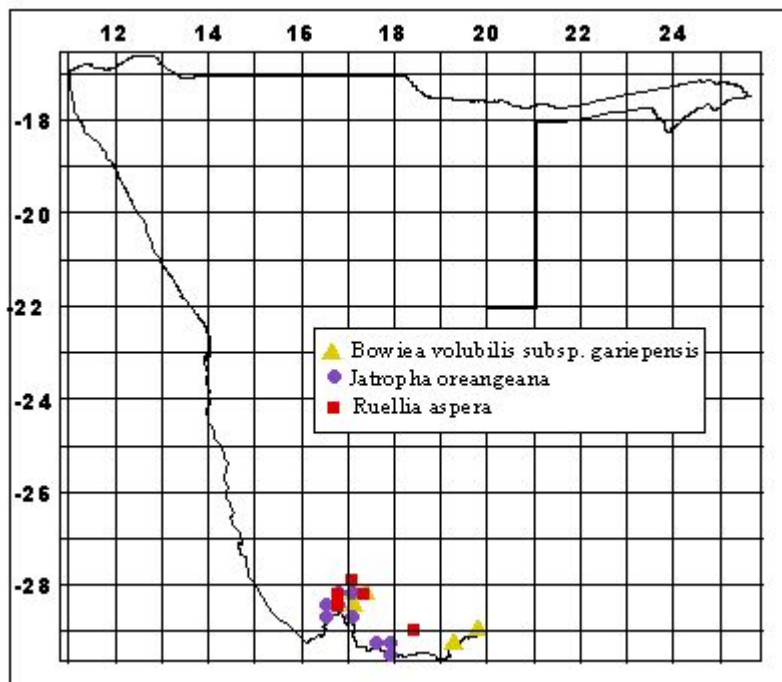


Figure 5.3.6. Huns-Orange Group

### 5.3.7 Gordonia Group

The area of this Group is outlined by the distribution patterns of *Euphorbia friedrichiae* Dinter, *Stipagrostis brevifolia* (Nees) De Winter, *Xerocladia viridiramis* (Burch.) Taub. and *Zygophyllum rigidum* Schinz (Figure 5.3.7). A number of species also extend northwards and their ranges match that of *Phaeoptilum spinosum* to some extent. This Group also corresponds to the Karoo-Namib region of Volk (1964, 1966), but with altitude a determining factor, in that species only occur at lower elevations (up to 800 m above sea level). *Phaeoptilum spinosum* occurs on the fringe of the northern escarpment, extends through the area between the north and south escarpments and then to an area east of the southern escarpment. It basically follows the rainfall isohyets of less than 300 mm annually. This pattern is also seen in the distribution of *Parkinsonia africana* Sond..

The southern border of this Group is the Orange River, but the hilly parts along the river are included in the Huns-Orange Group (6) and the Karasberg are included in the Highland Group (3). The small, often quartzitic outcrops are included in this Group. The Kalahari-sand Group (8) occurs in the east and the Hunsberg Mountains in the west. The altitude varies from 900 to 1200 m. The area basically lies within the catchment of the Orange River and non-perennial rivers like the Gamkab and Löwen, while the upper reaches of the Konkiep and Fish Rivers cross this area as well. The area includes more pans and brackish areas than any of the other Groups. Rain falls in summer, but surprisingly the most humid month is given by the Atlas of Namibian (Mendelsohn *et al.* 2002) as June. Although the species diversity is low, there are at least 75 species present in the area, most with extensions into the Kakamas, Upington, Kenhardt and Prieska areas of the Northern Cape Province and perhaps even as far as the Free State. Included in this distribution are *Lapidaria*, *Schwantesia* and *Titanopsis* species. The most speciose families are the Acanthaceae, Chenopodiaceae, Poaceae and Sterculiaceae, along with a few members of the Asteraceae, Euphorbiaceae Geraniaceae and Leguminosae. Members of the Mesembryanthemaceae and Crassulaceae are generally confined to the quartz outcrops and pebbles. Succulents like *Conophytum friedrichiae* (Dinter) Schwantes, *Dinteranthus* and *Lapidaria* species differ from those in the Southern Namib succulent desert Group (5) and are generally range restricted. Three *Monsonia* species occur in the Gordonia Group, namely *M. luederitziana* Focke & Schinz, *M. parviflora* Schinz and *M. trioloba* Kers. Other genera that are well-represented here are *Hermannia*, *Monechma*, *Salsola*, *Stipagrostis* and *Zygophyllum*. There are also groups of species associated with pans, for example in the Hardap/Helmeringhausen region (e.g. *Crinum paludosum* Dinter ex Overkott) and brackish substrates (e.g. *Tetragonia schenckii* (Schinz) Engl.). The most common habit is dwarf shrubs or shrubs without succulent leaves, with some species such as *Tetragonia schenckii* and the *Salsola* species representing notable exceptions.



### 5.3.8 Kalahari-sand Group

This Group is characterized by *Acacia haematoxylon* Willd., *Neuradopsis austro-africana* (Schinz) Bremek. & Oberm. and *Helichrysum arenicola* M.D. Hend. (Figure 5.3.8). Botswana lies in the east and the Group borders the Gordonia Group (7) in the south, where a fair number of species overlap, including for example *Petalidium linifolium* T. Anderson. Kalahari sandveld is also found in north east Namibia, but it is separated from this Group by a westward extension of the Komashochland Plateau and in having a distinctly different climate characterized by higher rainfall, less frost and higher minimum temperatures. The Weissrand Plateau, which is floristically very under-explored, forms the southwestern border of the Kalahari-sand Group. This Group occurs at an altitude that varies from 900 to 1500 m. Rivers flowing eastwards include the Nossob, Olifants and Auob. Rainfall is in summer. There are only about 10 species limited to this area, but there are a number of sand-loving species, like *Terminalia sericea* Burch. ex DC., which occur here as well as in the Zambesian Domain (9), despite the lower rainfall. Families represented in this Group include the Amaranthaceae, Apocynaceae, Asteraceae, Capparaceae, Chenopodiaceae, Leguminosae, Neuradaceae and Poaceae. The included species often also occur in Botswana and the Northern Cape Province and may also be present in northern Africa (Werger 1983). These disjunct species are not present in the Zambesian Domain (9) and thus placement of them in Karoo-Namib (Volk 1964) is valid.

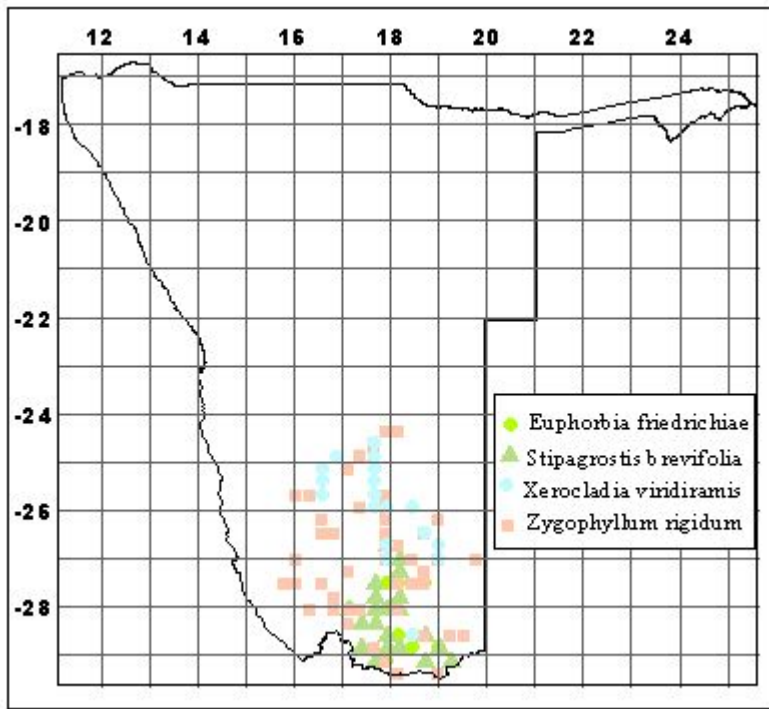


Figure 5.3.7. Gordonia Group

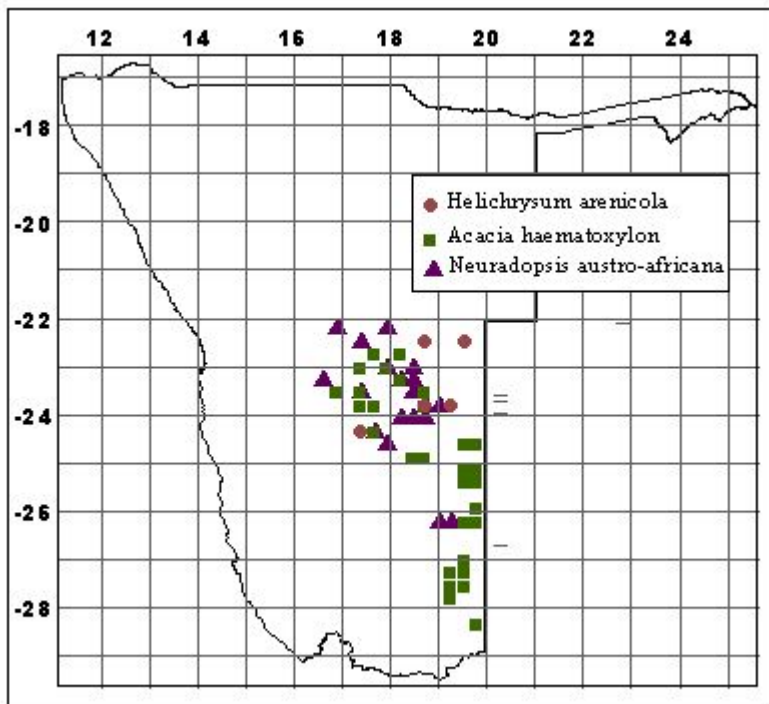


Figure 5.3.8. Kalahari-sand Group

### 5.3.9 Zambesian Domain of White (1971)

This Group coincides with the area outlined by White (1971) as the Zambesian Domain. It includes tropical floral elements (i.e. species with their main distributions in tropical areas of Africa), and can be divided into three based on the distributions of *Burkea africana* Hook., *Terminalia sericea* and plants restricted to the Caprivi. Analysis of which elements belong to the Sudan-Sambesi, Sambezi, or Kalahari elements as outlined by Volk (1964) has not been addressed here. Nor have the species occurring in Namibia that belong to the other African elements, e.g. *Trema orientalis* (L.) Blume from the Guineo-Congolian region or the Batotse Centre of White (1965) with *Baikiaea plurijuga* Harms as an example.

### Floristic Map

The areas occupied by each Group are outlined and mapped together in Figure 5.3.9.

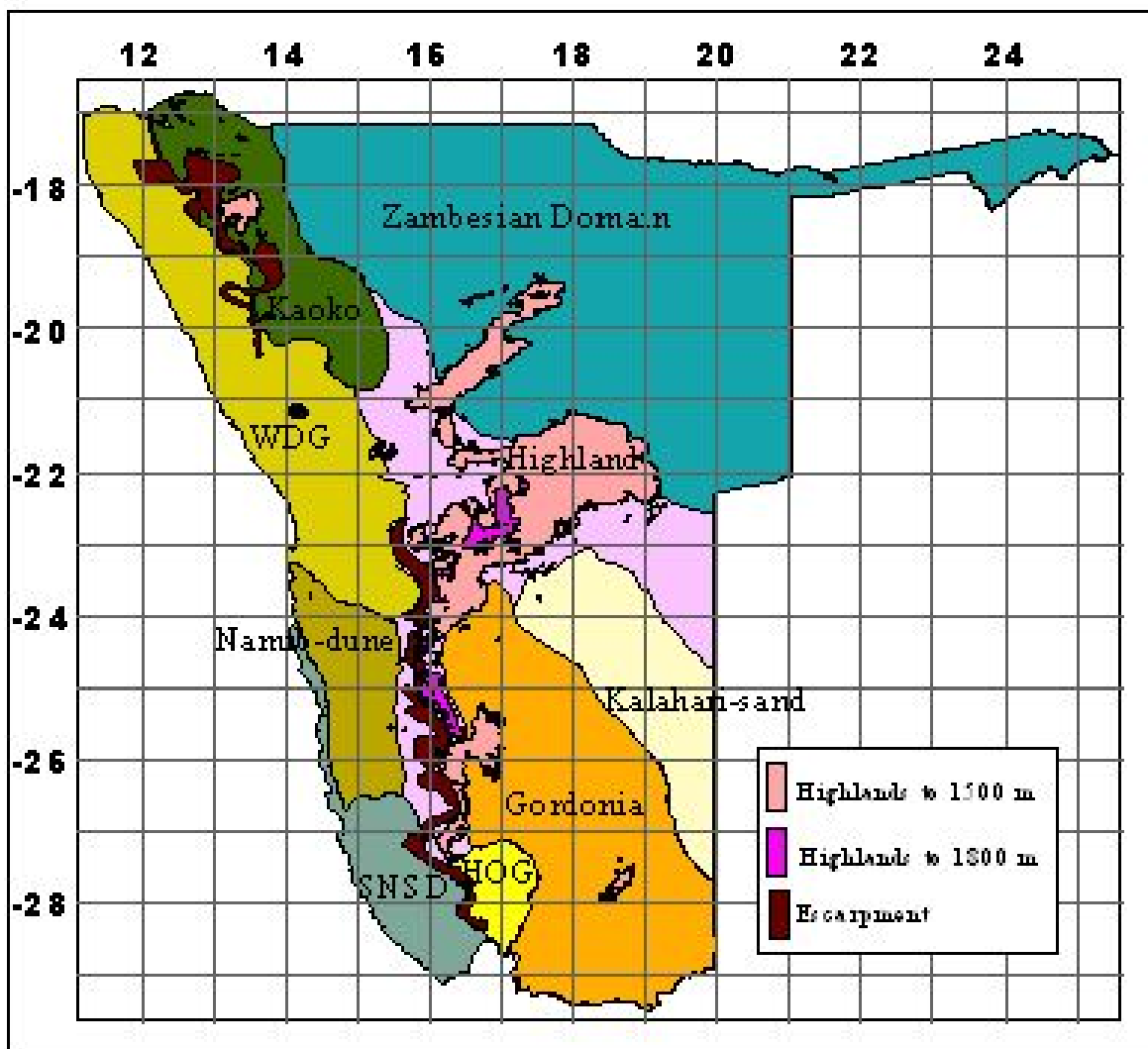


Figure 5.3.9. The nine floristic Groups identified within the Namibian flora based on distributions of species

## 5.4 Discussion

One of the objectives of floristic analysis is the identification and classification of floristic elements and their corresponding areas (Stott 1981). Results of this work have achieved this objective for Namibia, as areas based purely on congruent species distributions have been identified. Evaluation of these areas showed a remarkable number of physical attributes that correspond to these areas. Examples include: a) The disjunct distributions of the Highland Group (3) were found to correspond to mountain tops. b) Where the escarpment breaks down in central Namibia, species such as *Welwitschia* in the Welwitschia-desert Group (1) can be found further inland. c) The eastern extensions of Kaoko (2) species follow not only the karstveld, but also the contour lines. Although boundaries between Groups are sometimes fuzzy due to lack of detail, a high enough percentage of species is recorded within a specific area to be able to draw a provisional border. Outlines often included river catchments, for example the area covered by the Gordonia Group (7) is the same as the Orange River catchment in Namibia.

There are few taxa associated with South American in the Namibian flora, but when present they seem to be associated with northwestern Namibia. In addition a number have NE-SW African distributions indicative of the arid corridor (Craven 2009, Chapter 4). The study of Bellstedt *et al.* (2008) shows repeated migration of *Zygophyllum* species from southern African to the arid areas in the Horn of Africa and Asia that *Z. orbiculatum* and *Z. stapffii*, which are important endemics to the Welwitschia-desert Group (1), are the earliest diverging taxa in genus *Zygophyllum*. The number of endemic genera in this Group, many of which are small, also supports the opinion that this is a unique area of considerable age. Robinson's (1975–77) contention that no species confined to this Group has extensions in the Karoo-Namib region is confirmed here. It is interesting to note that the southern boundary of the Welwitschia-desert Group (24° S) is also the limit found by Holm (1990) based on distribution maps of beetles and three of the species belonging to this Group have their closest relatives in East Africa and Somalia.

Evaluating the affinities of all species confined to an area with their overall ranges, showed particular tracks. When not endemic to the Huns and Aus areas, for example, species do not occur with the succulent flora further west. The Huns-Orange Group (6) has more affinities with the Eastern Cape Province and this was also noticed because of the many misidentified species. *Pegolettia gariiepina* Anderb. in Namibia, for example, was mistaken for *P. baccaridifolia* Less. in the Eastern Cape (Anderberg 1985). Another example is the recently described *Dicoma obconica*

S.Ortiz & Pulgar, which was previously erroneously identified as *D. picta* (Thunb.) Druce, from the Eastern Cape Province (Ortiz & Pulgar 2002). Schrire *et al.* (in press) also noted that the *Indigofera nudicaulis* belongs to a clade with *Indigofera merxmuelleri* that includes species from the Albany area of the eastern Cape of southern Africa.

One of the most interesting results of this study was the indications from a number of different taxa that the Huns-Orange Group (6) may be very old, and it possibly contains the oldest flora of Namibia. Schrire *et al.* (in press) has recently estimated that the age of *Indigofera nudicaulis* to be over 20 Ma and suggests that this species may be the only species of *Indigofera* not belonging to one of the four main subclades in the genus. The next branching species in this study was another endemic to the Huns-Orange Group (6), namely *I. merxmuelleri*. Another example is the subgenus *Moraea*, found in winter rainfall areas, but with several unusual species considered ancient relics found near the Orange-Fish River confluence in southern Namibia. The ancestors of these are thought to have once thrived here when the climate was wetter (Goldblatt 1986). Another species in this Group, *Wellstedia dinteri* Pilg. has a NE-SW disjunct distribution that Thulin & Johansson (1996) proposed dates back to the late Tertiary. Another potential example is that of *Dauresia*, which Pelter *et al.* (2007) identified as the most earliest diverging taxon in the subtribe Senecioninae (Asteraceae). It is presently described as being monospecific with its main distribution within the Kaokoveld Centre of Endemism. However the few specimens known from the Hunsberg area may be confirmed as a different species. *D. alliariifolia* (O. Hoffm.) B. Nord. & Pelter is sister to another endemic to the Kaokoveld Centre of Endemism, *S. engleranus* O. Hoffm., and to *S. flavus* (Decne.) Sch.Bip. from southern Namibia.

One of the main problem areas is the Highland Group (3), because of the lack of knowledge of the Angolan highlands (Hilliard 1994). No definitive answers or thorough testing with modern procedures will be possible until more is known about this flora and its geographic affinities. The challenges to obtaining this information will, however, be great. Hilliard (1994) noted, for example, that some species such as *Jamesbrittenia heucherifolia* (Diels) Hilliard are montane in Namibia, but occur near sea level in Angola. Taxa above 1700 m could be related to the Great Escarpment zone of southern Africa and those above 1500 m to the highlands of the eastern parts of South Africa (Bredenkamp & Van Wyk 2006). It is interesting that Russell & Van Rooy (1986) showed the distribution of the bryophyte flora of the Namibia Highlands region to be concentrated on the highlands as identified here. Like the phytogeographic region in eastern Africa, the Afro-montane region (White 1978), that includes disjunct tops of mountains, this Group is also very difficult to map.

Born *et al.* (2007) describe the area between the Holgat River (located between the Orange River mouth and Port Nolloth) and Lüderitz, which is the area of the Southern Namib succulent desert Group (5), as being a “highly specialized flora, adapted to the dry and extremely windy climate that typifies this area”. They also consider it different to the flora of Namaqualand. This confirms the findings of this study, as different species were found in the Southern Namib succulent desert Group (5), the environs of Aus, and the Huns-Orange Group (6). This distinct difference was also noted by Range (1932). The boundary of the Southern Namib succulent desert Group (5), the factors that differentiate it from other Groups, and the fact that the limited rain is not limited to winter, should discourage generalizations about attributing any species in southwestern Namibia to a winter rainfall regime and region. The genus *Monsonia* provides a good example of this. Venter (1983) deduced that precipitation is derived from fog and winter rainfall for three members of the Section *Plumosae* (*Monsonia deserticola*, *M. drudeana* Schinz and *M. ignorata*) all with orthotropous subterrestrial rhizomes, as they occur in the southern part of the Namib Desert. A closer examination, however, shows the three species occupy areas with different rainfall regimes. One species is here included in the Southern Namib succulent desert Group (5), another occurs further inland around Aus and extends southward, while the third is included in the Namib-dunes Group (4) where rain is more likely in March.

Flowering in summer time as opposed to the normal time for winter rainfall taxa is not a sure indication of assignment to this Group. Some winter rainfall Iridaceae from South Africa grow in the summer rainfall area on the northern side of the Orange River (Goldblatt & Manning 1998). Perhaps an excellent indication of the uniqueness of this southwestern corner is the absence of many of the included taxa further north and east. The largest family in this area, the Mesembryanthemaceae subfamily Mesembryanthemoideae, is remarkable for the diversity of life and growth forms (Klak *et al.* 2007). They are believed to have diversified very recently and rapidly and estimated to be between 3,8 and 8,7 million years old (Klak *et al.* 2007).

The occurrence of coastal deserts along the western shore of most continents is well-documented and the Namib Desert along Namibia’s coast is no exception. The divisions of the coastal strip resulting from this study differ from previous evaluations, for example those of Giess (1971), because of being based purely on congruent distribution ranges of higher plant species. The most noticeable difference lies in the succulent vegetation in the southern part being separated from the *Welwitschia* desert Group (1) species by taxa confined to the sand dune habitat.

The Sahara Desert and Namibia are the regions in Africa with the most variable rainfall (Mendelsohn *et al.* 2002). Frequent shortages of rain are normal and total rainfall in some years may be several times greater than the amounts received in other years (Du Pisani 2001). For this reason it is necessary to consider floristic Groups as the norm over decades, not just based on data gathered over a few seasons. Unusually distributed disjuncts have most often been collected following very good rain years (e.g. 1933, 1964, 1975 and 2008). Another misconception is the idea of “average” rainfall, which is so often correlated with the distribution of a species. The microclimate is often more important than the coarse estimate of “average rainfall” over a given period. Run-off from condensation on granite sheets will account for far more available amounts of moisture than that falling as rain. More research is needed to identify species limited to certain altitudes, substrates or landscapes that have not been researched yet, like the Karstveld, Weissrand plateau and Limestones in the Otavi range. We also require detailed information on microclimatic or habitat preferences of the complete Namibian flora.

Many families show a preference for certain floristic Groups, for example the Acanthaceae (Welwitschia-desert, Kaoko and Huns-Orange), Apocynaceae (Highland and Kaoko), Asphodelaceae (mostly Southern Namib succulent desert), Burseraceae (Huns-Orange, Kaoko, Welwitschia-desert), Chenopodiaceae (Welwitschia-desert and Gordonia), Crassulaceae (Southern Namib succulent desert and Highlands), Geraniaceae and Iridaceae (Southern Namib succulent desert), Mesembryanthemaceae (Southern Namib succulent desert), Poaceae (Welwitschia-desert, Highlands, Gordonia), Scrophulariaceae (Highlands, Southern Namib succulent desert, Huns-Orange) and Sterculiaceae (Gordonia). Although species from the larger families have been used in this floristic evaluation, much is still unknown about many taxa in the Asteraceae, Leguminosae and Mesembryanthemaceae. The monocotyledons are also poorly known, especially families like Hyacinthaceae that are currently undergoing taxonomic revision. Examples of large genera not included because of poor taxonomy are *Aptosimum* (Scrophulariaceae), *Asparagus* (Asparagaceae), *Othonna* (Asteraceae) and *Polygala* (Polygalaceae).

Although the photosynthetic pathways of taxa are not known well enough to make major deductions here, some differences are apparent. In the Southern Namib succulent desert the Mesembryanthemaceae are all believed to utilize CAM photosynthesis, while the grasses employ C3 photosynthesis (Ellis *et al.* 1980). According to Vogel *et al.* (1978) temperate C3 grass genera only occur in the Southern Namib succulent desert Group (5), and the growing season of these temperate species corresponds with the cooler winter months when water stress is not severe. Recent analyses of the contribution of C3 and C4 plants to the food of zebra excavated in the

Apollo 11 Cave on Farm Uitsig, revealed that the proportion of C3 plants in their diet was only slightly higher than at present (Vogel 1983). This questions whether the winter rainfall did, in fact, extend appreciably further northwards in former times (Vogel *et al.* 1978). Plants in the Welwitschia-desert (1) utilize diverse photosynthetic pathways, for example *Zygophyllum stapffii* is C3, while *Welwitschia* has CAM photosynthesis (Von Willert 2005) and *Kaokochloa* C4.

Although some widespread species occur throughout the north, in the centre or south of Namibia, very few extend all the way down the west of Namibia. There are no obviously pan-biogeographical distributions that link these Groups with other areas and they number only a few compared to the other Groups mentioned above. It is probable that their methods of dispersal or other biotic facts may have contributed to these widespread distributions.

Centres of Endemism and Diversity (CPED) in Namibia were covered by Hilton-Taylor (1994a & b); Van Wyk and Smith (2001); Craven (2005) and Craven & Vorster (2006) and comprise different floristic Groups. The Gariiep centre comprises four of the Groups described here, namely the Southern Namib succulent desert, Huns-Orange, the quartz outcrop division of the Gordonia Group and the higher parts of the Karasberg mountains that are included in the Highland Group. The Kaokoveld centre of endemism elements include both the Kaoko and Welwitschia-desert Groups, along with elements of the Highland Group on the Brandberg. The more extensive study of the grouping of taxa with congruent distributions presented here should improve our understanding and definition of the CPED in Namibia in future studies.

A hierarchical arrangement of geographic areas is a useful way of depicting floristic data (McLaughlin 1992). As many names have been used for different concepts and areas in Namibia, new terminology was used for the Groups identified here. The area traditionally believed to receive winter rainfall is called the Southern Namib succulent desert (5) for two reasons. Firstly, Mendelsohn *et al.* (2002) have shown that the average rainfall per month in southwestern Namibia are about the same throughout the year. Secondly, a succulent subgroup of plants occurs just north of Namibe in Angola. This is called the Northern Namib succulent desert in Craven (2009, Chapter 7). Both the Gordonia (7) and Kalahari-sand (8) Groups take their name from Volk (1964). They indicate the close relationships with those areas in South Africa and Botswana. The Highland Group (3) still requires better definition and may be separated into “highlands” and “montane” groups.

A major goal of floristic phytogeography is the classification of regions into floristic areas. These arrangements are often hierarchical (i.e. smaller areas nested within larger ones). Such a system



would only be possible for Namibia if neighbouring countries were studied similarly. Based on present evidence and that of Born *et al.* (2007), a hierarchical arrangement for floristic regions in Namibia is proposed and the inclusion of the southwestern part of Namibia and a narrow strip up the coast in the Succulent Karoo section of the Greater Cape Floristic region by Jürgens (1997) is rejected.

#### The Palaeotropical Kingdom

The Sudano-Zambesian region

Zambesian Domain

The Highveld [The Highland and Kaoko Groups]

The Karoo-Namib region [Gordonia, Huns-Orange and Kalahari-sand Groups]

The Desert region [The Welwitschia-desert, Namib-dunes and the Southern Namib succulent desert Groups]

Reasons why plants occur where they do and clues to their origins were sought by assessing all available phylogenies, palaeoclimate data and vegetation analyses (Craven 2009, Chapter 3 and 4). Very little evidence of value was obtained from the fossil record for Namibia, as it is fragmentary. Published research results on palaeobotanical elements also lack quality input from botanists. Unfortunately there are also very few phylogenies available for Namibia's flora. In their evaluation of the available evidence, Ward & Corbett (1990) attributed the development of the Namib to five main phases that span the last 130 million years. This rather complicated hypothesis does not contribute much to understanding the history of the taxa found in Namibia.

The value of the present study is its future contribution to other research on the Namibian biota. It can serve as a basis, not only for plant biological and conservation studies, but also for studies on all other biological groups. It should also contribute considerably to correct identifications of species, and provides a framework for evaluation of climate change models, palaeo-environmental studies and many others. It will add species distributions as another dimension when modeling future climates change, which is presently based on life form only (Midgley *et al.* 2005). It should help to clarify natural areas and reduce the tendency to use generalizations when referring to, for example, the winter-rainfall region, Sperrgebiet or Gariep.

The study of the Namibian flora, although still incomplete, is making progress. Targeted fieldwork to obtain knowledge of exact distributions, with these floristic areas in mind, is needed. The next step is a regional framework. Data from neighbouring countries on Groups identified in the same way, will be the first step after which floristic regions can be defined.

Every plant species is unique in its distribution and ecology, and despite this, simple explanations are often proposed. Detailed and focused further investigation of the patterns, habitats and diverse other biological features of individual species are still required.

## **5.5 Conclusions**

General patterns of distribution can be distinguished in Namibia and these are a useful means of organizing a different set of information on the flora of Namibia. These floristic divisions are based on recurrent patterns of plant distribution by shared species, which are not necessarily endemic taxa, although a remarkable number of endemic genera and species were found to be limited to certain Groups. The species do not show identical geographic ranges, but rather ranges that coincide because they have similar ecological tolerances, evolutionary histories or both. These patterns have not been linked to historical explanations, however suggestions are made in some Groups.

The contribution made by knowledge of contemporary floras to understanding the past is clearly shown here. Studying the phytogeography of a country rather than a region has its limitations, especially regarding its contribution to the understanding of floristic regions of the world. It is, however, important for the country involved to appreciate what occurs within its borders, and to document and evaluate this. The scale of such a study also allows the incorporation of more details on certain features and it highlights specific data that is still lacking. The principle phytogeographic elements of the Namibian flora have been summarized in an attempt to open the subject for further analysis, especially using numerical or other scientifically recent methodology.

## **5.6 References**

Adamson, R.S. 1958. The Cape as an ancient African flora. *The advancement of Science* 58: 1–10.

African Flowering Plants Database. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, "Retrieved 2007/2008", from <<http://www.ville-ge.ch/cjb/bd/africa/index.php>>.

Anderberg, A. 1985. A new species of *Pegolettia* (Compositae – Inulae) from Namibia. *Nordic Journal of Botany* 5: 57–59.

Atlas of Namibia Project. 2002. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek. <http://www.dea.met.gov.na/>.

Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. and Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.

Born, J., Linder, H.P. & Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147–162.

Bredenkamp, C.L. & Van Wyk, A.E. 2006. Phyto geography of *Passerina* (Thymelaeaceae). *Bothalia* 36: 191–199.

Burke, A. 2002. Implementation strategy for Sperrgebiet Conservation Planning Study. Unpublished Draft. November 2002. Conservation International and Ministry of Environment and Tourism, Windhoek.

Clarke, N.V. & Mannheimer, C.A. 1999. Cyperaceae of Namibia – an illustrated key. *Occasional Contributions* 1. National Botanical Research Institute, Windhoek.

Craven, P. 2002. Phyto geography of the Namibian flora: A taxon approach. Unpublished. MSc thesis, University of Stellenbosch, Stellenbosch.

Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET News* 9: 24–44.

Craven, P. 2009. Chapter 3, this volume. Plant geography in Namibia.

Craven, P. 2009. Chapter 4, this volume. Phyto geographical aspects of the flora of Namibia.

- Craven, P. 2009. Chapter 6, this volume. Demarcating the Kaokoveld Centre of Endemism: A numerical approach.
- Craven, P. 2009. Chapter 7, this volume. Floristic and environmental analysis of the Kaokoveld Centre of Endemism.
- Craven, P. 2009. Chapter 8, this volume. Flora of the Kaokoveld Centre of Endemism.
- Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.
- Craven, P. & Vorster, P.V. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.
- Crisci, J.V. 2001. The voice of historical biogeography. *Journal of Biogeography* 28: 157–168.
- Cron, G.V., Balkwill, K. & Knox, E.B. 2008. Phylogenetic evidence for the generic circumscription of *Cineraria* L. (Asteraceae-Senecioneae). *Taxon* 57: 779–798.
- Curtis, B.A. & Mannheimer, C.A. 2005. *Tree Atlas of Namibia*. National Botanical Research Institute, Windhoek.
- DIVA GIS. 2007. A Geographical Information System for the Analysis of Biodiversity data. International Potato Center (CIP), [www.cipotato.ORG](http://www.cipotato.ORG).
- Du Pisani, A.L. 2001. The idiosyncrasies of Namibian rainfall. *Agricola* 2001: 28–32.
- Ellis, R.P., Vogel, J.C. & Fuls, A. 1980. Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. *South African Journal of Science* 76: 307–314.
- ESRI. 2000. *ArcView 3.2a Software*. Environmental Systems Research Institute, Redlands, USA.
- Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4: 5–114.
- Goldblatt, P. 1986. The *Moraeas* of Southern Africa. *Annals of Kirstenbosch Gardens*. Volume 14.

- Goldblatt, P. & Manning, J. 1998. *Gladiolus in southern Africa*. Fernwood Press, Vlaeberg.
- Hilliard, O. M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Hilton-Taylor, C. 1994a. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.
- Hilton-Taylor, C. 1994b. Centres of plant diversity: Karoo-Namib region: Western Cape domain (Succulent Karoo). In Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 204–217. Oxford University Press, Oxford.
- Holm, E. 1990. Notes on faunas bordering on the Namib Desert. In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 55–60. Transvaal Museum Pretoria.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495–514.
- Klak, C., Bruyns, P.V. & Hedderson, T.A.J. 2007. A phylogeny and new classification for the Mesembryanthemoideae (Aizoaceae). *Taxon* 56: 737–756.
- Levyns, M.R. 1964. Migrations and origin of the Cape Flora. *Transactions of the Royal Society of South Africa* 37: 85–107.
- McLaughlin, S.P. 1992. Are floristic areas hierahically arranged? *Journal of Biogeography* 19: 21–32.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, A. 2002. *Atlas of Namibia: A portrait of the land and it's people*. David Phillip Publishers, Cape Town.
- Midgley, G., Hughes, G., Thuiller, G., Drew, G. & Foden, W. 2005. Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function. Report for *Namibian National Biodiversity Programme*.

- Myers, A.A. & Giller, P.S. 1988. Process, pattern, and scale in biogeography. In: *Analytical biogeography*. Myers, A.A. & Giller, P.S. (eds). Pp. 3–12 Chapman & Hall, London.
- Ortiz, S. & Pulgar, I. 2002. A new species of *Dicoma* Cass. (Asteraceae: Mutisieae) from Namibia. *Botanical Journal of the Linnean Society* 139: 317–322.
- Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Posadas, P. & Donato, M. 2007. Everything you always wanted to know about historical biogeography, but were afraid to ask: A preliminary overview based on papers published in Journal of Biogeography. 2005–2006 *Biogeografía* 2: 1–6.
- Range, P. 1932–38. Die Flora des Namalandes I–XIII, *Feddes Repertorium* 1–13.
- Robinson, E.R. 1975–77. Phytogeography of the Namib Desert of South West Africa and its significance to discussions of the age and uniqueness of the desert. *Palaecoecology of Africa* 67–74.
- Russell, S. & van Rooy, J. 1986. Biogeographical relationships of the Namibian Bryoflora. In: Deacon, H.J. (ed.). Proceedings of the South African Society for Quaternary Research. Stellenbosch 1985. *Palaecoecology of Africa* 17: 201–203.
- Schrire, B.D., Lavin, M., Barker, N.P. & Forest, F. Phylogeny of the tribe Indigofereae (Leguminosae-Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments. *American Journal of Botany* (in press).
- Stott, P. 1981. *Historical plant geography. An introduction*. George Allen & Unwin, London.
- SKEP (Succulent Karoo Ecosystem Planning Strategy). 2002. Conservation International, Cape Town. [www.cepf.net](http://www.cepf.net).
- Takhtajan, A. 1986. *Floristic regions of the world*. University of California Press, Berkeley.

- Thulin, M. & Johansson, A.N.B. 1996. Taxonomy and biogeography of the anomalous genus *Wellstedtia*. In: Van der Maesen, L.J.G., van den Burgt, M. & van Medebach de Rooy, J.M. (eds). *The Biodiversity of African Plants*. Pp. 73–86. Kluwer Academic Publishers, Dordrecht.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Venter, H.J.T. 1983. Phyto geography and interspecies relationships in *Monsonia* (Geraniaceae). *Bothalia* 14: 865–869.
- Vogel, J.C. 1983. Isotopic evidence for the past climates and vegetation of southern Africa. *Bothalia* 14: 391–394.
- Vogel, J.C., Fuls, A. & Ellis, R.P. 1978. The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science* 74: 209–215.
- Volk, O.H. 1964. Die afro-meridionale-occidentale Floren-Region in Südwestafrika. *Beiträge zur Phytologie zu Ehren Prof. H. Walters 65 Geburtstages*. Ulmer, Stuttgart.
- Volk, O. H. 1966. Die Florengebiete von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.
- Von Willert, D.J., Armbruster, N., Drees, T. & Zaborowski, M. 2005. *Welwitschia mirabilis*: CAM or not CAM – what is the answer? *Functional Plant Biology* 32: 389–395.
- Ward, J.D. & Corbett, I. 1990. Towards the age of the Namib. In: Seely, M.K. (ed.). *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 17–26. Transvaal Museum, Pretoria.
- Werger, M.J.A. 1983. Vegetational geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa. *Bothalia* 14: 405–410.
- White, F. 1965. The savanna woodlands of the Zambebian and Sudanian Domains. An ecological and phytogeographical comparison. *Webbia* 19: 651–681.

White, F. 1971. The taxonomic and ecological basis of chorology. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 91–112.

White, F. 1976. The vegetation of Africa - the history of a completed project. *Boissiera* 24: 659–666.

White, F. 1978. The afromontane region. In: Werger, W.J.A. *Biogeography and ecology of southern Africa*. Pp. 463–513. Junk, The Hague.





The Kaokoveld in Southwest Angola



The Kaokoveld in Northwestern Namibia

## **SECTION B**

## Chapter 6

### Demarcating the Kaokoveld Centre of Endemism:

#### A numerical approach

##### Abstract

6.1	Introduction.....	123
6.2	The survey area.....	124
6.3	Materials and methods.....	124
6.4	Results.....	125
6.5	Discussion.....	128
6.6	Conclusions.....	130
6.7	References.....	131

## **Demarcating the Kaokoveld Centre of Endemism: A numerical approach.**

### **Abstract**

Distributional data for over 350, mainly range-restricted species found in northwestern Namibia and the southwestern part of Angola were evaluated numerically to delimit the Kaokoveld centre of endemism. The geographic ranges, in quarter degree squares, were analysed using the TWINSpan software package. Results of the study show, that the distinctive complement of species with congruent distribution patterns (i.e. floristic elements) that are traditionally listed for the Kaokoveld Centre of Endemism (KCE) covered a wider area than usually depicted in maps. In addition some of these species lay marginally outside the core area and would be better described as near-endemic KCE species. Concentrations of taxa in large and smaller subdivisions were also identified.

### **6.1 Introduction**

Quantitative approaches to analyse data are commonly used in plant ecology (especially phytosociology), but less so in historical phytogeography, because the identity and presence of taxa in a given area, and the completeness of species lists for such areas, are often problematic. Numerical analyses, based on species distributions only, have been carried out by for example Pedersen (1990), Moreno Saiz *et al.* (1998), Lawesson & Skov (2002), Van Rooy (2000) (on the moss flora of southern Africa) and Born *et al.* (2007) (who evaluated the delimitations of the Greater Cape Floristic Region including the southern part of Namibia). Numerical phytogeographical analyses of some botanically well-known areas like North America (McLaughlin 1994), included additional features of the taxa in the analyses, because the flora is well documented and additional features and attributes of the plants are readily available. Although numerical techniques have not previously been used in arid areas when based exclusively on locality data, and not supplemented by other features of the flora, the amount of available locality data for the study area suggested that the vaguely defined Kaokoveld Centre of Endemism would benefit from such techniques.

The Kaokoveld has long been considered biogeographically important for both flora and fauna, however its definition and delineation have often focused mostly on a Namibian perspective and depending on the circumscription of the user. The first person to identify the Kaokoveld as a biogeographical centre was Shortridge (1934). In his study, the coastal zone was not included, and the centre stretched from the Kunene River in the north, to as far south as the Ugab River.

Shortridge (1934) considered the area to be “mountainous practically everywhere”. Volk (1964, 1966) was the first phytogeographer to group southwestern Angola with northwestern Namibia. Other subsequent treatments of the area include those of Hilton-Taylor (1994), Van Wyk & Smith (2001) and Craven (2002, 2005), while Nordenstam (1974) and Hilliard (1994) assigned endemic taxa to this area after taxonomic revisions. Steenkamp *et al.* (2005) outlined a Kaokoveld centre based on a numerical analysis, using TWINSpan, of endemic genera. Kers (1967) was the first to note that the distribution range of *Welwitschia*, differed from nearly all the other species enumerated as elements, because it has a considerable distribution in the coastal plains to the west, while most were restricted to the mountainous parts. The name Kaoko has also been used for other phytogeographic units. Jürgens (1991), for example, called an undefined narrow strip the Damaraland-Kaokoland Domain in a phytogeographic evaluation of the Namib (Becker 2002). The result is that this intriguing area, frequently cited as one of Africa’s most species- and endemic-rich areas by the World Conservation Union (IUCN) (Beetjie 1994) needs definition.

In this paper, the geographical ranges of the plant species are evaluated using numerical classification techniques with the purpose of identifying the boundaries and floristic elements (groups of taxa with similar geographic distributions) more precisely and contribute to defining the KCE as a centre with a high concentration of endemics, the elements of which may not necessarily have had similar evolutionary developments (Van Wyk & Smith 2001).

## **6.2 The survey area**

The study area stretches from about 13° S in Angola (i.e. between Namibe/Benguela) to 24° S in Namibia (i.e. the Kuiseb River). The stoneless plains with Kalahari sand, called Karstveld, is more or less the eastern border, around 16° E and the Atlantic Ocean lies in the west. It includes the province of Namibe in Angola and the Kunene and Erongo regions of Namibia. The area was based on the outlines of various authors discussed in Craven (2002a & b, 2005), as well as the area outlined by the distributions of defining elements, like *Welwitschia*.

## **6.3 Materials and Methods**

All the information required for analysis was stored in the ACCESS database of Craven & Kolberg (on-going). This included species known to occur in the study area and georeferencing herbarium specimens, following the grid-reference system of Edwards & Leistner (1971). Using a table created in ACCESS, distribution data in quarter degree squares for each species was entered via

Turboveg 1.97 (International Single User Version, Stephen Hennekens) and Megatab 2.2 (Elsware) into the computer program TWINSPAN (two-way indicator species analysis) (Hill 1979) for numerical analysis. We chose TWINSPAN because it has been shown to be a good method with which to analyse a “complex, noisy, large or unfamiliar” dataset (Steenkamp *et al.* 2005). Other reasons for the choice included its “proven combination of effectiveness, robustness, relative objectivity, availability and speed” (Gauch & Whittaker 1981, Moreno Saiz *et al.* 1998, Van Rooy 2000). TWINSPAN is a divisive hierarchical classification technique that detects overall patterns of differences in biological data (Van Rooy 2000). Default settings were used for all TWINSPAN parameters. This included 428 quarter degree grid squares (subsequently used as relevés). The number of species recorded per relevés is shown in Figure 6.1. The data set contained the grid squares in which seed plants were recorded in the Kaokoveld and surrounds, but underlying specimens were not checked.

Due to the large number of both species and relevés (in this study quarter degree squares) with only one or two entries, the dataset was run in TWINSPAN using different units. Amalgamation and separation of units was done in different ways, for example, squares were joined in one level in order to pin point coastal species. Results of both the original TWINSPAN classification (the widespread) and of some subsequent classifications of subsets (restricted distribution) are presented. A geographic information system (DIVA GIS 2007) was used to overlay abiotic features onto the distribution maps to try and explain the observed patterns. This allowed for proof-reading and correction of errors.

## 6.4 Results

The TWINSPAN classification resulted in five divisions with component species, and they are named here after a representative species (e.g. *Welwitschia*) or area (e.g. Angola and Coast). Two of these divisions (Kaoko and *Welwitschia*) were further subdivided. The five divisions are depicted in Figure 6.2 and the two additional subdivisions in Figures 6.3 and 6.4. They are summarized below, along with examples of diagnostic taxa of each:

1. Kaoko: *Commiphora multijuga* (Hiern) K.Schum., *Sesamothamnus guerichii*
  - 1.1 Kaoko North: *Hoodia parviflora* N.E.Br., *Sesamothamnus benguellensis*
  - 1.2 Kaoko South: *Cyphostemma currorii* (Hook.f) Desc., *Setaria finita* Launert

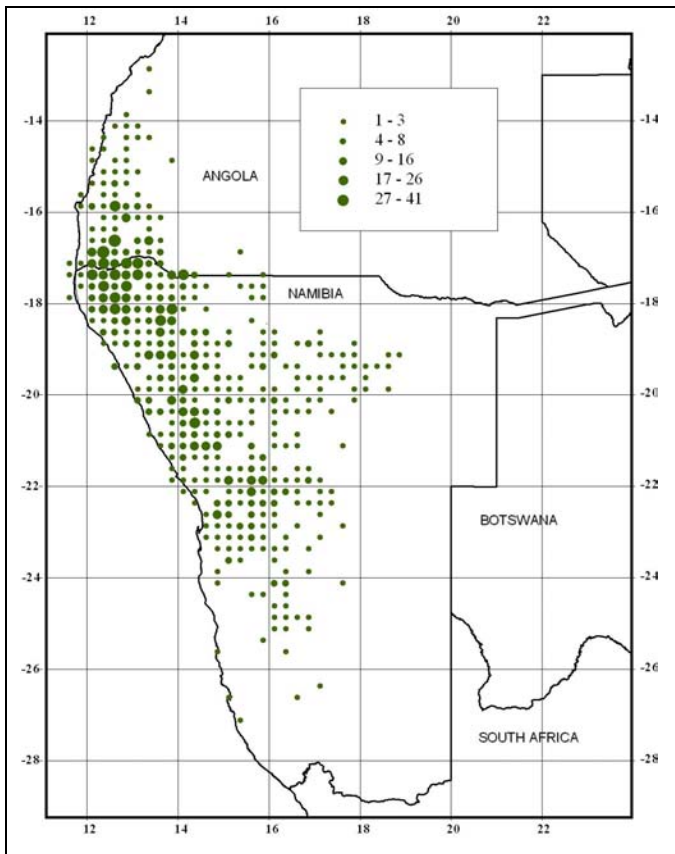


Figure 6.1: The number of species per relevé used in the numerical analysis

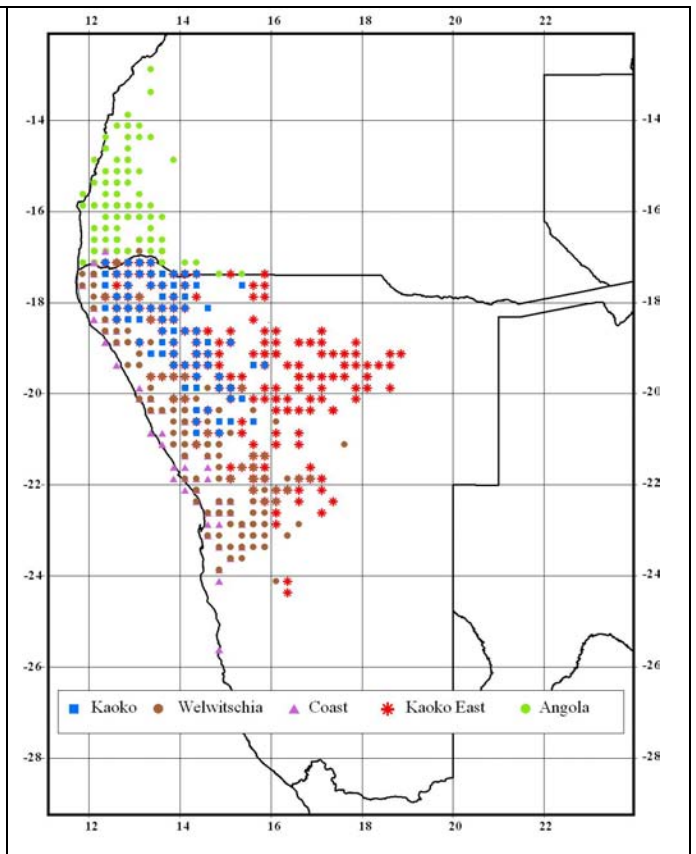


Figure 6.2: Five divisions resulting from the TWINSpan classification

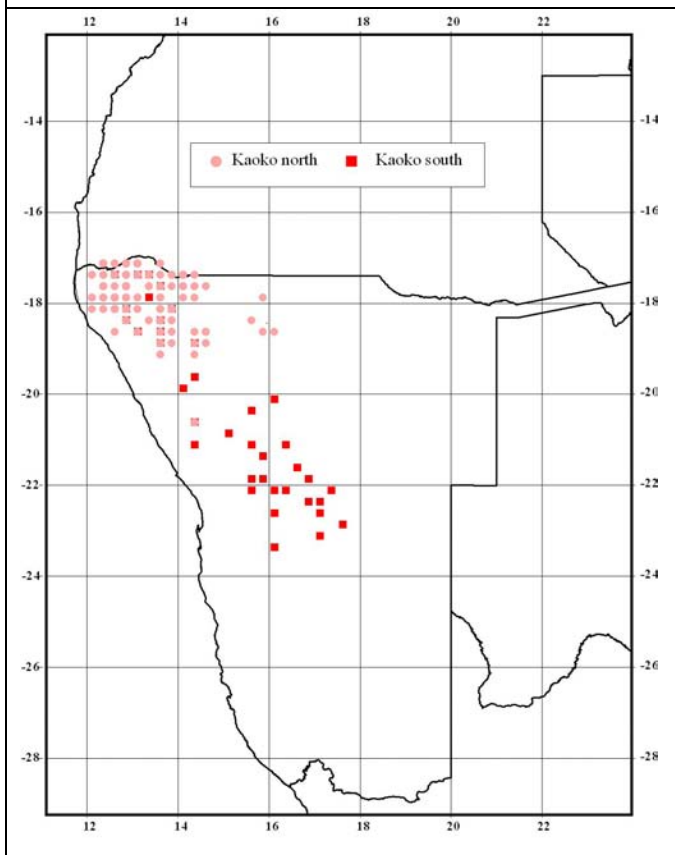


Figure 6.3: North and south concentrations of the Kaoko division after TWINSpan analysis

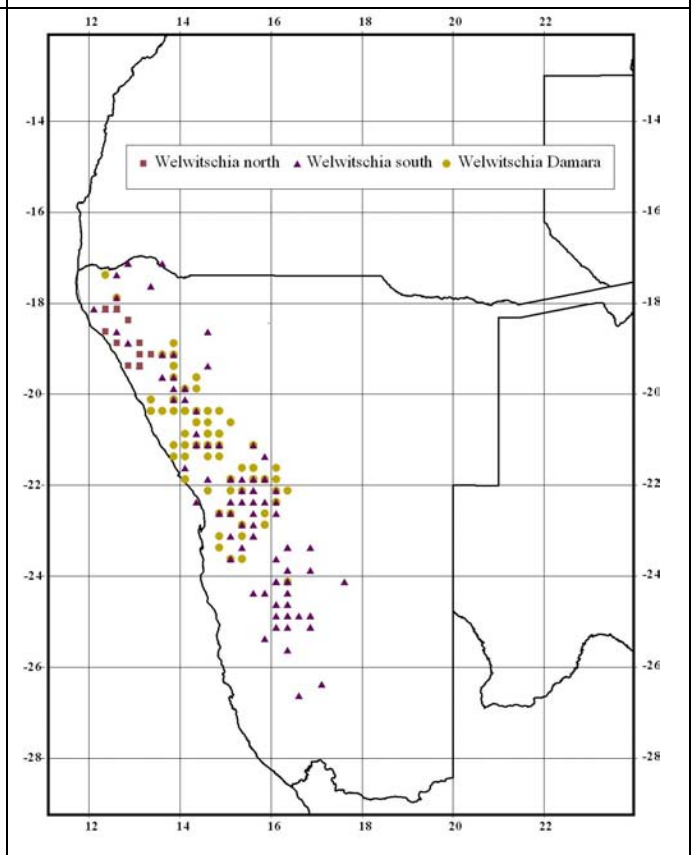


Figure 6.4: North and south concentrations of the Welwitschia division after TWINSpan analysis

2. Kaoko East: 2.1 *Cissus nymphaeifolia*, *Hiernia angolensis* S.Moore, *Pachypodium lealii*  
2.2 East and south: *Adenium boehmianum* Schinz
3. Welwitschia: *Welwitschia mirabilis*, *Adenia pechuelii*
  - 6.1 Welwitschia North: *Lotononis tenuis* Baker, *Petalidium angustitubum* P.G.Mey.
  - 6.2 Welwitschia “damara”: *Barleria solitaria*, *Syncolostemon floccosus* (Launert) D.F. Otieno
  - 6.3 Welwitschia South: *Petalidium canescens* (Engl.) C.B.Clarke, *Sarcocaulon marlothii*
4. Coast: *Arthraerua leubnitziae*, *Mesembryanthemum kuntzei* Schinz, *Zygophyllum orbiculatum/stapffii* complex
5. Angola: *Indigofera benguellensis* Welw. ex Baker, *Polygala mossamedensis* Paiva

The first run of TWINSPAN showed the data to be too busy and complex and species known from one grid only were removed when no other species was recorded from that grid. The second run separated the Angolan species from the rest. Subsequent divisions separated out Kaoko East, Kaoko, Welwitschia and Coast divisions. The Kaoko and Welwitschia divisions were rerun and Kaoko divided into North and South. Subdivisions in the Welwitschia division also showed concentration in the North and South and a “Damara” subdivision.

Angola was the first division to separate out, as it includes many species not found elsewhere. There was no noticeable difference between coastal or inland taxa in Angola. Very few connections were seen with the flora south of the Kunene River despite the fact that some of the same species are found in both areas.

The number of taxa that separated out into the Kaoko East division was not high, relative to the other divisions. Their main ranges were in the Kaoko division, but they had eastward extensions. Because the analysis was based on range restricted species, and those more or less confined to the study area, the floristic component of the area covered by these extensions could not be identified. The species were identified as taxa mentioned in previous delimitation of the KCE, but are included as near-endemic elements. Further evaluation of the floristic composition of the area of their eastern



extensions is required, but it would appear that because only a limited number extend here, the area should not be considered to be part of the Centre of Endemism.

The species from the Coast division were evident in the analysis, however, because the area in which they occur is long and narrow, attributing species to this division was complex. The analysis was aided by using the relevés in which a known coastal species, e.g. *Arthraerua*, occur to find the members of this division.

The ranges of species in the Kaoko division did not extend as far south as those in the *Welwitschia* division, however, both the *Welwitschia* and Kaoko divisions clearly displayed a need to subdivide northern and southern species. Although most divisions were clear because of concentrations of species, the borders between the divisions were almost impossible to designate because of overlapping distributions. Shape-files of physical features were overlaid onto these divisions and features of the environment that coincided with the divisions were highlighted. Species known from only one relevé, which had been removed in the first division because of the “busy” dataset, were manually placed within relevant divisions.

## 6.5 Discussion

The interpretation of a TWINSpan table is subjective (Kent & Coker 1996) and because of the few species records per grid, various amalgamations could be done. In addition, where for example rare species or those occurring in very few relevés are often excluded in vegetation mapping in order to reduce the “noise” of the data set, an adjustment had to be made manually here. It would be nonsensical to exclude localized endemics when the objective of the study is to analyse regions in which exactly such entities are localized. The analysis was successful in that it indicated concentrations of species and divisions. It also contributed to suggesting an outline for the extent of the KCE. It was clear that the inclusion of additional explicit factors, as was done by McLaughlin (1989), to the relevés, that presently consist of locality data only, would greatly enhance the results. Such additional elements could be a feature like altitude or area related, like coastal strip. This would be especially beneficial for analyzing plant species with discontinuous distribution ranges. *Welwitschia mirabilis* and *Adenia pechuelii* for example, are present in many relevés scattered over a wide area. Because various combinations of the TWINSpan table can be made it is essential that such disjunct distributions remain in the same divisions during the analysis. The value of including altitude as an additional element to the relevé data is clear when one considers the two grids in

which the Brandberg Mountain occurs. Some species may be restricted to lower slopes, while others are exclusively found at higher altitudes.

The analysis will also be greatly improved when the taxonomic differences between the flora of the Angolan and Namibian parts of the study area are better understood. Discrepancies are considerable and this merits further attention. Although there are many species that occur in both Namibia and Angola, there are a considerable number that are confined to either country. It is very likely that further taxonomic work will reveal that species presently considered as taxonomically distinct are, in fact, conspecific and should be combined.

The ecological demands on the species in this region are very varied and when systematically recorded and compared, they will undoubtedly improve the resolution of the analysis. At present, only broad scale differences are evident, for example altitudinal variations were noticed between three divisions, namely Kaoko, Welwitschia and Coast when abiotic elements such as topography, were overlaid using a geographic information system onto mapped outlines of the divisions. The divisions corresponded to physical features of the area as suggested by Shortridge (1934), who separated the low-lying coastal zone from the mountainous region. There was, however, considerable overlap of species between the Kaoko and Welwitschia divisions, especially in the north. This may be due to the lack of detail at the scale of our analysis.

Although Linder (2001) suggests that it is possible to objectively delimit areas of endemism, the similarities or differences between observed patterns in an arid area, with a high percentage of species known from only a few records, are small. In a numerical analysis of the African continent, Linder (1998) attributed the problem with arid areas like the Horn of Africa, Namibia and Botswana to be “too poorly sampled to give a robust indication of their phytogeographic affinities”. Although this is undoubtedly an issue, the low diversity and species numbers inherent in arid areas may actually have been the reason, rather than poor sampling. The scale of the study is also important. The Twinspan analysis that delimited the greater Cape Floristic region (Born *et al.* 2007) also showed that the centres north of the Orange River (D centres) always group together, irrespective of whether they are on the Karasberg plateau, along the escarpment, or from the Namib.

Northwestern Namibia and southwestern Angola were shown here to consist of two main divisions of plant species, namely those in high lying area, i.e. higher altitudes, and those nearer the coast and are influenced by the cold Benguela Current (for example *Welwitschia mirabilis*). This poses the question of what constitutes the KCE. Should it be separated into two distinct units or remain

one larger area, with the western part extending much further southward? The answer probably lies in the definition. If it is to be considered as a centre with a high concentration of endemics that do not necessarily have the same history (Van Wyk & Smith 2001), i.e. a **Centre** of Endemism, then recognition of the larger area is acceptable. However, if the aim is to have natural floristic region determined by only the endemic component of the flora with the same history, i.e. an **Area** of Endemism (Linder 2001), then smaller units will be needed. The results of this analysis indicated both a centre and potential regions according to these definitions, but both need further investigation. Optimal delimitation should include analyses of species and generic components, floristic patterns and relationships, as well as the physical environment and its history.

The results from the numerical analysis highlight the problems associated with areas containing a limited number of species per area. A numerical analysis starting with a larger area, including, for example all species in Namibia and its closest neighbors, would be an essential first step before an analysis of a smaller region can attain high levels of accuracy. Analysis at the family, genus and species level would also contribute towards improving resolution. Results presented here summarize available information, and can certainly guide the demarcation of this Centre of Endemism.

It is generally accepted that borders between phytogeographic areas cannot be drawn with exactitude and no method allows us to draw a map which is fully reproducible in the strict scientific meaning of the word (Friis 1986). Using Geographic information system and more criteria, however should allow for much improved resolution. BASED on the TWINSPAN analysis, a Larger Kaokoveld Centre of Endemism has been identified with subdivisions. Two main subdivisions consist of a higher inland area, and the other, which includes *Welwitschia mirabilis* is in the west and is influenced by the cold Benguela current.

## **6.6 Conclusions**

It is evident from the numerical analysis of over 350, mainly range-restricted species found in northwestern Namibia and the southwestern part of Angola, that the Kaokoveld is a Centre of Endemism. The total area is however, larger than is traditionally given. Because of the arid environment with low species numbers and members, there are a large number of relevés with few species. Further investigation is recommended to offset this problem.

## 6.7 References

- Becker, T. 2002. Zur Phytogeographie des Kaokolandes. In: Bollig, M., Brunotte, E. & Becker, T. (eds), *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 69–74. *Kölner Geographische Arbeiten 77*, Köln.
- Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.
- Beentje, H.J. 1994. Regional overview: Africa. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 101–116. Oxford University Press, Oxford.
- Born, J., Linder, H.P. & Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147–162.
- Craven, P. 2002a. Plant species diversity in the Kaokoveld, Namibia. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 75–80. *Kölner Geographische Arbeiten 77*, Köln.
- Craven, P. 2002b. Phytogeography of the Namibian flora: a taxon approach. M.Sc. thesis, University of Stellenbosch, Stellenbosch.
- Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET news* 9: 24–44.
- Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.
- DIVA GIS 2007. A Geographical Information System for the Analysis of Biodiversity data. International Potato Center (CIP), [www.cipotato.ORG](http://www.cipotato.ORG)
- Edwards, D. & Leistner, O.A. 1971. A degree reference system for citing biological records in South Africa. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 501–509.

- Friis, I. 1986. Ethiopia in regional phytogeography. *Symbolae Botanicae Upsaliensis* 26: 68–85.
- Gauch, H.G. & Whittaker, R.H. 1981. Hierarchical classification of community data. *Journal of Ecology* 69: 537–557.
- Hill, M.O. 1979. TWINSpan - A FORTRAN program for arranging data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*. Cornell University. Ithaca, New York.
- Hilliard, O.M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Hilton-Taylor, C. 1994. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.
- Jürgens, N. 1991. A new approach to the Namib region. I. Phytogeographic subdivision. *Vegetatio* 97: 21–38.
- Kent, M. & Coker, P. 1996. *Vegetation description and analysis*. John Wiley & Sons. Chichester.
- Kers, L.E. 1967. The distribution of *Welwitschia mirabilis* Hook.f. *Svensk Botanisk Tidskrift* 61: 97–125.
- Lawesson, J.E. & Skov, F. 2002. The phytogeography of Denmark revisited. *Plant Ecology* 158: 113–122.
- Linder, H.P. 1998. Numerical analyses of African plant distribution patterns. In: Huxley, C.R., Lock, J.M. & Cutler, D.F. (eds). *Chorology, taxonomy and ecology of the floras of Africa & Madagascar*. Pp. 67–86. Royal Botanic Gardens, Kew.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.

- McLaughlin, S.P. 1989. Natural floristic areas of the western United States. *Journal of Biogeography* 16: 239–248.
- McLaughlin, S.P. 1994. Floristic plant geography: The classification of floristic areas and elements. *Progress in Physical Geography* 18: 185–208.
- Moreno Saiz, J.C., Castro Parga, J. & Sainz Ollero, H. 1998. Numerical analysis of distributions of Iberian and Balearic endemic monocotyledons. *Journal of Biogeography* 25: 179–194.
- Nordenstam, B. 1974. The flora of the Brandberg. *Dinteria* 11: 3–67.
- Pedersen, B. 1990. Distributional patterns of vascular plants in Fennoscandia: A numerical approach. *Nordic Journal of Botany* 10: 163–189.
- Shortridge, G.C. 1934. *The mammals of South West Africa*. Heineman, London.
- Steenkamp, Y., van Wyk, A.E., Smith, G.F., & Steyn, H. 2005. Floristic endemism in southern Africa: A numerical classification at generic level. *Biologiske skrifter* 55: 253–271.
- Van Rooy, J. 2000. Diversity and phytogeography of the moss flora of southern Africa. PhD thesis University of Pretoria, Pretoria.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Volk, O.H. 1964. Die afro-meridionale-occidentale Floren-Region in Südwestafrika. *Beiträge zur Phytologie zu Ehren Prof. H. Walters 65 Geburtstages*. Ulmer, Stuttgart.
- Volk, O. H. 1966. Die Florengebiete von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.

## Chapter 7

# Floristic and environmental analysis of the Kaokoveld Centre of Endemism

### Abstract

7.1	Introduction.....	135
7.2	Material and method .....	136
7.3	Results.....	137
7.3.1	Floristic Groups .....	137
7.3.2	Floristic subgroups .....	140
7.3.3	Comparison of the floristic Groups and Divisions of the numerical analysis .....	141
7.3.4	Areas of Endemism .....	142
7.3.5	Extra-regional distributions .....	142
7.3.6	Phylogenies .....	144
7.3.7	Plant characteristics .....	145
7.3.8	Physical features: The present environment.....	146
7.3.9	Palaeo-environment.....	147
7.3.10	Age and origin of the KCE flora .....	147
7.4	Conclusions.....	148
7.5	References.....	148

## **Floristic and environmental analysis of the Kaokoveld Centre of Endemism**

### **Abstract**

The flora of the Kaokoveld Centre of Endemism (KCE) is not only distinct from that of surrounding regions in terms of taxonomic composition, but also in its affinities and origins. This paper compares and combines information obtained in a numerical analysis of the area with facts about floristic Groups in the region. The floristic elements can be separated into three distinct Groups that occupy different areas with different histories. The Kaoko Group is the most species-rich, but the *Welwitschia*-desert Group is the most unique and probably considerably older. The upper parts of Brandberg Mountain belong to the Highland Group with completely different relationships to the other two Groups.

### **7.1 Introduction**

The validity of defining a Kaokoveld Centre of Endemism (KCE), defined as a high concentration of endemics, the elements of which may not necessarily have similar evolutionary developments (Van Wyk & Smith 2001), was confirmed by numerical analysis (Craven 2009, Chapter 6). It covers the full distribution ranges of KCE elements, resulting in it being larger than indicated by previous assessments. A number of subdivisions were also identified. Although a Centre of Endemism can be identified using numerical methods, further investigation is needed if one is to understand why such centres exist, and why the flora is distinct. The flora of an area may be the result of climatic, geological, migrational or evolutionary events, the inherent biology of the plant, or even anthropogenic causes. It could also be due to various combinations of these elements. Consequently a wide variety of material must be scrutinized in order to explain the possible reasons for its existence.

The aim of this chapter was two-fold. Firstly, the divisions identified by the numerical analysis were compared with floristic Groups identified for the same area in Craven (2009, Chapter 5). We then investigated if any of these Groups and divisions are Areas of Endemism, i.e. natural floristic regions with the same biogeographic relationships that can provide evidence for explaining the history of the area (Linder 2001). The second aim was to assess other components of the flora and the environment, in order to define the KCE with regard to its relationships and history.



## 7.2 Materials and Methods

All the information required for the analyses in this paper was stored in the database of Craven & Kolberg (on-going). This database has a comprehensive index of all taxa in the Region, as well as information on both local and world-wide present day distribution, endemic status, phylogenies, the palaeoenvironment and other information relevant to this study. It is constantly updated from literature sources, study of herbarium specimens and through own field collections. The database setup allows manipulation of the data in many ways so as to produce different results.

In terms of methods, the floristic Groups and subgroups defined by Craven (2009, Chapter 5) for this area, were explored. These Groups are based on the overall distributions of the representative species, including their ranges in Angola. The floristic Groups were then compared with the divisions that resulted from the numerical analysis (Craven, 2009 Chapter 6). Although the underlying data for both these analyses are from the same dataset, the one used for floristic Groups was larger as it includes all species with congruent distributions, not only those with restricted ranges. Species are recorded for each quarter degree square in the numerical analysis, while the floristic Groups are based on congruent patterns displayed by the full distribution range of species. One of the problems encountered with the numerical analysis was a large number of relevés with few species, which resulted in a “busy” dataset that could be amalgamated in a few different ways. Some species may therefore be misplaced.

Areas of Endemism were then located following the protocols suggested by Linder (2001): The areas should be narrower than the study area; they should be mutually exclusive; species need to be largely, but not necessarily exactly, congruent and the areas should allow for disjunct distributions. Data on extra-regional distributions, phylogenies and plant characteristics of taxa in the KCE were obtained from Craven (2009, Chapter 4). Summarised information relevant to the KCE on the past environment (Craven 2009, Chapter 3) and the present environment (Mendelsohn *et al.* 2002) was also used.

## 7.3 Results

### 7.3.1 Floristic Groups

The Welwitschia-desert Group and the Kaoko Group (Craven 2009, Chapter 5) coincided with the KCE outlined by the numerical analysis. The examples given as representative of these Groups by Craven (2009, Chapter 5) also occur in Angola. Limits of the Groups in Angola were based on their ranges. An additional Group was identified and named the Northern Succulent Namib Desert. The differences between the two main Groups in the study area are summarized in Table 7.1.

The coastal strip, which is affected by fog and cooler temperatures, has very different endemic species, in terms of taxa and morphology, to those on the highlands where rainfall is higher, or the gravel plains at the base of the escarpment. In addition the relationships of the species to adjacent floras are noticeably different. Species with overlapping distributions occur where the two Groups join, but this may be due to the scale of the study. For example, it is possible that members of the Welwitschia-desert Group will generally be found in low lying areas, while the Kaoko Group members will occur above 900 m. The Welwitschia-desert Group has a more unique flora compared to the Kaoko Group, based on the number of endemic genera and species, as well as being the only Group including an endemic family. The Kaoko Group has closer ties to the rest of Africa and even to India, than the Welwitschia-desert Group.

Table 7.1. Comparison of biotic and abiotic features of the Welwitschia-desert and Kaoko Groups proposed by Craven (2009, Chapter 5) supplemented with additional information for species that occur in Angola

Feature	Welwitschia-desert Group	Kaoko Group
Examples	<i>Welwitschia mirabilis</i> , <i>Zygophyllum orbiculatum/stapffii</i> , <i>Adenia pechuelii</i>	<i>Sesamothamnus guerichii</i>
Location	Namibe to Kuiseb along coast and inland to 23° S, 15° E west of the escarpment	Benguela to 20° S, 15° E, between escarpment in the west and the 1500 m contour in the east
Altitude	Sea-level to 900 m	1200 to 1500 m; 1800 m in the mountains
Rivers	Kunene River and numerous western flowing non-perennial rivers	Kunene River and its catchment area in north Namibia, no other rivers
Terrain	Coastal sand, gravel plains to hills and rocky outcrops	Rocky slopes, water courses, rugged mountains and hills

Climate	Mist reaching up to 60 km inland from the Benguela current, less than 200 mm summer rainfall, strong, hot, dry east winds alternating with cold, moist west winds	Summer rainfall, <i>ca</i> 200 mm in the west and up to 350 mm in the east, no frost in winter, no mist
No. of species in Group	More than 200 species, 100 endemic to Namibia and 55 to Angola	More than 150 species, > 40 species endemic to Namibia and <i>ca.</i> 60 also in Angola
Endemic Families	Welwitschiaceae	None
Most speciose Families	Acanthaceae, Leguminosae, Poaceae	Acanthaceae, Leguminosae, Euphorbiaceae, Asteraceae
Monospecific endemic genera	<i>Arthraerua</i> , <i>Dewinteria</i> , <i>Eremiolirion</i> , <i>Kaokochloa</i> , <i>Lavrania</i> , <i>Phlyctidocarpa</i> , <i>Streptolophus</i> , <i>Welwitschia</i>	<i>Baynesia</i>
Endemic to KCE	<i>Marcelliopsis</i> (2 species)	<i>Marcelliopsis</i> (1 species)
Endemic rich genera	<i>Commiphora</i> , <i>Euphorbia</i> , <i>Indigofera</i> , <i>Lotononis</i> , <i>Merremia</i> , <i>Petalidium</i> , <i>Salsola</i> , <i>Stipagrostis</i>	<i>Aloe</i> , <i>Euphorbia</i> , <i>Petalidium</i> , <i>Sesamothamnus</i>
Species with ranges extending from Angola / Namibia to Cape	<i>Acanthosicyos horridus</i> , <i>Cladoraphis spinosa</i>	None
Disjuncts	<i>Tribulocarpus dimorphanthus</i> also in NE Africa	<i>Leucophrys mesocoma</i> also in southern Namibia
Extra-regional distributions (excluding disjuncts)	Very few northward into Africa	Tropical Africa, India and the Middle East.
Life strategies	Varied, short-lived non-woody, dwarf shrubs with deciduous succulent leaves or rodlike stems	Trees and shrubs, few unusual growth forms compared to Welwitschia-desert Group

The Highlands Group is represented here on the Brandberg Mountain, which was previously viewed as an outlier of the KCE (Hilton-Taylor 1994) and known to consist of species with various phytogeographical relationships (Nordenstam 1974). The mountain lies within the area covered by the Welwitschia-desert Group and because it has numerous endemic species (Craven & Craven 2000; Craven 2009, Chapter 5), it is included in the KCE. Taxa on the lower slopes belong to the Welwitschia-desert Group, and some species, for example *Acacia montis-usti*, are found in the Kaoko Group, especially in Angola. The upper parts of the mountain, however, have more species in common with mountains or highland areas at altitudes of over 1500 m (or even 1700 m), especially in the centre of Namibia or further south, i.e. the Highland Group. Very little is known

about the climate of such highlands, especially orographic rainfall figures are unknown. Over 200 species are recorded for the Highland Group and two of the four endemic genera are found on the Brandberg, namely *Manuleopsis* and *Chamaegigas*. Extra-regional relationships are with the Free State and Highveld of South Africa and a few taxa in this Group (although not found on the Brandberg) are also found in the highlands of Angola. Life forms vary with shrubs or dwarf shrubs being the most common types, but also including localized succulents in the Apocynaceae, Crassulaceae, Euphorbiaceae and Mesembryanthemaceae (*Lithops* species).

The Northern Succulent Namib Desert is a narrow strip extending from north of Namibe to Lucira, where steep cliffs occur very close to the coast. It is characterized by an uncommon set of species, many of which are succulents. It lies north of the distribution of examples given for the Welwitschia-desert Group, including *Welwitschia mirabilis*. The name Northern Succulent Namib Desert is designated here in order to differentiate it from the Southern Succulent Namib Desert (Craven 2009, Chapter 5). Families and genera found in the two areas are completely different, but, a succulent type life form is the most characteristic in both Groups. Examples include a selection of Apocynaceae: *Hoodia mossamedensis*, *Huernia lopanthera* Bruyns (L.C.Leach) Plowes and *Stapelia parvula* Kers., along with non-endemic species like *Huernia oculata* Hook.f., and *Tavaresia angolensis* Welw. Various members of the Portulacaceae, including *Talinum portulacifolium* (Forssk.) Asch. & Schweinf. are found, as well as *Euphorbia carunculifera* L.C.Leach, *E. indurescens* L.C.Leach and *E. subsalsa* Hiern; and *Kalanchoe* and *Kleinia* species. Although the taxa found here have previously been recorded for the KCE, this area was not. This section in Angola is also sometimes (e.g. Ward & Corbett 1990), but not always (e.g. Bruyns 2008) included in the Namib Desert. Field work during this study confirmed that the northern boundary of the Namib Desert lies north of Namibe at the Carunjamba River, and that this section, although comparatively different floristically, should be included in the KCE.

Genera with a number of species each, that are characteristic of both Groups, include: *Commiphora*, *Euphorbia* and *Petalidium*. The only difference between the species of the two groups, is that those from the western ranges tend to be smaller in stature or prostrate compared to the species at higher altitudes. A noteworthy feature of the KCE area is that it appears to be one of the more important centres of diversity in *Acacia* in South Tropical Africa (Ross 1981). The highest number of *Acacia* species in Namibia occurs in the NW and the highest number in Angola in the SW, that is, within the KCE. What is more interesting, however, is that the two endemics found south of the Kunene River belong to a different subgenus to the two north of the River in Angola.

### 7.3.2 Floristic subgroups

Smaller concentrations of endemic species were found in both the floristic Groups (called subgroups) and in the numerical analysis (called subdivisions). In our discussion of them below, terminology is standardized as far as possible and examples of a few taxa provided.

#### 1. Kaoko Group

North: This subgroup consisted of species occurring on the mountains, just south of the Kunene River including the Baynes and Otjihipa Mountains and high lying areas. The species included, amongst others, are: *Aloe corallina*, *A. kaokoensis*, *A. omavandae*, *Baynesia lophophora*, *Hibiscus merxmulleri* and *Stapelia remota* R.A.Dyer. This subgroup is also represented in Angola, but then at lower altitudes, by species such as *Maerua kaokoensis* Swanepoel and *Sesamothamnus benguellensis*. The highlands include many localized endemics: *Phaulopsis semiconica* P.G.Mey., *Petalidium ohopohense* P.G.Mey., *P. welwitschii* S.Moore. and *Priva auricoccea* A.Meeuse. *Hoodia parviflora* N.E.Br. is also present here and not localized.

#### 2. Kaoko Group, near-endemics

While the main area of distribution for these species is within the KCE, they also extend to *ca.* 19° E above 1500 m in altitude. This area is part of the Zambesian Domain of White (1983) and the floral composition and relationships are therefore considerably different. Examples of included species are: *Cissus nymphaeifolia*, *Pachypodium lealii* and *Stigmatorhynchus hereroensis* Schltr.

#### 3. Welwitschia- Desert Group

There is a coastal subgroup occurring from Namibe southward to the Kuiseb River, including species such as *Arthroa leubnitziae* (Kuntze) Schinz, *Brachiaria psammophila* (Welw. ex Rendle) Launert, *Ectadium rotundifolium* (H.Huber) Venter & Kotze, *Mesembryanthemum kuntzei* Schinz, *Stipagrostis hermannii*, and the *Zygophyllum orbiculatum/stapffii* complex.

The Damara subgroup lies inland from the coast, where the northern escarpment breaks down. Species included are for example: *Aloe asperifolia*, *Barleria solitaria*, *Blepharis gigantea* Oberm., *Commiphora kraeuseliana* Heine and *Sarcocaulon marlothii* Engl. Examples from the Sesfontein region include: *Kirkia dewinteri* Merxm. & Heine and *Lavrana haagnerae* Plowes.

### 7.3.3 Comparison of the floristic Groups and Divisions of the numerical analysis

Some floristic Groups and subgroups, discussed above, coincided with the divisions and subdivisions of the numerical analysis (Craven 2009, Chapter 6). There were, however, other marked differences between Groups/subgroups and Divisions/subdivisions, and these are summarized in Table 7.2. The fact that all species north of the Kunene River separated out into an Angolan division could be due to: 1. the large number of both species and relevés with only one or two entries in the dataset; 2. a considerable number of species are endemic to Angola, which may be due to taxonomic problems and/or 3. disjunctions between populations of the same species on either sides of the Kunene River made amalgamations in the numerical analysis more difficult. This sort of lumping of relevés was also seen in the numerical analysis of Born *et al.* (2007), where all taxa north of the Orange River were included in one division. Mapping and overlaying the full distribution patterns of the species allowed for better placement of such taxa.

Table 7.2. Similarities and differences between the Divisions and the Groups in the KCE

<b>Divisions of the Numerical analysis</b>	<b>Groups of the floristic analysis</b>
Kaoko	Kaoko Group
Kaoko East	Near-endemic
Brandberg	Highland Group
Welwitschia	Welwitschia-desert Group
Coast:	Included in Welwitschia-desert Group
Angola:	Separated into Kaoko, Welwitschia-Desert and Northern Succulent Namib Desert Groups

Although the Coast was identified as both a division and a subgroup, the ranges of a number of species overlap and thus it was included in the Welwitschia-desert Group. Both analyses identified species that occurred east of the main concentrations. The floristic relationships of the majority of species in this area differ from that in the core KCE area and these species are therefore regarded as near-endemics. In the numerical analysis, the two relevés housing the Brandberg Mountain indicated a concentration of endemics. Based on the floristic Groups, however, the upper Brandberg is placed in the Highland Group because they have closer ties.

### 7.3.4 Areas of Endemism

The *Welwitschia*-desert Group and the Kaoko Group comply with the criteria of Linder (2001) for recognition as Areas of Endemism in all but one criterion, namely there is an overlap of species on the borders between the two Groups. Despite this they are recognized in this study as being Areas of Endemism with the same history. Reasons for doing so include that the species found to overlap are generally in need of revision and because when more is known about the habitats of these species it is likely that the separation will become clearer.

### 7.3.5 Extra-regional distributions

The world-wide distributions of the families and genera found in the KCE, as well as the ranges of non-endemic species in Craven (2009, Chapter 8) were summarized. Distribution ranges of species that are also found in neighbouring floras followed three paths, which can be summed up by using the proposed hierarchical arrangement for floristic Regions in Namibia (Craven 2009, Chapter 5) as follows:

- Karoo-Namib Region of Namibia and Northern Cape (South Africa).
- Sudano-Zambesian Region, Zambesian Domain
- The Highveld

The summary also pointed to tracks, i.e. distributions of taxa that show the areas and floras that had previous contact with the KCE flora (Linder *et al.* 1992).

- NE African track resulting from the Arid Corridor, which developed after the split of Europe from Africa.
- South American track resulting from the Tethys Seaway (Brown & Lomolino 1998)
- Afromontane track, which includes the Great Escarpment of eastern southern Africa and the Angolan Highlands.

There are two explanations for the establishment of tracks. The track may be due to long-distance dispersal across the barriers in the track, or the distributions could have been broken up by the establishment of barriers between the two related areas. Evidence here suggests that all three tracks were the result of the latter option, although dating of the associated areas is still needed in some cases. That numerous taxa with varying dispersal mechanisms are grouped in the same tracks suggests that dispersal was not the cause. Other evidence is provided by one of the key elements of the KCE, namely *Welwitschia mirabilis*, which is closely related to the South American genus

*Gnetum* (Lewis *et al.* 2005). The link between *Gnetum* and *Welwitschia* is thought to have resulted from a persistent dry vegetation type that was linked in the Tertiary, from South America, through Central America, Mexico and the Caribbean, along the Tethys Seaway to Africa, Arabia and India (Ickert-Bond & Wojciechowski 2004).

More evidence comes from the genera represented in the KCE with distributions in NE Africa and sometimes in Arabia and India, implying an Afro-arid disjunction. These include: *Citrullus*, *Dicerocaryum*, *Lotononis*, *Pterodiscus*, *Sesamothamnus*, *Tetrapogon*, *Turnera*, *Walleria*, *Xerophyta* and *Zygophyllum*. Genera in the KCE with sister species in North Africa and Arabia are *Heliotropium*, *Kissenia*, *Stipagrostis* and *Tricholaena*. The KCE endemic, *Camptoloma rotundifolia* Benth., has two sister species in North Africa. *Cucumella cinerea* (Cogn.) C.Jeffrey occurs in four disjunct areas and one of these is the KCE. The others are Northern Province of South Africa, SE Kenya & NE Tanzania and Madagascar (Kirkbride 1994). Although *Dactyliandra welwitschii* is a KCE near-endemic, it is mentioned here as it has a very interesting disjunction to the Thar Desert in India. Other species with known disjunct distributions from the KCE to NE Africa are: *Geigeria alata* (Hochst. & Steud. ex DC.) Benth. & Hook.f. ex Oliv. & Hiern, *Gossypium anomalum* Wawra ex Wawra & Peyr. disjunct with Niger, Chad & Sudan (Fryxell 1967), *Sesamum rigidum* Peyr., *Tribulocarpus dimorphanthus* and *Trichodesma africanum* (L.) Lehm.

Van Jaarsveld & Van Wyk (2006) consider the presence of species of *Othonna* and *Pelargonium* on the upper parts of the Otjhipa and Baynes Mountains to indicate the presence of Cape elements. Although these two genera are representative of the Cape flora, the two species are not indicators of Cape floristic elements in the KCE flora.

A few habitat or substrate specific taxa are also found along the coast as far north as Luanda in Angola or southwards to the Orange River, but in general very few species in the Welwitschia-desert Group occur outside of the Region. Some occur northward into Africa, but are generally associated with small inselbergs or certain substrates, like granite. This is in contrast to the Kaoko Group that has more species in common with Tropical Africa, the Middle East and even India. Due to the steep escarpment in Angola there is very little exchange of species between the Angola KCE portion and the rest of the Angolan flora.



### 7.3.6 Phylogenies

The intensive search found very few molecular phylogenetic studies focused on or even just including Namibian plant taxa (Craven 2009, Chapter 4). The only phylogenies of significance to the KCE are:

*Zygophyllum*: Results of Bellstedt *et al.* (2008) showed that *Zygophyllum orbiculatum* and *Z. stapffii*, KCE endemics, are the earliest diverging taxa in genus *Zygophyllum*. Their results also suggested that there have been repeated migrations of *Zygophyllum* species from southern Africa to the arid areas in the Horn of Africa and Asia.

*Indigofera*: The range of variation in the large genus *Indigofera* (Leguminosae) has been analysed using molecular sequence data (Schrire *et al.* 2003; Schrire pers. comm). Results of the most recent research (Schrire *et al.* in press) show that a range restricted KCE endemic, *Indigofera anabibensis* A.Schreib., belonging to the Tethyan crown clade which is linked to the arid corridor in NE Africa, is the second oldest clade in the genus and estimated to be about 11.7 million years old.

*Dauresia*: Analyses of subtribe Senecioninae revealed the genus *Dauresia* to be the earliest diverging taxon of this lineage (Pelser *et al.* 2007). It is presently described as being monospecific, with its main distribution within the KCE. However, the few specimens known from the Hunsberg area may be confirmed as a different species. *D. alliariifolia* is sister to another KCE endemic, *Senecio engleranus* O.Hoffm. and to *S. flavus* (Decne.) Sch.Bip. from southern Namibia.

A genus that is well-represented in the KCE, but not elsewhere in the Region, namely *Xerophyta*, is one of the few taxa shared between South America and Africa (De Melo *et al.* 1997). Karyological information supports the hypothesis that the Velloziaceae originated in South America where the other six endemic genera occur.

*Syncolostemon*: Using both morphological and molecular characters, the genus *Syncolostemon* (including *Hemizygia*) was studied to determine evolutionary relationships among the species and to use the phylogeny to investigate their biogeography (Otieno *et al.* 2006). Their results suggested that *S. floccosus*, a KCE endemic, is not closely related to the other species found in Namibia. The closest are two species from the Highveld of South Africa and *H. comosa* (Wright ex Benth.) D.F.Otieno, the only species found in India. Unfortunately only 19 of the 44 taxa were sequenced and the KCE endemic and *H. comosa* were not included. This is unfortunate, given the many known

links between the arid areas of SW Africa and NE Africa extend as far as India. For example *Dactyliandra welwitschi*, is also only found here and in the Thar Desert in India.

A much debated disjunction is that of the KCE near-endemic *Nicotiana africana* Merxm. It is the only indigenous *Nicotiana* species in southern Africa and is limited to the Brandberg and a few mountains in western-central Namibia. The rest of the genus is known from semi-arid habitats in Australia and South America. Merxmüller & Buttler (1975) believed its taxonomic position to be obscure and that it was neither a hybrid of the few naturalized or cultivated species in Africa, nor was it likely to have resulted from a recent long range dispersal of a still unknown species or hybrid. Goodspeed (1954) in Gerstel *et al.* (1979) dated the diversification of *Nicotiana* in South America to the mid or late Tertiary. Unlike several South American species, *Nicotiana africana* is insensitive to tentoxin, a character inherited through the cytoplasm. It also possesses another marker which occurs in only two species from southern South America, which may be regarded as ancestral. This species is now considered to be most closely related to a group from Australia and New Caledonia (Knapp *et al.* 2004). This is the only taxon in Namibia with such an unusual range and relations, and is possibly an endemic relict of considerable age.

Although published work is not based on molecular studies yet, the phytogeography of the Pedaliaceae has been comparatively well-researched and *Sesamum rigidum* Peyr., a species from the KCE, is considered to be the ancestor of its group, and has given rise to species that colonized NE Africa (Ihlenfeldt 1994). This family also includes an undescribed tree-like species of *Sesamothamnus* (De Winter & Leistner 5504) from the KCE. It is probably the species from which the others species in *Sesamothamnus* are derived (Ihlenfeldt pers. comm.).

### **7.3.7 Plant characteristics**

A comparatively high proportion of taxa endemic to particularly the western part of the KCE, consists of monospecific genera or have a low average number of species. This has been put forward as evidence of considerable age for the flora, that speciation is probably not occurring and that the environment has been stable for a long time (Robinson 1975-77). The reason behind this deduction is that the taxa are limited in range, because they are at the end of their existence. However, as Good (1974) points out, species may also have very narrow ranges when they are very young. In most cases there is no means of knowing whether an individual species is new or old, however information from dated phylogenies, terminal versus basal taxa, as well as the presence of endemic genera contribute. Based on all available evidence it would appear that KCE endemics in

the *Welwitschia*-Desert Group are of considerable age, however, those in the Kaoko Group (for example some *Petalidium* species) are younger as there is evidence of hybridization (Meyer 1973).

### **7.3.8 Physical features: The present environment**

The main environmental factors that have contributed to the ranges of species found here are discussed in 7.3. They can be summarized as follows:

#### **Altitude**

The coastal plain ranges from sea-level to 900 m, while the plateau can be 1200 m and higher above the escarpment. Mountains just south of the Kunene River reach 1800 m, while the altitude of the highest point on the Brandberg Mountain is 2 579 m. The escarpment is steep in the far north and breaks down around 21° S. It becomes steep again south of 24° S, which is also south of the KCE. The coastal plain north of Namibe in Angola is very narrow and the escarpment very steep.

#### **Rivers**

The perennial Kunene River dissects the northern part of the KCE, where it generally flows through deep gorges. Numerous western flowing non-perennial rivers are found in the area below the escarpment, but no significant water courses are present in the higher parts.

#### **Terrain**

Landforms are very variable. The coastal areas are sandy or have gravel plains that are crossed by wide, dry water courses. There are hills, rocky outcrops, and small inselbergs in the west, while rocky slopes and rugged mountains are more common inland.

#### **Climate**

The weather along the coast is considerably different to that inland. The average annual rainfall is recorded as being less than 50 mm, while that on the higher inland areas ranges between 250 to 350 mm. Rain falls in summer and the precipitation at the coast is increased by fog from the Benguela current. Strong, hot, dry east winds and cold, moist west winds also occur.

### 7.3.9 Palaeo-environment

The environmental history of Namibia is complex. This is reflected in the diverse range and amount of information on Namibia (Craven 2009, Chapter 3) and by the variety of view points published. Trying to date the origins of the flora in the KCE is made more difficult because the age of the Namib Desert remains controversial. The various arguments were summarized by Ward & Corbett (1990) and although more research has been carried out since then, the matter remains unresolved. The evaluation of relevant literature showed that most research is limited in scope (e.g. the northern sand sea – Teller *et al.* 1990) and specific (e.g. fish moths – Irish 1990). Many research papers concentrated on the sand desert and pollen from ocean cores, while the Central Namib Desert has received the most attention. According to Deacon & Lancaster (1988) palaeoclimatic evidence is variably preserved in the Namib. Studies of fluvial deposits in the Namib, for example, have “assisted in the elucidation of the geomorphic history of the area, but provided little precise palaeoclimatic information”. This fragmented information renders it difficult to combine and apply any holistic concepts to the whole Namib Desert. No particular research output could be identified that may contribute to the palaeo-historic understanding of the KCE area.

### 7.3.10 Age and origins of the KCE flora

The history of the flora is best traced by summarizing the evidence provided by the various phytogeographic analyses and three components of the taxa themselves (i.e. extra-regional distributions, phylogenies and plant characteristics) discussed above.

1. The extra-regional distributions of taxa show links to NE Africa, South America and Afro-montane Regions of Africa and are thought to be the results of the continuous distributions being broken up by some barrier or event in the past.
2. Repeated migration of some taxa, for example *Zygophyllum* species, from southern Africa to the arid areas in the Horn of Africa and Asia took place (Bellstedt *et al.* 2008) and the earliest taxa, *Zygophyllum orbiculatum* and *Z. stapffii*, are KCE endemics.
3. An estimated age for certain species in the KCE can be based on *Indigofera anabibensis*, which belongs to a clade estimated to be about 11.7 Ma years old (Schrire *et al.* in press).
4. The richness of monospecific genera and endemic taxa suggests an ancient flora. Linder *et al.* (1992) propose that this type of phylogenetic diversity is an indication of a Tertiary or even older flora. Unfortunately no fossil record can verify this, but the presence of an

endemic monospecific family of the gymnosperms, with links to South America, does testify to it being an ancient flora.

When combining the evidence it is clear that the history of the KCE flora dates back to the Tertiary, however, it is also clear from the taxa involved, that this age pertains to the flora in the west and not to that found on the highlands. The latter is clearly a younger flora such as is found in tropical Africa. The KCE therefore consists of two different backgrounds based on the delimited Areas of Endemism. There is no evidence to suggest links to an ancient Gondwanan flora.

#### **7.4 Conclusions**

This newly defined larger KCE includes the full distribution range of one of the most intriguing plants in the world, *Welwitschia mirabilis*. The flora consists of three different floristic Groups, each with their own compliment of species, environmental conditions and relationships. Many species are still taxonomically difficult, but the components of the flora justify the definition of the area as a Centre of Endemism. The flora of the Kaokoveld must continue to receive conservation attention because of its many rare and unique taxa.

#### **7.5 References**

Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.

Born, J., Linder, H.P. & Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147–162.

Brown, J.H. & Lomolino, M.V. 1998. *Biogeography*. 2nd edition. Sinauer Associates, Sunderland.

Bruyns, P.V. 2008. Notes on African plants Apocynaceae: A new species of *Huernia* (Asclepiadoideae–Ceropegieae) from Angola. *Bothalia* 38: 83–85.

Craven, P. 2009. Chapter 3, this volume. Plant geography in Namibia.

- Craven, P. 2009. Chapter 4, this volume. Phytogeographical aspects of the flora of Namibia.
- Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.
- Craven, P. 2009. Chapter 6, this volume. Demarcating the Kaokoveld Centre of Endemism: A numerical approach.
- Craven, P. & Craven, D. 2000. The flora of the Brandberg, Namibia. In: Kirk-Sprigs, A.H. & Marais, E. (eds). Biodiversity of the Brandberg Massif, Namibia. *Cimbebasia* 9: 49–67.
- Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.
- Deacon, J. & Lancaster, N. 1988. *Late Quarternary Palaeoenvironments of Southern Africa*. Clarendon Press, Oxford.
- De Melo, N.F., Guerra, M., Benko-Iseppon, A.M. & de Menezes, N.L. 1997. Cytogenetics and cytotaxonomy of Velloziaceae. *Plant systematics and evolution* 204: 257–273.
- Gerstel, D.U. Burns, J.A. & Burk, L.G. 1979. Interspecific hybridisations with an African tobacco, *Nicotiana africana* Merxm. *The Journal of Heredity* 70: 342–344.
- Good, R.D. 1974. *The geography of flowering plants*. Wiley, New York.
- Hilton-Taylor, C. 1994. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.
- Ickert-Bond, S.M. & Wojciechowski, M.F. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): Evidence from nuclear and chloroplast DNA sequence data. *Systematic Botany* 29: 834–849.
- Ihlenfeldt, H.-D. 1994. Phytogeography of Pedaliaceae R.Br. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the XIIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1063–1075. National Herbarium and Botanic Gardens of Malawi, Zomba.

- Irish, J. 1990. Namib biogeography, as exemplified mainly by Lepismatidae (Thysanura: Insecta). In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 61–66.
- Kirkbride, J.H. 1994. Revision of *Cucumella* (Cucurbitaceae, Cucurbitoideae, Melothrieae, Cucumerinae). *Brittonia* 46: 161–186.
- Knapp, S., Chase, M.W. & Clarkson, J.J. 2004. Nomenclatural changes and a new sectional classification in *Nicotiana* (Solanaceae). *Taxon* 53: 73–82.
- Kent, M. & Coker, P. 1996. *Vegetation description and analysis*. John Wiley & Sons. Chichester.
- Knight, R.S. & Siegfried, W.R. 1982. Distribution and evolution of aril-bearing trees in southern Africa. *South African Journal of Botany* 1: 117–123.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.
- Linder, H.P., Meadows, M.E. & Cowling, R.M. 1992. History of the Cape flora. In: Cowling, R.M. (ed.). *The ecology of fynbos. Nutrients, fire and diversity*. 5: 113–134. Oxford University Press, Oxford.
- Merxmüller, H. & Buttler, K.P. 1975. *Nicotiana* in der Afrikanischen Namib – ein pflanzengeographisches Rätsel. *Mitteilungen aus der Botanischen Staatssammlung, München* 12: 91–104.
- Meyer, P.G. 1973. Neue und wenig bekannte Acanthaceen aus dem Kaokoveld (SWA). *Mitteilungen aus der Botanischen Staatssammlung, München* 11: 101–103.
- Nordenstam, B. 1974. The flora of the Brandberg. *Dinteria* 11: 3–67.
- Otieno, D.F., Balkwill, K., Paton, A.J. & Savolainen, V. 2006. A reassessment of *Hemizygia* and *Syncolostemon* (Ocimeae—Lamiaceae). *Taxon* 55 : 941–958.

- Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Robinson, E.R. 1975–77. Phytogeography of the Namib Desert of South West Africa and its significance to discussions of the age and uniqueness of the desert. *Palaecoecology of Africa* 67–74.
- Ross, J.H. 1981. An analysis of the African *Acacia* species: Their distribution, possible origins and relationships. *Bothalia* 13: 389–413.
- Schrire, B.D., Lavin, M., Barker, N.P., Cortes-Burns, H., Von Senger, I. & Kim, J.-H. 2003. Towards a phylogeny of *Indigofera* (Leguminosae-Papilionoideae): Identification of major clades and relative ages. In: Klitgaard, B.B. & Bruneau, A. (eds). *Advances in Legume Systematics 10 Higher Level Systematics*. Pp. 269–302. Royal Botanic Gardens, Kew.
- Schrire, B., Lavin, M., Barker, N.P. & Forest, F. Phylogeny of the tribe Indigofereae (Leguminosae-Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments. *American Journal of Botany*. In press.
- Teller, J.T., Rutter, N.W. & Lancaster, N. 1990. Sedimentology and palaeohydrology of late Quaternary lake deposits in the northern Namib Sand Sea, Namibia. *Quaternary Science Reviews* 9: 343–364.
- Van Jaarsveld, E.J. & van Wyk, A.E. 2006. *Pelargonium vanderwaltii*, a new cliff-dwelling species from the Otjihipa Mountains, Northern Namibia. *Aloe* 43: 32–34.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Ward, J.D. & Corbett, I. 1990. Towards the age of the Namib. In: Seely, M.K. (ed.). *Namib ecology: 25 years of Namib research*. Pp. 17–26. Transvaal Museum Monograph 7, Transvaal Museum, Pretoria.
- White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.



## Chapter 8

### Flora of the Kaokoveld Centre of Endemism

#### Abstract

8.1	Introduction.....	153
8.2	Data compilation.....	153
8.3	Results.....	155
8.3.1	Families .....	155
8.3.2	Genera .....	156
8.3.3	Species.....	157
8.3.4	Disjunct species.....	159
8.3.5	Disjunction through anthropogenic activity.....	160
8.3.6	Comparison of species within the Region.....	160
8.3.7	Life form, habit and habitat.....	161
8.4	Discussion.....	164
8.5	Conclusions.....	166
8.6	References.....	166

# Flora of the Kaokoveld Centre of Endemism

## Abstract

The Kaokoveld Centre of Endemism (KCE) comprises over 1600 species in nearly 550 genera and one of the 130 families is endemic. The phytogeographic characteristics were examined based on an analysis of these indigenous families, genera and species. Local and wider distributions as well as taxa with disjunct distributions both within the KCE and in the Regions were reviewed. The diversity of unusual structural features and ecological requirements in many species is summarized. The flora is portrayed as being rich in numbers of taxa and diversity, especially for an arid area.

## 8.1 Introduction

The number of species and infraspecific taxa of indigenous vascular plants recorded for the Kaokoveld Centre of Endemism (KCE) exceeds 1600. This figure is expected to rise as the larger KCE (Craven 2009, Chapter 6 and 4) is better surveyed. The actual numbers are also changing constantly as new species are described and revisions completed. It will be considerably enhanced when the Flora of Angola online (FLAN), which is currently still in preparation, is completed (Soares *et al.* 2007). This paper focuses on the flora of the KCE as a whole. It provides details on the taxa at different levels (families, genera and species), then compares these data with taxa beyond the Centre, but still present in the broader Region, and concludes with a discussion of the life forms, habits and habitats present in the KCE flora. More than 350 species are endemic to the KCE (Craven 2009, Chapter 9) and a few species previously listed as endemic are now known to be near-endemic KCE floristic elements, i.e. they are marginally present elsewhere.

## 8.2 Data compilation

Data compilation has been ongoing since the first preliminary checklists of Kaokoveld plant species of Craven & Maggs (1993), Craven (2001) and Hilton-Taylor (pers. comm.). These lists were based on *Prodromus einer Flora von Südwestafrika*, (Merxmüller 1966–1972), *Flora of southern Africa* (various editorial teams; 1963–ongoing) and *Conspectus Florae Angolensis* (various editorial teams; 1937–1970), as well as numerous other sources referred to in the database of Craven & Kolberg (on-going). This database includes fields for a variety of information, including both local and wider distributions, voucher specimens, life forms, uses, local names and endemic status. Accepted, code-compliant taxon names generally follow Germishuizen & Meyer (2003), except for

species not included in this checklist or where current and/or preferred systematic concepts are followed. Individual taxonomic judgements were made to standardise species concepts in Angola with Namibia based on available literature or expert opinion. Besides a grass checklist for Angola (Costa *et al.* 2004), legume endemics (Soares *et al.*, 2007), Rubiaceae (Figueiredo 2008), a few isolated publications (Bruyns, 2005) and Lebrun & Stork (2003, 2006), information on the plants in Angola is very limited. There are also no up to date national plant lists. Electronic data of herbarium specimens were not available for this exercise. Information was, however, obtained from herbarium specimens in K, M, PRE, NBG, BOL and personal collections of the main author and the collecting lists of De Winter & Leistner (pers. comm.). The taxonomy is inadequate in some areas due to the lack of specialist studies on large numbers of the taxa, limited representation of KCE taxa in taxonomic studies, and the number of undescribed species in the area.

Targeted collecting as well as wide-ranging field work by Craven and Kolberg (pers. comm.) has resulted in many new plant records for Namibia, as well as finding species previously known only from type collections or not collected for many years. Recent field work by Craven in this centre in Angola contributed much needed first hand information on many aspects of the Centre. Although extensive identification of taxa was not possible, numerous taxonomic problems were identified or ironed out. Soares *et al.* (2007) found that recent plant collections were rare in Angola and difficult to access, thus their analysis of legumes refers mostly to the period up to 1975, after which collection activities practically ceased due to the war in that country. The most productive period for collections in Angola was between 1960 and 1973, and an absence of specimens from the period is believed to reflect rarity (Soares *et al.* 2007). This assumption is not necessarily correct for the centre covered by this paper, as it is extremely arid and longer periods of collecting are required to cover the flora that is present when conditions allow. A personally compiled list of over 1600 species and infraspecific taxa was recorded for the area and forms the basis of this investigation.

The word *Region* is used here for the wedge-shaped southwestern part of Angola, south of Benguela and west of the escarpment, Namibia and marginally into neighbouring countries in the south and southwest. This more or less corresponds to White's (1983) Karoo-Namib Regional centre of endemism and Kalahari-Highveld Regional transition zone, however this demarcation is used for convenience only as it is defined differently.

## 8.3 Results

### 8.3.1 Families

The families with the most species in Kaokoveld are Poaceae [169], Leguminosae [168], Asteraceae [124], Acanthaceae [105], Apocynaceae s.l. [63] and Euphorbiaceae s.l. [58]. The first three families also rate amongst the largest families in the world. Other globally large families are poorly represented in the Kaokoveld, for example: Rubiaceae [16], Orobanchaceae [7], Brassicaceae [4]; Apiaceae [3] and Orchidaceae [1]. The Burseraceae is also well-represented and although Acanthaceae is found throughout Namibia, they are very numerous in this Centre, both in numbers of individuals and in species. Families that are large in both the world and southern Africa, but are not represented in the Kaokoveld include: Araceae, Myrsinaceae, Proteaceae, Rosaceae and Zingiberaceae. The Mesembryanthaceae, Amaryllidaceae and Iridaceae are also very poorly represented. Table 8.1 provides a breakdown of the numbers of taxa of higher plants in the KCE. These numbers vary continually as new species are found and described or revisions result in adjustments to taxonomic concepts.

Predominantly African families with species in the KCE include the Balanitaceae, Eriospermaceae, Hydrostachyaceae, Kirkiaceae, Melianthaceae, Montiniaceae, Myrothamnaceae, Ptaeroxylaceae, Tecophilaeaceae and Vahliaceae. All of these include only a few taxa within the KCE. The Moringaceae and Salvadoraceae, both of which are represented in the KCE, occur in Africa and Asia.

Despite the arid climate a number of hydrophytic families are found either in the perennial Kunene River or in pans (only after rain). These include the Aponogetonaceae, Ceratophyllaceae, Hydrocharitaceae, Lythraceae, Podostemaceae, Ruppiaceae and Zannichelliaceae. One family mainly associated with humid forests elsewhere, the Sapotaceae, is also represented in the KCE.

Table 8.1. Number of taxa (families, genera and species) present in the KCE, with reference to the representation of the main seed plant groups

	<b>Gymnosperms</b>	<b>Monocotyledons</b>	<b>Dicotyledons</b>
Families	1	25	104
Genera	1	112	467
Species	1	293	1263

### 8.3.2 Genera

Besides the genera endemic or near-endemic to the KCE (Craven 2009, Chapter 9), the following range restricted genera have species in the KCE: *Chamaegigas*, *Ectadium*, *Manuleopsis*, *Ondetia* (endemic to Namibia); *Antiphiona*, *Engleria*, *Entoplocamia*, *Monelytrum* (endemic to Namibia and Angola); *Cladoraphis*, (Namibia and neighbouring parts of the Cape, South Africa); *Leucophrys* and *Leucosphaera* (Namibia, Cape (South Africa) and Angola). Genera with most of their species restricted to the KCE include: *Aeollanthus* (9 of 10 species), *Maerua* (6 of 7 species and two undescribed taxa), *Sesuvium* (5 of 5 species) and *Solanum* (8 of 11 species). *Solanum* is, however, currently under revision and changes in these species numbers are expected. The most speciose genera relative to the Region are summarized in Table 8.2.

Table 8.2. Genera in the KCE with the most species, along with the number of species present in the Region

Genus	No. of spp. in Centre	No. of spp. in Region
<i>Euphorbia</i>	35	73
<i>Indigofera</i>	29	54
<i>Petalidium</i>	27	33
<i>Commiphora</i>	24	30
<i>Eragrostis</i>	24	59
<i>Stipagrostis</i>	23	33
<i>Barleria</i>	23	30
<i>Hibiscus</i>	22	36
<i>Acacia</i>	21	30
<i>Cleome</i>	18	20
<i>Grewia</i>	18	21

The genera with the least species compared to the rest of the Region are *Crassula*, *Mesembryanthemum*, *Oxalis*, *Pelargonium*, *Pteronia* and *Wahlenbergia*. Over 100 genera are represented in the Region by only one species, and this representative is only present in the Kaokoveld. Examples include: *Ansellia*, *Australluma*, *Berchemia*, *Diplorhynchus*, *Gyrocarpus*, *Lepidagathis*, *Priva* and *Zanthoxylum*. Many genera have very localized distributions, but where the species occur they tend to be locally abundant. This is particularly true of some of the endemics (e.g. *Barleria*).

A number of genera in the KCE have ranges in Africa, Arabia and Asia. These include: Acanthaceae: *Blepharis*, *Monechma*, *Petalidium*, *Phaulopsis* and *Rhinacanthus*; Asteraceae: *Dicoma*, *Grangea*, *Kleinia*, *Laggera* and *Sphaeranthus*; Leguminosae: *Lablab*, *Lotononis*, *Macrotyloma*, *Mundulea* and *Neonotonia*. The most species-rich genus in this group is *Petalidium*, followed by *Commiphora* and *Lotononis*. Some genera, such as *Dyerophytum*, are noteworthy for having only one species in each of Africa, India and Sumatra.

*Zygophyllum* is one of only a few genera that are present in Africa, Asia and Australia. Genera that occur in the KCE and also in America and Africa include *Anthepphora*, *Dalechampia*, *Eriocaulon*, *Lantana*, *Lippia*, *Loudetia*, *Parkinsonia* and *Rogeria*. Two disjunct, mainly xeromorphic genera that occur in arid SW Africa and NW America are *Thamnosma* and *Turnera*. This is of particular interest when the relationships and origins of the flora of the KCE are considered. Genera that are in urgent need of revision include: *Cordia*, *Ficus*, *Hermannia*, *Melhania*, *Petalidium*, *Rhynchosia*, *Salsola* and *Solanum*. Few of the pantropical genera with numerous species in Namibia (Craven 2009, Chapter 4) occur in the KCE, and are then represented by only a few taxa.

### 8.2.3 Species

Besides the species endemic to this Centre, there are a number of species confined to the Region. A total of 43 of these species have distributions similar to that of *Phaeoptilum spinosum* (Craven 2009, Chapter 5). Those confined to Namibia include: *Cleome suffruticosa* Schinz, *Felicia smaragdina* (S.Moore) Merxm., *Indigofera pechuelii* Kuntze, *Indigofera rautanenii* Baker f., *Monechma desertorum* (Engl.) C.B.Clarke, *Monechma genistifolium* (Engl.) C.B.Clarke subsp. *genistifolium* and *Solanum rigescentoides* Hutch. A second group of taxa have a similar distribution, but are also found in Angola. They include: *Entoplocamia aristulata* (Hack. & Rendle) Stapf, *Justicia platysepala* (S.Moore) P.G.Mey., *Leucas pechuelii* (Kuntze) Gürke, *Monechma cleomoides* (S.Moore) C.B.Clarke, *Polygala guerichiana* Engl., *Sesbania sphaerosperma* Welw., *Stipagrostis hirtigluma* (Trin. & Rupr.) De Winter subsp. *pearsonii* (Henrard) De Winter and *Stipagrostis hochstetteriana* (L.C.Beck ex Hack.) De Winter var. *hochstetteriana*. About 20 species have distribution patterns similar to *Adenium boehmianum* Schinz, *Cissus nymphaeifolia* (Welw. ex Baker) Planch., *Kirkia acuminata* Oliv. and *Pachypodium lealii*. They occur within the centre and extend further eastwards into the karstveld. *Stigmatorhynchus hereroensis* is the only one of these species endemic to Namibia. *Combretum mossambicense* (Klotzsch) Engl. and *Fockea multiflora* K.Schum. also follow this distribution pattern, but have a disjunct range in the Caprivi. The range of *Rhinacanthus kaokoensis* is restricted to the Kunene River in Namibia. The distributions of

*Entandrophragma spicatum* (C.DC.) Sprague and *Ledermanniella warmingiana* (Gilg) C.Cusset are similar, but are also found in Angola. The range of the latter species is unusual, as the rest of the Podostemaceae in the KCE have much wider distributions, extending all the way into South America.

Nearly 200 species are found throughout the north of the Region, but many, like the following examples, have restricted ranges: *Barleria kaloxytone* Lindau, *Felicia smaragdina* (S.Moore) Merxm., *Geigeria odontoptera* O.Hoffm., *Heliotropium albiflorum* Engl., *Hygrophila gracillima* (Schinz) Burkill, *Indigofera rautanenii* Baker f. and *Peristrophe namibensis* K.Balkwill subsp. *brandbergensis* K.Balkwill. The rest generally occur in tropical Africa.

There are more than 130 species in the KCE that are also widely distributed in Namibia. Of these, 11 are endemic to Namibia, namely: *Acrotome fleckii* (Gürke) Launert, *Anisopappus pinnatifidus* (Klatt) O.Hoffm. ex Hutch., *Antiphonia pinnatisecta* (Klatt) O.Hoffm. ex Hutch., *Barleria lanceolata* (Schinz) Oberm., *Hibiscus fleckii* Gürke, *Ondetia linearis* Benth., *Ornithogalum stapffii* Schinz, *Ornithoglossum calcicola* K.Krause & Dinter, *Pelargonium otaviense* R.Knuth, *Searsia marlothii* (Engl.) Moffett and *Tripteris nervosa* Hutch.

Altogether ca. 220 species that are restricted to Namibia occur within this centre, and a further 130 also only occur in South Africa, of which 70 are only found in the Cape, South Africa. A number of species found in the west of the centre extend their ranges south from Angola along the west coast to the Cape. Examples include *Acanthosicyos horridus* Welw. ex Hook.f., *Adenolobus garipensis* (E.Mey.) Torre & Hillc., *Blepharis grossa* (Nees) T.Anderson, *Cryptolepis decidua* (Planch. ex Hook.f. & Benth.) N.E.Br., *Euphorbia virosa* Willd. subsp. *virosa*, *Ficus ilicina* (Sond.) Miq., *Stipagrostis subacaulis* (Nees) De Winter and *Tetragonia reduplicata* Welw. ex Oliv. Few species also extend their ranges to the Bushmanland part of the Northern Cape, South Africa. Among these, two families are well represented, namely Capparaceae: *Cleome foliosa* Hook.f. var. *lutea* (Sond.) Codd & Kers, *Cleome semitetrandra* Sond. and *Cleome paxii* (Schinz) Gilg & Benedict and Sterculiaceae: *Hermannia minutiflora* Engl. and *Hermannia affinis* K.Schum.

More than 120 species occur in the KCE and then also in southern and South Tropical Africa. Examples include: *Ficus cordata* Thunb., *Montinia caryophyllacea* Thunb. and *Pterocarpus lucens* Guill. & Perr. subsp. *antunesii* (Taub.) Rojo. Far fewer (ca. 30 species) extend from South Africa all the way into tropical Africa. More than 100 species are confined to Africa. Many of these occur elsewhere in Angola, but are then not restricted to Angola or specifically characteristic of the flora

of Angola. Few species in the centre have cosmopolitan distributions or even just extend from Africa to Asia and Australia. Most of these belong to the Poaceae, and are generally associated with moisture, for example *Cynodon dactylon* (L.) Pers., *Chloris virgata* Sw., *Phragmites australis* (Cav.) Steud. and the legume *Mimosa pigra* L.. *Leptochloa fusca* (Nees) Cope & N.Snow is one of the few species (less than 10) in the centre that also extends its range from Africa to Asia and Australia. Very few species are common to this centre and South America. All of these are associated with rivers, for example *Jasminum fluminense* Vell. and *Tristicha trifaria* (Bory ex Willd.) Spreng.

#### 8.3.4 Disjunct species

A number of species found in the Kaokoveld have disjunct distributions to nearby eastern parts like Kavango or Caprivi. Most of these are also found in tropical Africa. A large number of them are trees, although a few, like *Eriocaulon abyssinicum* Hochst and *Gloriosa superba* L., are monocotyledons. In Kaokoveld the disjuncts are generally found either along the Kunene River or in sandy substrates in the east of the centre. In Namibia they appear to be represented by isolated outliers, and could be excluded from the list of species occurring within the KCE, however, they are more frequent in Angola. Examples include: *Baikiaea plurijuga* Harms, *Burkea africana* Hook., *Philenoptera nelsii* (Schinz) Schrire and *Terminalia sericea* Burch. ex DC. Nearly 20 species have been collected a few times in the eastern parts of the Kaokoveld and Caprivi. Examples include *Crabbea velutina* S.Moore, *Garcinia livingstonei* T.Anderson, *Paropsia brazzeana* Baill., *Syzygium cordatum* Hochst. ex O.Krauss and *Tricliceras lobatum* (Klotzsch) R.R.Fern.

*Ptaeroxylon obliquum* (Thunb.) Radlk. was recorded in two completely different environments in the Kaokoveld. White (1990) described the habitat of this species in Angola as sub-desert with rocks in sparse Mopane woodland, while it is associated with limestone and sandstone in Namibia. Both of these areas receive less than 250 mm rain annually, but in KwaZulu-Natal, South Africa, it occurs in habitats with an annual rainfall of up to 1300 mm. The species displays remarkable variation in leaf shape, which may in part be correlated with this geographical range, but intermediates do exist, rendering the recognition of more than one taxon impossible. *Ormocarpum kirkii* S.Moore is another example of a species known only from a few specimens in the KCE, but which is well-known in an area ranging from northern South Africa all the way north into Somalia. It is possible that closer comparison of specimens from these diverse regions may reveal differences, but in practice the ovaries and young fruit are almost always subject to insect attack, obscuring the details of potentially diagnostic differences (White 1990).



Other disjunct patterns that can be identified include:

- Kaokoveld to southern Namibia: *Leucophrys mesocoma*
- Kaokoveld (Brandberg Mountain) to southern Namibia and the Northern Cape: *Diospyros acocksii*

Species that display marked disjunct distributions within the Kaokoveld, that do not appear to be substrate specific are *Commiphora oblanceolata* Schinz and *Dauresia alliarifolia* (O.Hoffm.) B.Nord. & Pelser, although the latter is only found in shaded rocky areas. Disjunct distributions from Kaokoveld to North Africa and India include: *Tribulocarpus dimorphanthus*, which was considered to be *T. somalensis* Schellenb. in Somalia by Thulin (1994), but has been combined again under *T. dimorphanthus* in the new Flora of Ethiopia (Edwards *et al.* 2000); *Dactyliandra welwitschii* is known from NW Namibia and SE Angola and the Thar Desert in India (Craven 2009, Chapter 7).

### **8.3.5 Disjunction through anthropogenic activity**

Transfer of plant material by humans may account for disjunct distribution of some species, for example *Searsia leptodictya*, and *Trema orientalis* (L.) Blume (if the specimen reported from the Baynes Mountains is verified as correctly identified). Both species have well-documented indigenous uses and their ranges in the KCE are very distant from their core ranges.

### **8.3.6 Comparison of species within the Region**

The KCE is floristically very different to the rest of the Angolan flora (Exell & Gonçalves 1973; Huntley 1974; White 1983) in terms of the taxa present, as well as growth forms and relationships. It has closer ties to the floras further south. Unfortunately there are no figures quantifying the number of taxa in the Region as defined here, or in any other defined unit that could be used for statistical comparison. Data for Namibia includes the country as a whole and that for Angola is outdated. It is, however, fair to say that more than half of the families in the Region occur in the KCE and this also applies to genera. There are, however less than half the number of species in the KCE, than in the Region. Differences between the diversity in number of species and taxa in the two main floristic Groups, namely the Welwitschia-desert Group and the Kaoko Group were recorded (Craven 2009, Chapters 4 and 9). The total number of species found in the former Group is lower than in the latter, but the proportion of range restricted taxa is higher. There are also more species in the western low altitude areas with distributions extending to the Cape of South Africa

compared to the flora of the higher altitudes. Many more species in the higher areas co-occur in tropical Africa and southern Africa.

### 8.3.7 Life form, habit and habitat

A remarkable diversity of life forms is found in the Kaokoveld Centre of Endemism. This may be ascribed to the mixture of landforms and climatic conditions present in the area. Plants vary from annuals to trees, woody to succulent, parasitic to hydrophytic, while habitats range from exposed slopes or shaded clefts in dry rocky areas to gravel planes or sand dunes. Identification and classification of life forms and habitats is hampered by inconsistent terminology in literature. A wider range of morphological features is needed to describe and classify both the taxa and the habitats, followed by a completely new analysis of every species. Other problems encountered include: the life form of the same species may vary according to the season or position within the Centre; many features and forms, e.g. underground structures are extremely poorly known; plants called “trees” in some sources do not fit a generally accepted definition of a tree, while others may also be documented as trees for this Centre when they actually never reach such status here; the term succulent is also generally based on conjecture and not scientific investigation. Plants listed as succulents include vastly different forms and a finer measure is needed for any valuable discussion.

On a broad scale, no particular life form preference was seen for any area. Height classes decrease westward and tall trees in the east may only occur in this Centre as shrubs or even dwarf shrubs, while near the coast they may even be prostrate. Most types of succulent life form can be found here, with rod-like stems being the most numerous. This character is present in many different families, including Amaranthaceae, Apocynaceae, Asteraceae, Euphorbiaceae and Passifloraceae. They may have early deciduous leaves in some seasons depending on availability of moisture.

Some families, such as the Apocynaceae, show a great variety of life forms varying from trees (*Strophanthus amboensis* (Schinz) Engl. & Pax), dwarf shrubs (*Stigmatorhynchus hereroensis*), herbaceous geophytes (*Raphionacme inconspicua* H.Huber), leafless stem succulents (*Hoodia* spp.), rod-shaped stems (*Orphanthera albida* Schinz), climbers (*Marsdenia* spp.), shrub or climbers (*Tylophora fleckii* (Schltr.) N.E.Br.) and geophytes with succulent leaves (*Raphionacme haeneliae* Venter & R.L.Verh.). The presence of succulent leaves in *R. haeneliae* is unique in the genus (Verhoeven & Venter 1996). Another genus, *Ectadium*, which is confined to extreme conditions along the coast, has coriaceous leaves (Venter *et al.* 1990).

Entirely succulent species such as *Mesembryanthemum dimorphum* (Welw. ex Oliv.) N.E.Br. are few in number, and do not appear annually, but these are locally common and are generally confined to the coast. *Aloe* species with large succulent leaves are present, including the tree *Aloe dichotoma* on the Brandberg Mountain and at isolated places on the plains further south, where they are very large. The cactoid tree form in *Euphorbia* is found only in *E. eduardoi* L.C.Leach in the KCE. It is a feature more commonly associated with the eastern side of Africa (White 1990). Other *Euphorbia* species are either prostrate or erect annuals (e.g. *Euphorbia chamaesycoides* B.Nord.), trees with peeling bark, e.g. *Euphorbia guerichiana* Pax, thick succulent-stemmed shrubs such as *Euphorbia virosa* Willd., and dwarf shrubs with thinner angular stems, e.g. *Euphorbia otjipembana* L.C.Leach.

Trees or tall shrubs make up about 13% of the flora. Another 13% are Poaceae or Cyperaceae, about half of which are annual and the other half perennial. There are few holoparasites (e.g. *Striga gesnerioides* (Willd.) Vatke), but hemiparasites are represented by a considerable number of individuals from the families Loranthaceae, Orobanchaceae (*Hiernia angolensis*) and Viscaceae. The spines found range from large in *Balanites angolensis* (Welw.) Welw. ex Mildbr. & Schltr., to prickles as in *Acacia ataxacantha* DC. They may also be the remains of leaves, such as in *Aptosimum* species.

Plant pubescence is characteristic of many taxa in harsh moisture regimes, but no particular pattern of occurrence could be detected between different localities or between different types of hairs. Their role in decreasing the high radiation levels encountered in the desert need to be investigated and confirmed. A phenomenon that is difficult to explain is the ability of some specimens to be glabrous, while the same population may also include plants with hairy leaves. This is noticed in the genus *Commiphora* in particular, a genus also known to display considerable variation in leaf size within the same species. Another common feature is the change in leaf shape from juvenile to adult stages. This is displayed particularly prominently in *Adansonia digitata* L. Species in the genera *Boscia* and *Maerua* produce very different leaves at ground level when the plants coppice from the base. The leaves are much longer, have a pink tinge and may be more hairy. Other noteworthy adaptations to arid climates were encountered in literature pertaining to individual taxa. Many legumes, for example, “adapt to seasonally dry, warm climates by producing compound leaves that photosynthesize rapidly during favourable periods (and exhibit leaf nyctinasty to promote efficiency)” (Schrire *et al.* 2005). They avoid excessive water loss by losing their leaflets in unfavourable periods. The high nitrogen metabolism of all legumes allows them to be more competitive when they colonize arid areas and they only produce leaves when the climate allows.

Some plants only produce leaves after rain (e.g. *Euphorbia damarana* L.C.Leach, *Adenia pechuelii*) and then they are early deciduous. Another feature that needs investigation is what appears to be two types of leaves on some species of *Petalidium*, a genus that is very well-adapted to this Centre. Thin green deciduous leaves are produced in good rain years, while the leaves that appear later in the season or only when there is insufficient rain are longer-lived, grey-green and much thicker. Both can be present on the plant at the same time. Other species in this genus vary considerably in the type and density of hairs as well as the indumentum on all plant parts. This does not only vary within a single population, but also across different seasons. Another inconsistent feature in this family is the aromatic state of most plant parts. Growth form varies from prostrate to dwarf shrubs, with the former only occurring in the west.

A surprising number of genera are dioecious, including *Adenia*, *Commiphora*, *Citrullus*, *Cucumella*, *Euphorbia* and *Welwitschia*. Gynodioecy, where plants of the same species bear either functionally female or bisexual flowers, is found in *Ceraria kaokoensis* (Swanepoel 2007) and *Cordia* species. The ecological advantage of this sexual state is unclear. *Phaeoptilum spinosum* produce both bisexual and unisexual flowers.

A waxy bloom has been recorded in species of *Adenolobus*, while many other genera have peeling barks, for example members of *Commiphora*, *Cyphostemma* and *Euphorbia*. The advantages of these adaptations are still poorly understood. Xeromorphic features that were observed, but which need further documentation include: the position and size of stomata, cuticle thickness, leaf size (i.e. production of smaller rotund leaves), leaf thickness and/or shape, and reductions in the size and number of vegetative and reproductive structures.

Seed adaptations such as the production of hard testas and prolonged periods of dormancy, and a range of chemical defences like alkaloid production, are also likely to be critical to the survival of species under these harsh conditions. The genus *Commiphora*, which is characteristic of this region, bears pseudo-aril, often considered to be a particularly important source of food for birds and mammals and thereby a means of seed dispersal. Fruiting periods of aril-bearing species are relatively short and the KCE has a relatively high incidence of species producing low-quality fruits at low cost (Knight & Siegfried 1982).

Many species evade dry periods by being annuals or geophytes and only appear after rain, which means that many years, maybe even decades, will pass before the plants are seen (e.g. *Cleome laburnifolia* Roessler). Another example is *Raphionacme haeneliae*, the only true desert species in a

genus of 38 species (Venter & Verhoeven 1996). It has numerous tubers (per plant), that weigh up to 1 kg each and these only produce above ground parts after rain, which may be only every few years. The showers are often so localized that the plants are easily missed when they do grow above ground bearing succulent leaves, most unlike the coriaceous leaves of the rest of the genus.

A structure so far only recorded from one endemic, *Phaulopsis semiconica*, is a filament curtain. It is a complex structure inside the corolla which is supposed to prevent nectar evaporation (Manktelow 2000). Besides being of importance for systematics and pollination, it may be advantageous in an arid environment and needs further study, especially as so many closely related taxa (e.g. *Petalidium*) are found in the KCE that may utilize similar mechanisms.

#### **8.4 Discussion**

Although the number of endemic taxa in the KCE has increased compared to earlier reports, the overall number of taxa in the area has increased more. No complete lists are available for the newly enlarged area, but the numbers are expected to be still higher when it is better surveyed. This is despite the near-endemic taxa no longer being included in this count. Previous investigations into the flora of the area in Namibia (Craven 2002a & b, 2005; Hilton-Taylor 1994) and Angola (Exell & Goncalves 1973) are outdated in both species numbers and area covered, while Van Wyk and Smith (2001) included mainly succulent species. In Namibia estimated numbers were for the area between the Kunene and Huanib Rivers, while in Angola, the analysis was based on a survey of endemism using an incomplete *Conspectus Florae Angolensis* (1937-1970). Exell & Goncalves (1973) estimated 256 species, (of which 46 were endemic), to occur more or less in the area of this Centre. The limited number of species that extended across the Kunene River was believed to be due to the desert or arid nature south of the Kunene River, not because the river acts as a barrier (Exell & Goncalves 1973). Only 33% of the species in the Namibe political area in their sample extended into Namibia, while only 16% of the Huila species reached Namibia. 12.5 % of the 256 species from Namibe also occurred in the Lunada area. Their analysis showed the relationship, but not the extent of the divergence, and is useful because Angolan data is limited.

Although a phylogeographic analysis of an area requires a thorough knowledge of the flora and good taxonomy, no attempt was made to sort out the numerous taxonomic problems encountered here as that was outside the scope of this study. In addition the present level of taxonomic revision, incomplete floras available, the expertise required in a wide variety of taxa and the problems associated with collecting sufficient specimens in an arid climate would have made the task

extremely difficult. The treatment of the floras of Angola and Namibia in various publications and in different languages posed a big problem. Studies restricted to the plants of only one of the areas have resulted in taxonomic differences. For example, *Boscia albitrunca* is considered to be common south of the Kunene River, but it has never been recorded north of the river. Instead, three potential Angolan endemic species are recorded (Lebrun & Stork 2003), but they have not been described. Numerous other species are expected to be combined after further study. Amongst the most problematic taxa are well-represented genera like *Ficus*, *Vangueria* and *Petalidium*.

The *Crotalaria* monograph (Polhill 1982) covers both countries well, but even in this treatment there is an uneven quality and quantity of information from Angola, with many species only known from types or a few collections. *Crotalaria nematophylla* Baker f. is a good example. It is only known from the type collection in a deciduous forest en route to the base of Serra da Chela. In a phytogeographic study where locality data is important, the limited distribution notes on many specimens, make it difficult to locate exact collection areas. In addition, as in the case of the Cyperaceae, even when an updated checklist is available (Archer & Craven 2004), information on the distribution patterns remain poor. Biogeographic work for the majority of the taxa in the area is very limited (e.g. Acanthaceae, Balkwill & Balkwill 1998).

Soares *et al.* (2007) provides evidence for the rarity of endemics by showing the year of the most recent collection records. Those applicable here include: *Acacia quintanilhae* Torre in 1956; *Crotalaria nematophylla* in 1909; *Lotononis newtonii* Dummer in 1892 (known from the type only) and *Rhynchosia ovatifoliolata* Torre in 1957, (known from the type only). Monocotyledons and annuals are also under-collected due to the aridity of the area and the difficulty of being in the area when the plants are visible. On the other hand, the relatively high number of succulent species recorded in Angola could be due to specialist collections of living plants that were cultivated elsewhere. It is likely that many species have larger distribution ranges than recorded at present.

The mechanisms used by plants to survive the arid conditions and how the various environmental factors affect them have not been studied. An attempt to classify species into habitat classes proved futile due to the very large diversity of habitats encountered in the KCE. This was especially problematic when attempting to take life form or the plant structure into account as well. The many species with discontinuous distributions suggest a high number could be classed as “niche taxa”, i.e. species that only occur in appropriate niches. It is presently not possible to classify taxa either with regard to their plant structure or habitat requirements, because in most studies these issues are too briefly defined or totally absent. There is a need for descriptions of both plant characters and those

of the environment, as well as criteria for placement in order to obtain some form of consistency, which will allow comparison and analysis. There is also a need for more complete lists of species occurring in localized areas of importance.

## 8.5 Conclusions

Any analysis of the KCE flora must be regarded as exploratory rather than definitive at present, because of the uncertainties with regard to many aspects of the flora, especially that in Angola. For this reason there are no statistics, but rather general comparisons with the surrounding floras and information on life forms, habits and habitats. Statistics will be possible in future studies that are based on phytogeographic groups identified here combined with more knowledge about the flora. The area is not necessarily the richest in species, but the diversity of taxa, forms and adaptations to the harsh environment show clearly that this profile of the KCE flora should be followed up and the plants must receive conservation attention.

## 8.6 References

Archer, C. & Craven, P. 2004. Cyperaceae in Namibia. *SABONET News* 9: 18–28.

Balkwill, M.-J. & Balkwill, K. 1998. A preliminary analysis of distribution patterns in a large, pantropical genus, *Barleria* L. (Acanthaceae). *Journal of Biogeography* 25: 95–110.

Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.

Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar* 1 & II. Umdaus Press, Hatfield.

*Conspectus Florae Angolense* (various editorial teams). 1937-1970. Centro de Botânica, Instituto de Investigação Científica Tropical, Lisboa.

Costa, E., Martins, T. & Monteiro, F. 2004. A checklist of Angola grasses – Checklist das Poaceae de Angola. *Southern African Botanical Diversity Network Report* 28. SABONET, Pretoria.

- Craven, P. 2001. *Checklist: Kaokoveld*. Unpublished. National Herbarium of Namibia, National Botanical Research Institute, Windhoek.
- Craven, P. 2002. *Phytogeography of the Namibian flora: A taxon approach*. Unpublished. MSc thesis, University of Stellenbosch, Stellenbosch.
- Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET News* 9: 24–44.
- Craven, P. 2009. Chapter 4, this volume. *Phytogeographical aspects of the flora of Namibia*.
- Craven, P. 2009. Chapter 5, this volume. *Natural floristic areas of Namibia*.
- Craven, P. 2009. Chapter 6, this volume. *Demarcating the Kaokoveld Centre of Endemism: A numerical approach*.
- Craven, P. 2009. Chapter 7, this volume. *Floristic and environmental analysis of the Kaokoveld Centre of Endemism (KCE)*.
- Craven, P. 2009. Chapter 9, this volume. *The endemic seed plants of the Kaokoveld Centre of Endemism*.
- Craven, P. & Kolberg, H. on-going. *DB Index of plant species for Namibia and surrounds*.
- Craven, P. & Maggs, G.L. 1993. *Checklist: Kaokoveld*. Unpublished. National Botanical Research Institute, Windhoek.
- Edwards, S., Tadesse, M., Demissew, S. & Hedberg, I. (eds). 2000. *Flora of Ethiopia and Eritrea* 2 Addis Ababa, Ethiopia.
- Exell, A.W. & Gonçalves, M.L. 1973. A statistical analysis of a sample of the flora of Angola. *Garcia de Orta, Ser.Bot.* 1: 105–128.
- Figueiredo, E. 2008. The Rubiaceae of Angola. *Botanical Journal of the Linnean Society* 156: 537–638.



*Flora of southern Africa* (various editorial teams). 1963–ongoing. National Botanical Institute, Pretoria.

Germishuizen, G. & Meyer, N.L. (eds). 2003. Plants of southern Africa: an annotated checklist. *Strelitzia* 14. National Botanical Institute, Pretoria.

Hilton-Taylor, C. 1994. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.

Huntley, B.J. 1974. Outlines of Wildlife Conservation in Angola. *Journal of South African Wildlife Management Association* 4: 157–166.

Knight, R.S. & Siegfried, W.R. 1982. Distribution and evolution of aril-bearing trees in southern Africa. *South African Journal of Botany* 1: 117–123.

Lebrun, J.-P. & Stork, A.L. 2003. *Tropical African flowering plants. Ecology and distribution. 1 – Annonaceae – Balanitaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.

Lebrun, J.-P. & Stork, A.L. 2006. *Tropical African Flowering plants. Ecology and distribution 2, Euphorbiaceae – Dichapetalaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.

Manktelow, M. 2000. The filament curtain: A structure important to systematics and pollination biology in the Acanthaceae. *Botanical Journal of the Linnean Society* 133: 129–160.

Merxmüller, H. (ed.) 1966–1972. *Prodromus eine Flora von Südwestafrika*. Cramer Verlag, Lehre.

Polhill, R.M. 1982. *Crotalaria in Africa and Madagascar*. Balkema, Rotterdam.

Schrire, B.D., Lavin, M., Barker, N.P., Cortes-Burns, H., Von Senger, I. & Kim, J.-H. 2003. Towards a phylogeny of *Indigofera* (Leguminosae-Papilionoideae): Identification of major clades and relative ages. In: Klitgaard, B.B. & Bruneau, A. (eds). *Advances in Legume Systematics* 10 Higher Level Systematics. Pp. 269–302. Royal Botanic Gardens, Kew.

Soares, M., Abreu, J., Nunes, H., Silveira, P., Schrire, B. & Figueiredo, E. 2007. The Leguminosae of Angola: Diversity and endemism. *Systematics and geography of plants* 77: 141–212.

Swanepoel, W. 2007a. *Ceraria kaokoensis*, a new species from Namibia, with notes on gynodioecy in the genus. *Bothalia* 37: 202–206.

Thulin, M. 1994. Aspects of disjunct distributions and endemism in the arid parts of the Horn of Africa, particularly Somalia. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the XIIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1105–1119. National Herbarium and Botanic Gardens of Malawi, Zomba.

Verhoeven, R.L. & Venter, H.J.T. 1996. *Raphionacme haeneliae* (Periplocaceae), a new species from the Namib Desert, Namibia. *South African Journal of Botany* 62: 316–320.

Venter, H.J.T., Kotze, J.D.S. & Verhoeven, R.L. 1990. A taxonomic revision of *Ectadium* (Periplocaceae). *South African Journal of Botany* 56: 113–124.

White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.

White, F. 1990. *Ptaeroxylon obliquum* (Ptaeroxylaceae), some other disjuncts and the Quarternary history of African vegetation. *Bulletin du Museum National d'Histoire Naturelle Section B. Adansonia* 2: 139–185.

## Chapter 9

# Endemic seed plants of the Kaokoveld Centre of Endemism

### Abstract

9.1	Introduction.....	171
9.2	Data compilation.....	171
9.3	Results.....	172
9.3.1	Endemic families.....	172
9.3.2	Endemic genera.....	173
9.3.3	Endemic species.....	178
9.3.4	New and problematic taxa.....	179
9.3.5	Distributions of endemic species.....	180
9.3.6	Near-endemics.....	184
9.3.7	Highly disjunct taxa.....	185
9.3.8	Distributions of relatives.....	185
9.3.9	Adaptations, life forms and habitats.....	185
9.4	Discussion.....	186
9.5	Conclusions.....	187
9.6	References.....	187

# Endemic seed plants of the Kaokoveld Centre of Endemism

## Abstract

The Kaokoveld Centre of Endemism (KCE) supports over 1600 species of seed plants and over 20% of these are endemic. There is also one endemic family and eight endemic genera. The majority of endemic genera occur on the western side of the escarpment in environmentally the harshest part of the area. There is a marked difference between the western and eastern parts of the KCE with regard to geological age and origin of the endemics. Acanthaceae is the family with the most endemics and is found throughout the KCE, while 50 other families also have endemics and these are not always the largest families in the flora. Genera with the most endemic species include *Petalidium*, *Euphorbia* and *Commiphora*. Many of the endemics are localised and rare with specific habitat preferences, but no particular life or growth forms are favoured.

## 9.1 Introduction

The purpose of this paper is to discuss the full quota of endemic higher plant taxa— gymnosperms and angiosperms— in the Kaokoveld Centre of Endemism (KCE) as accurately as possible. A considerable number in diverse families and genera require revision or description, or are under-collected and very little is known about them. There is, however, sufficient evidence on endemic species to validate the existence of the KCE. Much of the information on the overall flora of the KCE (Craven 2009, Chapter 8) applies to the endemics, especially information on the life form and habitats. Species occurring marginally outside the KCE, either with disjunct distributions or extending slightly into neighbouring parts are defined as near-endemics.

## 9.2 Data compilation

Almost 300 species were identified as endemic according to the definition of Major (1988), from the total index of species (*ca* 1600) recorded for the KCE (Craven 2009, Chapter 8). The lists of Kaokoveld endemics in Craven (2005) and Van Wyk & Smith (2001) were updated from literature sources and collections. Since the publication of these lists new endemic taxa have been described, amongst others by Van Jaarsveld & Van Wyk (2005, 2006), Van Jaarsveld *et al.* (2006), Bruyns (2007, 2008), Swanepoel (2007a.& b, 2008 a & b) and Van Wyk & Kolberg (2008). Two well-known endemic species have been transferred to new genera. *Hemizygia floccosa* Launert is now

placed in *Syncolostemon* (Otieno *et al.* 2006) and *Rogeria petrophila* De Winter is included in the monospecific genus *Dewinteria* Van Jaarsveld & van Wyk (2007).

Because a study of endemism is as sensitive to taxon names as to collection sites, steps were made to ensure precise taxonomic and distributional data. This was not always possible for the Angolan taxa and in particular their distributions. A number of taxa clearly require further taxonomic scrutiny, but this could not be carried out in the time period available for this study. Problems encountered included lack of updated or comprehensive botanical revisions, the variety of taxa involved which would require diverse expertise, and the problems related to obtaining Angolan plant material. Fortunately, the Angolan section of the KCE is small compared to the Namibian section and the difficulties should not affect the overall picture presented here. Statistics are expected to change as on-going and targeted collecting and study continues. Soares *et al.* (2007) identified 32 endemic legumes from the area covered in this centre, although this number may still include taxa from the Sera de Chela, as locality information is limited. A full list of taxa currently considered as endemic is supplied in Appendix 1.

### **9.3 Results**

#### **9.3.1 Endemic families**

No angiosperm families are restricted to the KCE, but one gymnosperm family, Welwitschiaceae, is endemic. Today it is represented by a single extant species, *Welwitschia mirabilis*, although it is known from a 110-My-old seedling from the Lower Cretaceous in northeastern Brazil (Won & Renner 2006). Despite enormous interest and research, little is known about many aspects of this family. Studies have concentrated on ecology, physiology and seed germination and a study on genetic variation (Jacobson & Lester 2003) does not take more recent facts and theories into consideration and attribute the close relationship of *Welwitschia* with the South American genus, *Gnetum* to the Gondwana landmass.

Recently more molecular studies have been carried out on the Gnetales and fossil-calibrated molecular clocks indicate that the split between *Gnetum* and *Welwitschia* had already occurred by 115 million years ago (Won & Renner 2003). *Welwitschia* is very different to *Gnetum*, (a genus of canopy climbers), but the two together are the sister clade to *Ephedra* (a genus of shrubby plants) (Ickert-Bond & Wojciechowski 2004). The Tethys Seaway is considered the reason for the close

relationship, not only of *Welwitschia* and *Gnetum*, but also for other genera such as *Xerocladia* and *Prosopis* (Lewis *et al.* 2005; Schrire *et al.* 2005; Craven 2009, Chapter 4).

Welwitschiaceae extends from Namibe in Angola south to the Kuiseb River in Namibia in discontinuous localities. It occurs in the desert just inland from the coast and further inland in the transition zone when in the catchment areas of west flowing rivers. Field observations as well as GIS evaluations indicate that *Welwitschia* extends eastwards where the escarpment breaks down and moisture (fog from the coast) is able to penetrate further inland.

About 50 of the 129 families in the KCE have endemic species. Of these, twenty two have only one endemic species each. Families with the most endemics are shown with the number of species in the KCE and the Region in Table 9.1. About a third of the Acanthaceae species in the Region are endemic to the KCE and half of the species found in the KCE area endemic. In comparison, both the Leguminosae and Asteraceae are neither represented well in numbers of endemics nor in total numbers of species.

One of the globally largest families in terms of numbers of genera and species, the Apiaceae, is not well-represented in the Region, but a monospecific endemic genus *Phlyctidocarpa* occurs in the KCE. Another cosmopolitan family of note is the Scrophulariaceae. The genera present in the Region are mainly confined to Africa with two of the three endemic to Namibia, namely *Chamaegigas* and *Manuleopsis*, in the KCE, while *Camptoloma* (which includes a KCE endemic species) is disjunct to northeast Africa. One of the biogeographically significant families is the Turneraceae, because it is one of the few families with endemic species in the KCE that is restricted to Africa and South America.

Table 9.1. Families present in the KCE with high numbers of endemic species and the total number of species in the KCE and in the Region

<b>Family</b>	<b>No. of species endemic to the KCE</b>	<b>Overall no. of species in the KCE</b>	<b>Overall no. of species in the Region</b>
Acanthaceae	55	105	155
Leguminosae	37	168	351
Asteraceae	21	124	378
Euphorbiaceae	21	58	132
Apocynaceae	19	63	174

Poaceae	18	169	406
Capparaceae	15	39	46
Burseraceae	14	24	30
Chenopodiaceae	12	24	80
Amaranthaceae	10	27	40
Tiliaceae	10	25	34

### 9.3.2 Endemic genera

Seven genera are endemic to the KCE, of which only one, *Marcelliopsis*, is not monospecific. Most endemic genera are only known from Namibia at present, for example *Arthraerua*, *Baynesia*, *Dewinteria*, *Kaokochloa* and *Lavrana*. *Streptolophus* only occurs in Angola, while *Welwitschia* has been collected in both countries. Two other monospecific genera, *Eremiolirion* and *Phytidocarpa*, are also endemic, but further field work may reveal that they grow sufficiently outside the KCE to be called near-endemic. Genera that are endemic to Angola and Namibia, mainly in the KCE and possibly near-endemic are *Aizoanthemum* and *Hiernia*. *Dacytliandra* has two species, one in the KCE and the other is in North Africa to India. A high proportion of the distribution ranges of *Chamaegigas* and *Manuleopsis* also occur in the KCE.

*Arthraerua* is included in tribe Amarantheae, subtribe Aervinae (Amaranthaceae). This subtribe includes other species-poor genera like *Calicorema*, *Leucosphaera*, *Marelliopsis* and *Nelsia* that are confined to the arid areas in southern Africa. *Arthraerua leubnitziae* (Kuntze) Schinz is confined to the west coast of Namibia where it very common on gravel plains. The eastern limit of its habitat corresponds to that of the fog belt. It frequently forms hummocks by trapping wind-blown sand.

*Baynesia*, represented by *B. lophophora*, in the Apocynaceae is only known from the mountainous areas just south of the Kunene River. It was placed in a new genus based on a combination of unusual features in the vegetative parts and flowers. Molecular evidence has shown that it is not closely allied to any other species (Bruyns 2005).

*Dewinteria* (family Pedaliaceae), previously included in the genus *Rogeria*, is also monospecific (*D. petrophila* (De Winter) Van Jaarsv. & Van Wyk). Unlike *Baynesia*, however, it occurs in the Welwitschia-desert Group (Craven 2009, Chapters 4 and 9). According to the locality data of the type specimen (De Winter & Leistner 5790) it occurs in red granite mountains consisting of large slabs and boulders with soil restricted to crevices, 30 miles south of Otinungua. Collections at the

same place and date as the type, and field work and collections of Kolberg and Craven, suggested that the habitat (i.e. cliff-faces on peaks) and associated species given in Van Jaarsveld & Van Wyk (2007) need to be verified. It is also not associated with any elements of the Cape flora mentioned by them, for example *Eriosephalus*, *Othonna* and *Pelargonium*.

*Eremiolirion* (family Tecophilaeaceae), represented by *Eremiolirion amboensis* (Schinz) J.C.Manning & Mannheimer (Manning *et al.* 2005) has recently been found on the coast north of Namibe in Angola. It has been found east of the KCE in exceptionally good rain years and is probably better defined as a near-endemic genus. Besides the two grass genera, it represents the only endemic monocotyledonous genus.

The presence of *Kaokochloa* (family Poaceae) in Angola has not yet been confirmed. It is an annual grass that may be very common after substantial rain on the plains and hill slopes. It is found in the western parts of the KCE and the seeds are reported to be eaten by humans.

*Lavrania* (family Apocynaceae) is distinguished from *Larryleachia*, a genus with members in the KCE, by the flowers being produced basally and the uniqueness of the 'bristle-tipped papillae' on the face of the corolla (Bruyns 2005). It is only found in the mountains around Sesfontein. It is presently only known from two localities 20 km apart, but is probably little collected due to its restricted occurrence on ledges on vertical cliffs.

*Marcellipsis* (family Amaranthaceae) consists of three species, two of which are perennial or dwarf shrubs, while the third is an annual. The latter is found in the Kaoko Group, while the other two occur in the Welwitschia-desert Group where they are generally found on hill sides or outcrops.

The monospecific genus *Phlyctidocarpa* contains the only member of the Apiaceae in the KCE (= *P. flava* Cannon & W.L.Theob.), besides *Steganotaenia araliacea*, a tree of the same family that is confined to the eastern parts. It is an annual that only occurs periodically after good rain, and for this reason has not been recorded very frequently. It also occurs on the eastern limits of the KCE and may be a near-endemic.

*Streptolophus* (family Poaceae, Panicoideae) is an annual only known from few collections in Angola. Very little is known about the genus and it could not be found during targeted field work after rain, over the past few years.



*Petalidium* is by far the most important for endemic species when comparing the number of endemics with the number of species present in the KCE and the Region. It is even more significant considering that the genus only consists of about 35 species, and that it is restricted to an area from Africa to India, a pattern often displayed by taxa representative of the Arid track. Unfortunately it is in great need of taxonomic revision. Targeted collecting in Namibia has resulted in a number of species previously known only from Angola also being found in Namibia. There are still numerous species that are limited to Angola and of which only very few collections have been made. Other genera in the Acanthaceae of importance for endemics in the KCE are *Barleria* (7), *Blepharis* (5) and *Ruellia* (5).

Cosmopolitan genera with endemic species in the KCE include *Acacia*, *Barleria*, *Cleome*, *Crotalaria*, *Euphorbia*, *Hibiscus*, *Indigofera*, *Polygala* and *Senecio*. Two pantropical genera, *Melhania* and *Grewia*, with their main distributions in Africa and Asia, have a number of endemic species recorded for the Angolan part of the KCE, but not for the Namibian part. In all probability some of the following species will also be found south of the Kunene River after further revision: *Melhania albiflora* (Hiern) Exell & Mendonça ex Hill & Salisb., *Melhania carrissoi* Exell & Mendonça, *Grewia argentea* Exell & Mendonça, *Grewia carrissoi* Exell & Mendonça, *Grewia cerocarpa* Exell & Mendonça, *Grewia elyseoi* Cav. & Simoes and *Grewia newtonii* Burret.

Table 9.2. Genera with high numbers of species endemic to the KCE, along with the number of species in both the Centre and in the Region

<b>Genus</b>	<b>Endemic species</b>	<b>No. of species in Centre</b>	<b>No. of species in Region</b>
<i>Petalidium</i>	26	27	33
<i>Euphorbia</i>	19	35	73
<i>Commiphora</i>	14	24	30
<i>Indigofera</i>	10	29	54
<i>Stipagrostis</i>	7	23	33
<i>Barleria</i>	7	23	30
<i>Grewia</i>	7	18	21
<i>Hibiscus</i>	6	22	36
<i>Cleome</i>	6	18	20

*Aeollanthus* (family Lamiaceae)

Western Angola is one of the areas with a particularly high frequency of *Aeollanthus* species and is the Area of Endemism for two sections of the genus. Discontinuities in the distribution of many of South Tropical African *Aeollanthus* species can probably be explained by the lack of suitable habitat in the intervening areas (Ryding 1986). They prefer well-drained soil and occur on rock outcrops and hill slopes. They usually grow in areas that are dry for a large part of the year, but are often found near small seasonal streams. *Aeollanthus rydingianus* Van Jaarsv. & A.E.van Wyk is only known from two localities, 300 km apart (Van Jaarsveld & Van Wyk 2005). The collection made in the area of the KCE is on the upper parts of the Baynes Mountains and that from Angola is from the Huila Plateau. It has only been collected once in 1968. The species is said to be an Afromontane element brought to the Baynes Mountains by birds (Van Jaarsveld & Van Wyk 2005). Considering that the Angolan specimen was represented by a single collection of which the material was considered insufficient (Ryding 1986), and the present poor state of knowledge of the Angolan highlands, this statement is considered premature. The species, like the others with which it co-occurs in the KCE, for example *Aloe omavandae*, are considered KCE endemics.

*Phaulopsis* (family Acanthaceae) is another genus represented by a few localized specimens of *Phaulopsis semiconica* in Namibia and two in Angola, many kilometers away. In the generic revision of the genus (Manktelow 1996) the Angolan specimens are said to differ in their inflorescences and flowers and that they may well represent a separate taxon. In addition the specimens were scant and few. The species is included as an endemic of the KCE, but further research is needed assess if the Angolan specimens should be recognised as a second species. The species is unusual as it has the densest and largest cover of glandular hairs of all species in the genus. In addition it does not have any short reflexed hairs on the stem and it occurs in the driest habitat.

### 9.3.3 Endemic species

As new species are found and described for the KCE, it is likely that the majority will be endemic, therefore the numbers will continue to increase. A workable definition for near-endemic is also necessary for more accurate assessments (see below). Table 9.3 divides the numbers of endemic taxa presently known into different categories. It excludes undescribed taxa that are often taken as endemic, for example *Sesamothamnus* (de Winter & Leistner 5504).

Table: 9.3. Estimates of the number of endemic taxa (families, genera, species and infraspecific taxa) in the KCE, divided between each of the main seed plant groups

	<b>Gymnosperms</b>	<b>Monocotyledons</b>	<b>Dicotyledons</b>	<b>Total</b>
Families	1	0	0	1
Genera	1	3	6	10
Species & infraspecific taxa	1	20	265	286

The genera with the highest number of species endemic to the KCE (Table 9.2) occur in a variety of families and these families are often represented by numerous endemic species in other genera as well (Table 9.4).

Table 9.4. Families and genera with the most endemic species in the KCE (the number of endemics in other genera of the same family given in brackets)

<b>Family</b>	<b>Genera with most endemics</b>	<b>Other genera with endemic species</b>
Acanthaceae	<i>Petalidium, Barleria</i>	<i>Blepharis</i> (4), <i>Justicia</i> (1), <i>Monechma</i> (4), <i>Phaulopsis</i> (1), <i>Rhinacanthus</i> (1), <i>Ruellia</i> (2)
Capparaceae	<i>Cleome</i>	<i>Boscia</i> (2), <i>Cadaba</i> (1), <i>Maerua</i> (1)
Euphorbiaceae	<i>Euphorbia</i>	<i>Bridelia</i> (1), <i>Phyllanthus</i> (1)
Leguminosae	<i>Acacia, Indigofera</i>	<i>Acacia</i> (3), <i>Adenolobus</i> (2), <i>Caesalpinia</i> (1), <i>Crotalaria</i> (4), <i>Indigostrum</i> (1), <i>Lotononis</i> (5), <i>Rhynchosia</i> (1), <i>Tephrosia</i> (7)
Malvaceae	<i>Hibiscus</i>	<i>Abutilon</i> (1), <i>Pavonia</i> (1)
Poaceae	<i>Stipagrostis</i>	<i>Brachiaria</i> (1), <i>Chloris</i> (1), <i>Eragrostis</i> (1), <i>Kaokochloa</i> (1), <i>Setaria</i> (1), <i>Streptolophus</i> (1), <i>Willkommia</i> (1)

Endemic species are found in an assortment of genera, many of which may not be associated with a desert. The example used to help define the Welwitschia-desert Group, *Adenia pechuelii* (Craven 2009, Chapter 5), belongs to a genus in the Passifloraceae that is adapted to habitats that differ from tropical rain forests to deserts. They usually have tuber-like stem bases, which in the case of this species may reach nearly a meter in diameter. Another example is that of *Aponogeton azureus* H.Bruggen, a hydrophyte that was only collected once in a seasonal fresh-water pool.

#### 9.3.4 New and problematic taxa

Specimens belonging to many genera have been collected (particularly by Kolberg and Craven), but cannot be identified. These genera include: *Abrus*, *Aptosimum*, *Boscia*, *Cineraria*, *Cyathula*, *Euphorbia* (particularly the annual species), *Hypoestes*, *Petalidium*, *Rhynchosia* and *Ruellia*. They are likely to represent new endemic species. Figueiredo (2008) also included *Amphiasma* sp. A, in a recent account of the Rubiaceae of Angola. Many endemics are only known from the type collection and those listed by Soares *et al* (2007) include: *Crotalaria longiclavata* Polhill, *Crotalaria nematophylla* Baker f. (collected in 1909), *Lotononis newtonii* Dummer (collected in 1892) and *Rhynchosia ovatifoliolata* Torre (collected in 1957). More Angolan species are only known from type collections than Namibian species, because collecting was impossible in Angola for many years due to the war, while ongoing targeted collection has produced results in Namibia (Kolberg pers. comm.). Species only known from types in Namibia include: *Aponogeton azureus* H.Bruggen, *Felicia gunillae* B.Nord., *Pentzia tomentosa* B.Nord. and *Jamesbrittenia fimbriata* Hilliard. Most of these were collected in the exceptionally good rainy season of 1974. *Euphorbia otjipembana* L.C.Leach was last collected in 1976, while *Monechma serotinum* P.G.Mey. was re-collected in 2006 after more than 30 years. Two infraspecific taxa have been recorded for Angola that are different to the taxa found south of the political border. They are *Euphorbia virosa* Willd. subsp. *arenicola* Leach and *Opilia campestris* Engl. var. *glabra* Hiepko (type only, collected in 1962).

Several newly described species from the KCE are based on very limited or no field work and few specimens, especially from Angola. Although type material from Angola may have been seen, the range of material is often very limited and it is likely that more field work would recover intermediates, that will then question the status of the new taxa.

### 9.3.5 Distributions of endemic species

The KCE has been divided into two main floristic Groups based on congruent distribution ranges of all the species present in the area (Craven 2009, Chapters 4 and 9). Further analyses of localities with concentrations of endemics within the Groups, do not show evidence of any particular taxa congregating, but the life form may sometimes be similar. For example:

- upper parts of the highest mountains in the north (Baynes and Otjihipa), have a succulent flora with various growth forms.
- species found only along the coast were not from any particular taxa. They showed no similarities in growth form and varied from rod-like stemmed shrubs, succulent-leaved dwarf shrubs, grasses to annual legumes.
- species found only in the vicinity of Sesfontein show the extent of the variety of endemics found together. There are two succulent species, one a monocotyledon (*Aloe dewinteri* Giess) and the other a dicotyledon (*Lavrania haagnerae*), as well as a tree that can reach heights of 10 m (*Kirkia dewinteri*).

A number of KCE endemics are holo-endemics as they have extremely restricted geographic distributions and may occupy just a few square kilometers (Richardson 1978). Although the inaccessibility of many areas of the KCE may be responsible for limited collecting and result in the assertion that some species are holo-endemics, the terrain and climatic conditions in the KCE lend themselves to numerous unique environments and many holo-endemics do occur. Endemic genera like *Baynesia* and *Lavrania* are good examples. This contrasts with species like *Petalidium subcrispum* P.G.Mey. that is undoubtedly under-collected and rare, but is not a holo-endemic as its known habitat is not peculiar to the vicinity. *Phaulopsis semiconica*, on the other hand, inhabits an uncommon niche, i.e. crevices in rocks facing south (away from the sun) where it grows close to the more or less vertical surface to keep in the shade. Here it can survive the dry, hot season seemingly without any xeromorphic structures, but it is densely covered with glandular hairs that, through their stickiness, protect the plant from grazing (Manktelow 1996).

*Commiphora* endemics may prefer either the western low-lying areas or the inland parts above 900 m in altitude (Table 9.5). Very few endemic species in this genus occur in both areas. The inland species attain more tree-like forms than those in the west, which may be low and sprawling, and the entire inland group has peeling bark, while some nearer the coast have smooth, non-peeling stems. Field observations of *Commiphora* species north of the Kunene River indicated that many of the low-growing Namibian species are taller and have more erect stems in Angola. This difference in

life-form north of the Kunene River has also been observed in other species, for example *Rhigozum* and *Cordia*.

Table 9.5. Distribution of *Commiphora* species within the two floristic Groups of the KCE

Group	Species
Kaoko Group	<i>Commiphora crenato-serrata</i> Engl.
	<i>Commiphora discolor</i> Mendes
	<i>Commiphora multijuga</i> (Hiern) K.Schum.
Welwitschia-desert Group	<i>Commiphora anacardiifolia</i> Dinter & Engl.
	<i>Commiphora giessii</i> J.J.A.van der Walt
	<i>Commiphora kaokoensis</i> W.Swanepoel
	<i>Commiphora krauseliana</i> Heine
	<i>Commiphora oblanceolata</i> Schinz
	<i>Commiphora saxicola</i> Engl.
	<i>Commiphora steynii</i> W.Swanepoel
	<i>Commiphora virgata</i> Engl.
	<i>Commiphora wildii</i> Merxm.
Both groups	<i>Commiphora kuneneana</i> W.Swanepoel
	<i>Commiphora otjihipana</i> W.Swanepoel

*Euphorbia*, with many species endemic in the KCE, can also be separated according to their ranges (Table 9.6). The only tree-like form occurs in the Kaoko Group, while the Welwitschia-desert Group consists mainly of dwarf shrubs with rod-like stems or shrubs. Five species have so far been recorded from the Angolan part of the KCE only, but this is likely to change with the on-going revision of the genus (Bruyns pers. comm.). A few indeterminate specimens have also been collected.

Table 9.6. Species of *Euphorbia* arranged according to their main ranges within the KCE

Group	Species
Welwitschia-desert group area	<i>Euphorbia berotica</i> N.E.Br.
	<i>Euphorbia chamaesycooides</i> B.Nord.
	<i>Euphorbia damarana</i> L.C.Leach
	<i>Euphorbia gariiepina</i> Boiss. subsp. <i>balsamea</i> (Welw. ex Hiern) L.C.Leach
	<i>Euphorbia giessii</i> L.C.Leach
	<i>Euphorbia insarmentosa</i> P.G.Mey.
	<i>Euphorbia pergracilis</i> P.G.Mey.
Angolan part of KCE only	<i>Euphorbia carunculifera</i> L.C. Leach
	<i>Euphorbia curocana</i> L.C.Leach
	<i>Euphorbia indurescens</i> L.C.Leach
	<i>Euphorbia negromontana</i> N.E.Br.
	<i>Euphorbia virosa</i> Willd. subsp. <i>arenicola</i> Leach
The Kaoko group (above 900 m)	<i>Euphorbia caperonioides</i> R.A.Dyer & P.G.Mey.
	<i>Euphorbia congestiflora</i> L.C. Leach
	<i>Euphorbia eduardoi</i> L.C.Leach
	<i>Euphorbia kaokoensis</i> (A.C.White, R.A.Dyer & B.Sloane) L.C.Leach
	<i>Euphorbia leistneri</i> R.H.Archer
	<i>Euphorbia otjipembana</i> L.C.Leach
	<i>Euphorbia subsalsa</i> Hiern subsp. <i>fluvialis</i> L.C.Leach

Besides a number of species already known to be restricted to the Brandberg Mountain (Table 9.7), a number of other unusual forms have been collected on the mountain that require attention. Many of these represent potentially new species. Specimens in the genera *Cyathula*, *Cineraria* and *Rhynchosia*, amongst others require revision, while *Lightfootia dinteri* still has to be transferred to *Wahlenbergia*. Although the *Cineraria* genus has recently been studied, the Namibian taxa were not completed (Cron *et al.* 2008). The endemics on the Brandberg are included in the KCE because they comply with the definition of a Centre of Endemism, i.e. an area with a high concentration of endemics (Wyk & Smith 2001), even if the overall floristic component of the area is more allied to another floristic group when it comes to having similar evolutionary developments.

Table 9.7. List of species restricted to the Brandberg Mountain

Family	Species
Crassulaceae	<i>Adromischus schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.
Tiliaceae	<i>Corchorus merxmuelleri</i> Wild
Amaranthaceae	<i>Eragrostis aristata</i> De Winter
Poaceae	<i>Felicia gunillae</i> B.Nord.
Asteraceae	<i>Hermannia merxmuelleri</i> Friedr.-Holzh.
Sterculiaceae	<i>Isolepis hemiuncialis</i> (C.B.Clarke) J.Raynal
Scrophulariaceae	<i>Jamesbrittenia tenella</i> (Hiern) Hilliard
Mesembryanthemaceae	<i>Lithops gracilidelineata</i> Dinter subsp. <i>brandbergensis</i> (de Boer) D.T.Cole
Asteraceae	<i>Nidorella nordenstamii</i> Wild
Asteraceae	<i>Pentzia tomentosa</i> B.Nord.
Asteraceae	<i>Philyrophyllum brandbergense</i> P.P.J.Herman
Acanthaceae	<i>Ruellia brandbergensis</i> Kers

There are also a number of range-restricted species on the mountain that are not included here as near-endemic (Table 9.8), because their ranges generally lie to the south and away from the core of the KCE. Most occur on isolated mountains or areas in the southern and central parts and not in the KCE itself. They are all included in the Highland Group of Craven (2009, Chapter 5).

Table 9.8. List of species occurring on the Brandberg Mountain that are also restricted to disjunct mountains or areas mainly in central or southern Namibia

Species	Associated Mountains or areas
<i>Alectra pseudobarleriae</i> (Dinter) Dinter	Naukluft, Otavi, Windhoek highlands
<i>Aloe viridiflora</i> Reynolds	Windhoek highlands
<i>Cineraria canescens</i> J.C.Wendl. ex Link	Gamsberg, Windhoek highlands
<i>Cucumella clavipetiolata</i> J.H.Kirkbr.	Etjo, Gamsberg
<i>Engleria africana</i> O.Hoffm.	Husab
<i>Eriocephalus dinteri</i> S.Moore	Aus, central & southern Mountains
<i>Euphorbia monteiroi</i> Hook.f. subsp. <i>brandbergensis</i> B.Nord.	Erongo, Spitzkop



<i>Euryops subcarnosus</i> DC. subsp. <i>vulgaris</i> B.Nord.	Central and southern Mountains, Otavi-Grootfontein
<i>Felicia hirsuta</i> DC.	Aus, Karasberg, Naukluft
<i>Manulea dubia</i> (Skan) Overkott ex Roessler	Aus, Karasberg, Waterberg
<i>Manuleopsis dinteri</i> Thell.	Kaoko, central & southern Mountains
<i>Melianthus comosus</i> Vahl	Windhoek highlands, Hunsberg
<i>Mentha longifolia</i> (L.) L. subsp. <i>wissii</i> (Launert) Codd	Naukluft
<i>Microlooma hereroense</i> Wanntorp	Gamsberg, Naukluft
<i>Nicotiana africana</i> Merxm.	Erongo, Spitzkop
<i>Orbea maculata</i> (N.E.Br.) L.C.Leach subsp. <i>rangeana</i> (Dinter & A.Berger) Bruyns	Central & southern Mountains (and one at the coast)
<i>Othonna brandbergensis</i> B.Nord.	Gamsberg, Namib Mountain southwest of Gamsberg
<i>Pentatrichia petrosa</i> Klatt	Karasberg
<i>Peristrophe namibensis</i> K.Balkwill subsp. <i>brandbergensis</i> K.Balkwill	Outcrops north east of Brandberg
<i>Plumbago wissii</i> Friedrich	Hunsberg
<i>Searsia burchellii</i> (Sond. ex Engl.) Moffett	Orange River outcrops
<i>Selago lepida</i> Hilliard	Gamsberg, Karasberg, Windhoek highlands and perhaps Aus
<i>Lightfootia dinteri</i> = <i>Wahlenbergia intricata</i> (Dinter & Markgraf) P.Craven ined.	Central & southern Mountains, Otavi Mountains

### 9.3.6 Near-endemics

Although the term *endemic* is useful, it is difficult to give an exact definition (Cain 1944). This is even more true when trying to define the concept near-endemic. Matthews *et al.* (1993) define a near-endemic as a taxon marginally present elsewhere, sometimes as distant satellite populations. The interpretation of the term ‘marginally’ leaves the definition open to various options. An endemic is defined in some biota as a large percentage (not necessarily 100%) of the population present in the area. However, because distribution ranges in many areas are not well known, a simpler approach has been taken here based on the presence or absence of a species in a different floristic Group based on evidence presented in Craven (Chapter 7 and 9). Three concepts have been used to classify species as near-endemics: 1. Species that have only been found to occur outside the core area in very good rain years are considered endemic to KCE (e.g. *Phyllanthus dinteri* Pax and *Merremia guerichii* A.Meeuse). 2. Species that are always found marginally outside the KCE in an area with a different flora are called near-endemics (e.g. *Hermannia solaniflora* K.Schum.). 3.

Species with disjunct distributions elsewhere are called near-endemic (e.g. *Tribulocarpus dimorphanthus*). Classification according to this scheme has not been conclusive, but presents a start based on objective criteria.

Plants limited to southern Angola, the Kaokoveld and other western parts of Namibia and occasionally the Cape, which are often listed as Kaokoveld elements, include *Acanthosicyos horridus*, *Cyphostemma currorii* and *Moringa ovalifolia*. These are now reclassified as near-endemics as they also occur partially outside the KCE. *Balanites angolensis* var. *welwitschii*, *Boscia microphylla* and *Cadaba schroepelii* occur in the KCE in Namibia, but also occur more widely in Angola and are therefore also called near-endemics.

### **9.3.7 Highly disjunct taxa**

*Commiphora oblanceolata* Schinz and *Dicoma cuneneensis* Wild are endemics with two disjunct localities within the KCE. However, whereas the morphology of the *Commiphora* plants appears to be the same, that of the *Dicoma* differs between the northern and southern populations. These may constitute a different infraspecific taxon. Differences include much less marked leaf dimorphism and generally shorter involucre, with glabrous or glabrescent phyllaries, contrasting with the tomentose phyllaries of the typical populations (Ortiz & Netnou 2005).

### **9.3.8 Distributions of relatives**

Due to the lack of phylogenetic studies on taxa present in the KCE, little is known about the species that are the closest relatives to KCE endemics. *Priva auricoccea*, which has not been re-collected since 1974, is said to be closely related to an East African species *P. curtisiae* Kobuski (Meeuse 1960) and may be another indicator of the arid corridor.

### **9.3.9 Adaptations, life forms and habitats**

No particular adaptation, be it in the morphology, behavior or physiology, is characteristic of the endemics of the KCE. Many specialized structures that have evolved for adaptation to arid conditions, for example succulent leaves or stems, are present, but attempts to tabulate or sort plant adaptations into categories proved futile. Life form, habit and habitats do not differ from that of the overall floristic composition (Craven 2009, Chapter 8). They show a remarkable diversity of growth forms and most of the acclimatization mechanisms are not yet described or understood.

The rich diversity of habitats available to plants in the KCE is not surprising, considering the variation in climate and topography. In addition the aridity is alleviated by coastal fog that may seep into cracks in the rocks or condense on the surface of the ground to be used by plants. Habitats include sandy river beds to gravel plains or rocky localities near the coast. Even small dunes develop around individual plants as wind-blown sand gathers against them e.g. *Ectadium rotundifolium*.

#### **9.4 Discussion**

A study of endemism is sensitive to species names and requires precise taxonomic data. Such a scenario is neither possible for a study involving Angolan taxa at this point, nor for certain taxa in Namibia. Two major factors thought to influence the degree of endemism, isolation and stability, can also not be discussed because even if the taxonomy of individual species is good, little is known about their relationships or derivation. This is mainly because of the lack of phylogenetic studies on taxa in the Region (Craven 2009, Chapter 4). Obtaining good herbarium specimens for further research is hampered by the inaccessibility of many areas, but mainly by the unpredictable and very localized rainfall that results in species being missed by botanists when they are available. A recent collection of an undescribed *Ammocharis* species is an example of the need to be in the right spot at the right time. The collection was made in an area well frequented by tourists, miners, and others, and plants were locally common but in a very restricted locality. This first record is probably due to the abnormally good rain that fell in a small area and was followed up the following season by another shower. For this reason, and many others, it is difficult to determine the ecological requirements that affect the endemic plant species.

It is not always easy to distinguish between different types of endemics based on their presumed origins. Neo-endemics are new or evolutionally young species, while palaeo-endemic are remnants of a species that formerly had a wider distribution. Endemics confined to restricted ranges or isolated location are neither of the above and called habitat specialist or holo-endemics (Richardson 1978). This type is probably the easiest to identify in the KCE, because of the very many and varied habitats occupied by endemic species. Evidence from molecular studies and relationships of taxa are likely to suggest that the endemic genera and many species in the western part of the KCE, below the escarpment, are palaeo-endemic (Craven 2009, Chapter 7). No phylogenies exist for taxa found above the escarpment, but these are thought to be neo-endemics, because of the relationships of the taxa overall.

The percentage of the flora that is endemic is often taken as a good guide to the length of time for which an area has been isolated. Also the longer an area has been isolated, the higher the taxonomic rank of its endemic plants is likely to be and *vice versa*. In the case of the KCE it is necessary to differentiate between the two Groups that make up the Centre. With an endemic family and many endemic genera, the western part, i.e. The Welwitschia-desert Group of the KCE, is considered to be older than the Kaoko Group. This is ascribed to the fact that where moisture is a limiting factor, local diversity in topography, soil, and other factors will have a much greater effect on the character of the vegetation than in regions where moisture is adequate. A statistical analysis of the percentage of the flora that is endemic was not carried because the data is inadequate and because information is often limited to political regions rather than phytogeographic regions.

## 9.5 Conclusions

The Kaokoveld Centre of Endemism has over 20% of its flora restricted to the area. The percentage of endemic genera and species is higher on the western side of the escarpment in the harshest environment. This profile needs to be followed up by detailed autecological studies of individual species and habitats. More complete listing of species within specific areas and the Groups is also necessary so that statistics will be possible and thereby a better gauge of the significance of smaller areas within the Centre. The alacrity with which new species are being described for the KCE is of concern, especially as many are based on very scant material and often without consulting material elsewhere. The family Acanthaceae includes the most endemics, while the other endemics are from a wide variety of families.

## References

- Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar* 1 & II. Umdaus Press, Hatfield.
- Bruyns, P.V. 2007. Apocynaceae. A new species of *Huernia* (Asclepiadoideae–Ceropegieae) from Southern Angola. *Bothalia* 37: 23–56.
- Bruyns, P.V. 2008. Notes on African plants. Apocynaceae: A new species of *Huernia* (Asclepiadoideae–Ceropegieae) from Angola. *Bothalia* 38: 83–85.
- Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET News* 9: 24–44.

- Craven, P. 2009. Chapter 4, this volume. Phytogeographical aspects of the flora of Namibia.
- Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.
- Craven, P. 2009. Chapter 7, this volume. Floristic and environmental analysis of the Kaokoveld Centre of Endemism.
- Craven, P. 2009. Chapter 8, this volume. Flora of the Kaokoveld Centre of Endemism.
- Cron, G.V., Balkwill, K. & Knox, E.B. 2008. Phylogenetic evidence for the generic circumscription of *Cineraria* L. (Asteraceae-Senecioneae). *Taxon* 57: 779–798.
- Figueiredo, E. 2008. The Rubiaceae of Angola. *Botanical Journal of the Linnean Society* 156: 537–638.
- Ickert-Bond, S.M. & Wojciechowski, M.F. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): Evidence from nuclear and chloroplast DNA sequence data. *Systematic Botany* 29: 834–849.
- Jacobson, K.M. & Lester, E. 2003. A first assessment of genetic variation in *Welwitschia mirabilis* Hook. *Journal of Heredity* 94: 212–217.
- Lewis, G., Schrire, B., Mackinder, B. & Lock, M. 2005. *Legumes of the World*. The Royal Botanic Gardens, Kew.
- Major, J. 1988. Endemism: A botanical perspective. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 117–146. Chapman & Hall, London.
- Manktelow, M. 1996. *Phaulopsis* (Acanthaceae) – a monograph. *Symbolae Botanicae Upsaliensis* 31: 1–184.
- Manning, J.C., Forest, F. & Mannheimer, C.A. 2005. *Eremiolirion*, a new genus of southern African Tecophilaeaceae, and taxonomic notes on *Cyanella alba*. *Bothalia* 35: 115–120.

- Matthews, W.S., Van Wyk, A.E. & Bredenkamp, G.J. 1993. Endemic flora of the north-eastern Transvaal escarpment, South Africa. *Biological Conservation* 63: 83-94.
- Meeuse, A. 1960. Verbenaceae. *Priva auricocca*. *Bothalia* 7: 424–5.
- Ortiz, S. & Netnou, N.C. 2005. A new species of *Dicoma* (Asteraceae, Mutisieae) from South Africa. *Botanical Journal of the Linnean Society* 147: 509–513.
- Otieno, D.F., Balkwill, K., Paton, A.J. & Savolainen, V. 2006. A reassessment of *Hemizygia* and *Syncolostemon* (Ocimeae—Lamiaceae). *Taxon* 55: 941–958.
- Peterson, A.T. & Watson, D.M. 1998. Problems with areal definitions of endemism: The effect of spatial scaling. *Diversity and Distributions* 4: 189–194.
- Richardson, I.B.K. 1978. Endemic taxa and the taxonomist. In: Street, H.E. (ed.), *Essays in plant taxonomy*. Pp. 245–262. Academic Press, London.
- Ryding, O. 1986. The genus *Aeollanthus* s.lat. (Labiatae). *Symbolae Botanicae Upsaliensis* 26: 1–152.
- Soares, M., Abreu, J., Nunes, H., Silveira, P., Schrire, B. & Figueiredo, E. 2007. The Leguminosae of Angola: Diversity and endemism. *Systematics and geography of plants* 77: 141–212.
- Schrire, B.D., Lavin, M. & Lewis, G.P. 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. *Biologiske skrifter* 55: 375–422.
- Swanepoel, W. 2007a. *Ceraria kaokoensis*, a new species from Namibia, with notes on gynodioecy in the genus. *Bothalia* 37: 202–206.
- Swanepoel, W. 2007b. *Commiphora kuneneana*, a new species from the Kaokoveld, Namibia. *Bothalia* 37: 40–48.
- Swanepoel, W. 2008a. *Ceraria kuneneana* (Didiereaceae/Portulacaceae), a new species from the Kaokoveld, Namibia. *South African Journal of Botany* 74: 71–75.

- Swanepoel, W. 2008b. *Commiphora otjihipana* (Burseraceae), a new species from the Kaokoveld, Namibia. *South African Journal of Botany* 74: 623–628.
- Van Jaarsveld, E.J. & Van Wyk, A.E. 2005. *Aeollanthus rydingianus*, a new species from northern Namibia and southern Angola. *Bothalia* 35: 157–173.
- Van Jaarsveld, E.J. & van Wyk, A.E. 2006. *Pelargonium vanderwaltii*, a new cliff-dwelling species from the Otjihipa Mountains, Northern Namibia. *Aloe* 43: 32–34.
- Van Jaarsveld, E.J., Swanepoel, W. & van Wyk, A.E. 2006. *Aloe kaokoensis*, a new species from the Kaokoveld, Northwestern Namibia. *Bothalia* 36: 75–77.
- Van Jaarsveld, E.J. & Van Wyk, A.E. 2007. *Dewinteria*, a new semisucculent, cliff dwelling genus endemic to the Kaokoveld, Namibia. *Bothalia* 37: 198–201.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Van Wyk, B.-E. & Kolberg, H. 2008. A new species of *Lotononis* section *Oxydium* (Fabaceae, Crotalarieae). *South African Journal of Botany* 74: 750–752.
- Won, H. & Renner, S.S. 2003. Horizontal gene transfer from flowering plants to *Gnetum*. *Proceedings of the National Academy of Science, USA*. 100:10824–10829.
- Won, H. & Renner, S.S. 2006. Dating dispersal and radiation in the Gymnosperm *Gnetum* (Gnetales)—Clock calibration when outgroup relationships are uncertain. *Systematic Biology* 55: 610–622.

## APPENDIX I

### List of species endemic to the Kaokoveld Centre of Endemism

- Acanthaceae
- Barleria cyanea* S.Moore
  - Barleria exellii* Benoist
  - Barleria meeuseana* P.G.Mey.
  - Barleria solitaria* P.G.Mey.
  - Blepharis ferox* P.G.Mey.
  - Blepharis gigantea* Oberm.
  - Blepharis linariifolia* Pers.
  - Blepharis noli-me-tangere* S.Moore
  - Justicia lazarus* S.Moore
  - Monechma salsola* (S.Moore) C.B.Clarke
  - Monechma serotinum* P.G.Mey.
  - Petalidium angustitubum* P.G.Mey.
  - Petalidium bracteatum* Oberm.
  - Petalidium canescens* (Engl.) C.B.Clarke
  - Petalidium cirrhiferum* S.Moore
  - Petalidium coccineum* S.Moore
  - Petalidium crispum* A.Meeuse ex P.G.Mey.
  - Petalidium elatum* Benoist
  - Petalidium giessii* P.G.Mey.
  - Petalidium glandulosum* S.Moore
  - Petalidium gossweileri* S.Moore
  - Petalidium halimoides* (Nees) S.Moore
  - Petalidium huillensis* C.B.Clarke
  - Petalidium lanatum* (Engl.) C.B.Clarke
  - Petalidium lepidagathis* S.Moore
  - Petalidium luteo-album* A.Meeuse
  - Petalidium ohopohense* P.G.Mey.
  - Petalidium physaloides* S.Moore
  - Petalidium pilosi-bracteolatum* Merxm. & Hainz
  - Petalidium rupestre* Moore
  - Petalidium spiniferum* C.B.Clarke
  - Petalidium subcrispum* P.G.Mey.
  - Petalidium variabile* (Engl.) C.B.Clarke
  - Petalidium welwitschii* S.Moore
  - Phaulopsis semiconica* P.G.Mey.
  - Rhinacanthus nasutus* (L.) Lindau
  - Ruellia currorii* T.Anderson
  - Ruellia diversifolia* S.Moore
- Aizoaceae
- Aizoanthemum mossamedense* (Welw. ex Oliv.) Friedrich
  - Aizoanthemum rehmannii* (Schinz) H.E.K.Hartmann
- Amaranthaceae
- Arthroa leubnitziae* (Kuntze) Schinz
  - Celosia benguellensis* C.C.Towns.
  - Hermstaedtia exellii* (Suess.) C.C.Towns.
  - Hermstaedtia spathulifolia* (Engl.) Baker
  - Marcelliopsis denudata* (Hook.f.) Schinz
  - Marcelliopsis splendens* (Schinz) Schinz



	<i>Marcellipsis welwitschii</i> (Hook.f.) Schinz
	<i>Nelsia angolensis</i> Bamps
Anacardiaceae	<i>Ozoroa benguellensis</i> (Engl.) R.Fern.
Apiaceae	<i>Phlyctidocarpa flava</i> Cannon & W.L.Theob.
Apocynaceae	<i>Baynesia lophophora</i> Bruyns
	<i>Ectadium rotundifolium</i> (H.Huber) Venter & Kotze
	<i>Hoodia currorii</i> (Hook.) Decne. subsp. <i>currorii</i>
	<i>Hoodia mossamedensis</i> (L.C.Leach) Plowes
	<i>Hoodia parviflora</i> N.E.Br.
	<i>Huernia calosticta</i> Bruyns
	<i>Huernia lophanthera</i> Bruyns
	<i>Huernia urceolata</i> L.C.Leach
	<i>Lavrania haagnerae</i> Plowes
	<i>Orbea maculata</i> (N.E.Br.) L.C.Leach subsp. <i>kaokoensis</i> Bruyns
	<i>Raphionacme haeneliae</i> Venter & R.L.Verh.
	<i>Stapelia parvula</i> Kers
	<i>Stapelia remota</i> R.A.Dyer
	<i>Stapelia schinzii</i> A.Berger & Schltr. var. <i>angolensis</i> Kers
	<i>Tavaresia thompsoniorum</i> Van Jaarsv. & R.Nagel
Aponogetonaceae	<i>Aponogeton azureus</i> H.Bruggen
Asphodelaceae	<i>Aloe asperifolia</i> A.Berger
	<i>Aloe corallina</i> I.Verd.
	<i>Aloe dewinteri</i> Giess
	<i>Aloe hereroensis</i> Engl. var. <i>lutea</i> A.Berger
	<i>Aloe kaokoensis</i> Van Jaarsv., Swanepoel & A.E.van Wyk
	<i>Aloe namibensis</i> Giess
	<i>Aloe omavandae</i> Van Jaarsv.
Asteraceae	<i>Antiphiona fragrans</i> (Merxm.) Merxm.
	<i>Calostephane marlothiana</i> O.Hoffm.
	<i>Dauresia alliarifolia</i> (O.Hoffm.) B.Nord. & Pelsner
	<i>Dicoma cuneneensis</i> Wild
	<i>Distephanus angolensis</i> (Hiern.) H.Rob. & B.Kahn
	<i>Engleria decumbens</i> (Welw. ex Hiern) Hiern
	<i>Eriocephalus pinnatus</i> O.Hoffm.
	<i>Geigeria spinosa</i> O.Hoffm.
	<i>Helichrysum erubescens</i> Hilliard
	<i>Helichrysum roseo-niveum</i> Marloth & O.Hoffm.
	<i>Macleodium sessiliflorum</i> (Harv.) S.Ortiz subsp. <i>sessiliflorum</i> var. <i>membranaceum</i> (S.Moore) S.Ortiz
	<i>Myxopappus hereroensis</i> (O.Hoffm.) Källersjö
	<i>Nicolasia felicioides</i> (Hiern) S.Moore
	<i>Pluchea lycioides</i> (Hiern) Merxm.
	<i>Senecio engleranus</i> O.Hoffm.
	<i>Tripteris microcarpa</i> Harv. subsp. <i>septentrionalis</i> (T.Norl.) B.Nord.
	<i>Vernonia obionifolia</i> O.Hoffm. subsp. <i>dentata</i> Merxm.
	<i>Vernonia vallicola</i> S.Moore
Balanitaceae	<i>Balanites angolensis</i> (Welw.) Welw. ex Mildbr. & Schltr. subsp. <i>welwitschii</i> (Tiegh.) Sands
Bignoniaceae	<i>Rhigozum virgatum</i> Merxm. & A.Schreib.
Burseraceae	<i>Commiphora anacardiifolia</i> Dinter & Engl.
	<i>Commiphora crenato-serrata</i> Engl.
	<i>Commiphora discolor</i> Mendes

	<i>Commiphora giessii</i> J.J.A.van der Walt
	<i>Commiphora kaokoensis</i> W.Swanepoel
	<i>Commiphora krauseliana</i> Heine
	<i>Commiphora kuneneana</i> W.Swanepoel
	<i>Commiphora multijuga</i> (Hiern) K.Schum.
	<i>Commiphora oblanceolata</i> Schinz
	<i>Commiphora otjhipana</i> W.Swanepoel
	<i>Commiphora saxicola</i> Engl.
	<i>Commiphora steynii</i> W.Swanepoel
	<i>Commiphora virgata</i> Engl.
	<i>Commiphora wildii</i> Merxm.
Capparaceae	<i>Boscia gossweileri</i> Exell
	<i>Boscia pestalozziana</i> Gilg
	<i>Cadaba benguellensis</i> Mendes
	<i>Cadaba schroepelii</i> Suess.
	<i>Cleome carnos</i> (Pax) Gilg & Benedict
	<i>Cleome foliosa</i> Hook.f. var. <i>foliosa</i>
	<i>Cleome foliosa</i> Hook.f. var. <i>namibensis</i> (Kers) Codd
	<i>Cleome gossweileri</i> Exell
	<i>Cleome laburnifolia</i> Roessler
	<i>Cleome mossamedensis</i> Exell & Mendonça
	<i>Maerua kaokoensis</i> Swanepoel
Chenopodiaceae	<i>Salsola angolensis</i> Botsch.
	<i>Salsola glabra</i> Botsch.
	<i>Salsola hoanibica</i> Botsch.
	<i>Salsola huabica</i> Botsch.
	<i>Salsola omaruruensis</i> Botsch.
	<i>Salsola parviflora</i> Botsch.
	<i>Salsola pillansii</i> Botsch.
	<i>Salsola procera</i> Botsch.
	<i>Salsola seydelii</i> Botsch.
	<i>Salsola swakopmundi</i> Botsch.
	<i>Salsola ugabica</i> Botsch.
	<i>Salsola unjabica</i> Botsch.
Combretaceae	<i>Combretum oxystachyum</i> Welw. ex M.A.Lawson
	<i>Combretum wattii</i> Exell
Convolvulaceae	<i>Merremia guerichii</i> A.Meeuse
	<i>Merremia multisecta</i> Hallier f.
	<i>Seddera schizantha</i> Hallier f.
Crassulaceae	<i>Kalanchoe scapigera</i> Welw. ex Britten
	<i>Kalanchoe teixeirae</i> Raym.-Hamet ex R.Fern.
Cucurbitaceae	<i>Citrullus rehmi</i> De Winter
	<i>Cucumella aspera</i> (Cogn.) C.Jeffrey
	<i>Momordica welwitschii</i> Hook.f.
Cyperaceae	<i>Bolboschoenus nobilis</i> (Ridl.) Goetgh. & D.A.Simpson
Euphorbiaceae	<i>Bridelia tenuifolia</i> Müll.Arg.
	<i>Euphorbia berotica</i> N.E.Br.
	<i>Euphorbia caperonioides</i> R.A.Dyer & P.G.Mey.
	<i>Euphorbia carunculifera</i> L.C. Leach
	<i>Euphorbia chamaesycooides</i> B.Nord.
	<i>Euphorbia congestiflora</i> L.C. Leach
	<i>Euphorbia curocana</i> L.C.Leach

- Euphorbia damarana* L.C.Leach  
*Euphorbia eduardoi* L.C.Leach  
*Euphorbia gariiepina* Boiss. subsp. *balsamea* (Welw. ex Hiern)  
L.C.Leach  
*Euphorbia giessii* L.C.Leach  
*Euphorbia indurescens* L.C.Leach  
*Euphorbia insarmentosa* P.G.Mey.  
*Euphorbia kaokoensis* (A.C.White, R.A.Dyer & B.Sloane) L.C.Leach  
*Euphorbia leistneri* R.H.Archer  
*Euphorbia negromontana* N.E.Br.  
*Euphorbia otjipembana* L.C.Leach  
*Euphorbia pergracilis* P.G.Mey.  
*Euphorbia subsalsa* Hiern subsp. *fluvialis* L.C.Leach  
*Euphorbia virosa* Willd. subsp. *arenicola* Leach  
*Phyllanthus dinteri* Pax  
Geraniaceae *Pelargonium vanderwaltii* Van Jaarsv.  
*Sarcocaulon marlothii* Engl.  
*Sarcocaulon mossamedense* (Welw. ex Oliv.) Hiern  
Kirkiaceae *Kirkia dewinteri* Merxm. & Heine  
Lamiaceae *Aeollanthus caudatus* O.Ryding  
*Aeollanthus haumannii* Van Jaarsv.  
*Aeollanthus lobatus* N.E.Br.  
*Aeollanthus namibiensis* O.Ryding  
*Leucas ebracteata* Peyr. var. *kaokoveldensis* Sebald  
*Plectranthus unguentarius* Codd  
*Syncolostemon floccosus* (Launert) D.F. Otieno  
*Tetradenia kaokoensis* Van Jaarsv. & A.E.van Wyk  
Leguminosae *Acacia montis-usti* Merxm. & A.Schreib.  
*Acacia quintanilhae* Torre  
*Acacia robynsiana* Merxm. & A.Schreib.  
*Adenolobus pechuelii* (Kuntze) Torre & Hillc. subsp. *mossamedensis*  
(Torre & Hillc.) Brummitt & J.H.Ross  
*Adenolobus pechuelii* (Kuntze) Torre & Hillc. subsp. *pechuelii*  
*Caesalpinia pearsonii* L.Bolus  
*Crotalaria colorata* Schinz subsp. *colorata*  
*Crotalaria longiclavata* Polhill  
*Crotalaria nematophylla* Baker f.  
*Crotalaria stenopoda* Baker f.  
*Indigastrum guerranum* (Torre) Schrire  
*Indigofera anabibensis* A.Schreib.  
*Indigofera benguellensis* Welw. ex Baker  
*Indigofera breviracemosa* Torre  
*Indigofera cunenensis* Torre  
*Indigofera desertorum* Torre  
*Indigofera maritima* Baker  
*Indigofera pruinosa* Welw. Ex Baker  
*Indigofera santosii* Torre  
*Indigofera teixeirae* Torre  
*Lotononis bracteosa* B.-E.van Wyk  
*Lotononis macroloba* B-E.van Wyk & H. Kolberg  
*Lotononis newtonii* Dummer  
*Lotononis schreiberi* B.-E.van Wyk

	<i>Lotononis tenuis</i> Baker
	<i>Rhynchosia ovatifoliolata</i> Torre
	<i>Tephrosia disperma</i> Welw. ex Baker
	<i>Tephrosia griseola</i> H.M.L.Forbes
	<i>Tephrosia monophylla</i> Schinz
	<i>Tephrosia oxygona</i> Welw. ex Baker subsp. <i>oxygona</i> var. <i>obcordata</i> Torre
	<i>Tephrosia oxygona</i> Welw. ex Baker subsp. <i>oxygona</i> var. <i>oxygona</i>
	<i>Tephrosia pallida</i> H.M.L.Forbes
	<i>Tephrosia pearsonii</i> Baker f.
	<i>Tephrosia sylvitroides</i> Baker f.
Loranthaceae	<i>Oncocalyx welwitschii</i> (Engl.) Polhill & Wiens
Lythraceae	<i>Nesaea lythroides</i> Welw. ex Hiern
Malvaceae	<i>Abutilon mendoncae</i> Baker f.
	<i>Hibiscus benguellensis</i> Exell & Mendonça
	<i>Hibiscus castroi</i> Baker f. & Exell var. <i>castroi</i>
	<i>Hibiscus merxmuelleri</i> Roessler
	<i>Hibiscus rubriflorus</i> Bak.f.
	<i>Pavonia gossweileri</i> Exell
Mesembryanthemaceae	<i>Lithops gracilidelineata</i> Dinter subsp. <i>gracilidelineata</i>
	<i>Lithops ruschiorum</i> (Dinter & Schwantes) N.E.Br.
	<i>Mesembryanthemum cryptanthum</i> Hook.f.
	<i>Mesembryanthemum dimorphum</i> (Welw. ex Oliv.) N.E.Br.
	<i>Mesembryanthemum kuntzei</i> Schinz
Molluginaceae	<i>Hypertelis caespitosa</i> Friedrich
	<i>Mollugo fragilis</i> Wawra ex Wawra & Peyr
Nyctaginaceae	<i>Boerhavia deserticola</i> Codd
Opiliaceae	<i>Opilia campestris</i> Engl. var. <i>glabra</i> Hiepko
Passifloraceae	<i>Adenia pechuelii</i> (Engl.) Harms
	<i>Basananthe littoralis</i> Peyr.
Pedaliaceae	<i>Dewinteria petrophila</i> De Winter
	<i>Sesamothamnus benguellensis</i> Welw.
	<i>Sesamothamnus guerichii</i> (Engl.) E.A.Bruce
	<i>Sesamum marlothii</i> Engl.
	<i>Sesamum pedalioides</i> Welw.
	<i>Sesamum rigidum</i> Peyr.
	<i>Sesamum schinzianum</i> Asch.
Poaceae	<i>Brachiaria psammophila</i> (Welw. ex Rendle) Launert
	<i>Chloris flabellata</i> (Hack.) Launert
	<i>Eragrostis pygmaea</i> De Winter
	<i>Kaokochloa nigrirostris</i> De Winter
	<i>Setaria finita</i> Launert
	<i>Stipagrostis damarensis</i> (Mez) De Winter
	<i>Stipagrostis dinteri</i> (Hack.) De Winter
	<i>Stipagrostis giessii</i> Kers
	<i>Stipagrostis hermannii</i> (Mez) De Winter
	<i>Stipagrostis ramulosa</i> De Winter
	<i>Stipagrostis uniplumis</i> (Licht.) De Winter var. <i>intermedia</i> (Schweick.) De Winter
	<i>Streptolophus sagittifolius</i> Hughes
	<i>Willkommia newtonii</i> Hack.
Polygalaceae	<i>Polygala mossamedensis</i> Paiva
Polygonaceae	<i>Oxygonum acetosella</i> Welw.

Portulacaceae	<i>Ceraria carrissoana</i> Exell & Mendonça <i>Ceraria kaokoensis</i> Swanepoel <i>Ceraria kuneneana</i> Swanepoel <i>Ceraria longipedunculata</i> Merxm. & Podlech <i>Talinum portulacifolium</i> (Forssk.) Asch. & Schweinf.
Rubiaceae	<i>Amphiasma benguellense</i> (Hiern) Bremek. <i>Amphiasma merenskyanum</i> Bremek. <i>Kohautia angolensis</i> Bremek.
Rutaceae	<i>Zanthoxylum ovatifoliolatum</i> (Engl.) Finkelstein
Scrophulariaceae	<i>Aptosimum angustifolium</i> F.E. Weber & Schinz <i>Camptoloma rotundifolium</i> Benth. <i>Jamesbrittenia barbata</i> Hilliard <i>Jamesbrittenia chenopodioides</i> Hilliard <i>Jamesbrittenia fimbriata</i> Hilliard <i>Jamesbrittenia heucherifolia</i> (Diels) Hilliard
Sterculiaceae	<i>Hermannia amabilis</i> Marloth ex K.Schum. <i>Hermannia glandulosissima</i> Engl. <i>Hermannia helianthemum</i> K.Schum. <i>Melhania albiflora</i> (Hiern) Exell & Mendonça ex Hill & Salisb. <i>Melhania carrissoi</i> Exell & Mendonça
Tecophilaeaceae	<i>Eremiolirion amboensis</i> (Schinz) J.C.Manning & C.A.Mannheimer
Thymelaeaceae	<i>Gnidia welwitschii</i> Hiern
Tiliaceae	<i>Grewia argentea</i> Exell & Mendonça <i>Grewia carrissoi</i> Exell & Mendonça <i>Grewia cerocarpa</i> Exell & Mendonça <i>Grewia elyseoi</i> Cav. & Simoes <i>Grewia newtonii</i> Burret
Turneraceae	<i>Turnera oculata</i> Story var. <i>oculata</i> <i>Turnera oculata</i> Story var. <i>paucipilosa</i> Oberm.
Verbenaceae	<i>Priva auricoccea</i> A.Meeuse
Violaceae	<i>Hybanthus mossamedensis</i> Mendes
Vitaceae	<i>Cyphostemma uter</i> (Exell & Mendonça) Desc.
Welwitschiaceae	<i>Welwitschia mirabilis</i> Hook.f.
Zygophyllaceae	<i>Tribulus echinops</i> Kers <i>Tribulus excrucians</i> Wawra <i>Zygophyllum orbiculatum</i> Welw. ex Oliv. <i>Zygophyllum stapffii</i> Schinz

*Sesamothamnus leistneranus* ined. (= De Winter & Leistner 5504) and *Zygophyllum inflatum* Van Zyl ined. are in manuscript form and not yet validly published

## APPENDIX II

### An overview of the newly defined Kaokoveld Centre of Endemism

#### Location

The centre stretches from north of Namibe in southwestern Angola southwards to the Kuiseb River in western Namibia. The eastern limit in Angola is the base of the Huila plateau. The demarcation is obvious as the plateau rises abruptly and has a very different flora. South of the Kunene River, the KCE stretches from the sea to the eastern sandveld *ca.* 15° E. Further south (from *ca.* 20° S) the eastern border is generally the plateau above 900 m. The southern boundary is the Kuiseb River (*ca.* 23° S). A few species have extended distributions between the dunes and the southern escarpment to *ca.* 24° S.

#### Topography

The KCE varies in altitude from sea level, through narrow coastal plains, to 1800 m above sea level in the northern Baynes and Otjihipa ranges. The perennial Kunene River cuts a deep gorge below the Ruacana Falls. Its catchment is outside the Kaokoveld in Angola, but in northern Namibia there is a small area that drains into the Kunene River. A number of ephemeral rivers flow westwards through the Kaokoveld, the Curoca is the main one in Angola, and the numerous river catchments in the Namibian section are mapped and described by Jacobsen *et al.* (1995). The coastal belt of Angola can be as narrow as 12 km wide and the escarpment towards the sea is steeper than in Namibia, sometimes forming steep cliffs. South of the Kunene River the northern escarpment runs more or less parallel to the Atlantic coast as far south as *ca.* 20 °E. West of this, dunes are found scattered near the coast. Gravel plains are characteristic and inselbergs and smaller Namib mountains also occur (Irish, 2003). The highest point in Namibia, the Brandberg Mountain, at 2,579 m above sea level, lies in the KCE (Mendelsohn *et al.* 2002).

#### Geology and soils

The geology is very diverse as can be seen by the many rock types and geological groups recorded for the Namibian section in Mendelsohn *et al.* (2002). Martin (1965) provided the first outline for the northwest and pointed out one of the most important attributes of geology from a phytogeographical point of view, namely its strong similarity to South America (Martin, 1961). Muller (2002) provides simplified geological descriptions of important mountains in the region and the geology of the Brandberg is discussed in detail by Muller (2000). The Anorthosite Complex of SW Angola/NW Namibia has attracted considerable interest and is documented by De Carvalho &

Alves (1990), Drüppel & Okrusch (2000) and Drüppel, Brandt & Okrusch (2000). A detailed survey of soils in Namibia is being carried out by the Agro-Ecological Zoning Programme (1996-ongoing). To date only a generalised map is available and the poor soil coverage in Kaokoveld is obvious from the high percentage that is classified as rocky outcrops. Bollig *et al.* (2002a), Brunotte & Sander (2002) and Brunotte *et al.* (2002b) have contributed to the understanding of the soils in Namibia, but little is known about soils north of the Kunene River.

## **Climate**

The most salient features of the rainfall in western Namibia, which also apply in Angola, have been summarised in Jacobsen *et al.* (1995) as follows:

1. Rainfall decreases from east to west, thus floods, originating from heavy rains in the inland, may provide essential water and food resources to people in lower desert reaches of rivers.
2. As rainfall decreases towards the west, the variability in annual rainfall increases. The mean is therefore not a good indicator of the rainfall that can be expected.
3. Drought is normal across the entire region.

Other important characteristics are that temperatures closer to the coast are much lower and fluctuate less, while inland temperatures may be very high. Fog occurs along the coast and is attributed to the cold Benguela Current and the high-pressure system from the south Atlantic. These cause precipitation to decrease as latitude and altitude increase (Dombo *et al.*, 2002). The climate is discussed for parts of this area by Malan & Owen Smith (1974), Viljoen (1980) and Sander & Becker (2002), while Olszewski (2000) discusses the climate of the Brandberg. The scarcity of meteorological stations, shown by Irish (2002b), and the problems encountered with automatic weather stations in the heat of northwest Namibia means that little accurate information is available. Estimates of isohyete positions and the percentage variation in annual rainfall are however indicated by Mendelsohn *et al.* (2002).

## **Regional historical phytogeography**

The KCE lies in Karoo-Namib regional centre of endemism and the Kalahari-Highveld regional transition zone of White (1983). According to Werger (1978) the KCE falls into the Karoo-Namib Region, with a coastal Namib Domain and an inland Namaqualand Domain, including a Kaoko section in the northern part. Both Robinson (1975) and Craven (2009 Chapter 5) found few links between the KCE flora and the flora of the Karoo-Namib Region.

## **Ecological phytogeography**

The KCE is included in the Namib Desert, Nama-Karoo and tree and shrub biomes of Mendelsohn (2002) and further subdivision into vegetation zones are given. No comparable vegetation surveys have been carried out north and south of the Kunene River and the only detailed studies are for Namibia: Viljoen (1980) for the area between the Kunene and the Hoanib River; Becker & Jürgens (2000) looked at three transects from the Atlantic inwards in the same area as Viljoen. The community structure of the Central Namib was studied by Robinson (1977) and Hachfeld (1996). Wittneben (2003) surveyed the vegetation of the Brandberg Mountain. No detailed vegetation surveys have been carried out in Angola. Matos (1970) divided the vegetation of the Iona National Park, into four zones. Huntley (1974) calls the southwestern corner of Angola, along with a coastal strip extending north to Luanda, the “south-west arid biome”. The vegetation types are said to vary considerably according to soil and climatic conditions, however, plants are all deciduous and can endure long rainless periods. Grasses occur on the dunes near the coast and *Acacia-Commiphora* thickets are found further inland.

## **Fairy Circles**

Circular, slightly concave depressions, devoid of vegetation and often surrounded by a fringe of tall grass is the definition of Fairy circles given by Van Rooyen *et al.* (2004). Despite considerable interest in these conspicuous features of the landscape present from Angola to the Orange River, their origins remain speculative. Various hypotheses have been advanced, but these are sometimes based on limited sound research. The most recent work, which is on-going and based in Kaokoveld, is that of Van Rooyen *et al.* (2004) and further south by Jankowitz *et al.* (2008).

## **Conservation**

There are a number of formally protected areas in the KCE. In Namibia, the Skeleton Coast National Park covers a narrow portion from the Kunene River, about 500 km south to the Ugab River. North of the Unijab River is a wilderness area closed to the public. A small section of the Namib-Naukluft, from the Swakop to the Kuiseb Rivers, lies in the KCE. North of this Park is the National West Coast Tourist Recreation Area. Etosha National Park included the Kaokoveld in the early 1900's, but by 1971, it only included a strip between the Ugab and Hoanib Rivers and is not linked today. There are numerous conservancies and these have contributed to increasing wildlife numbers, but few if any, have management plans that include the plant life. The recently declared World Heritage site situated at Twyfelfontein lies on the border of this centre. Threats to the area include severe overstocking, as well as the Hydroelectric scheme planned for the Epupa falls or Baynes area on the Kunene River. In Angola, Iona is the largest and oldest park having been



established in 1937 (Huntley, 1974). It stretches from the Kunene to the Curoca Rivers. Nomadic pastoralists utilise the park in good years. Reserva de Namibe was established in 1957 and is 4,684 km<sup>2</sup> (Huntley, 1974). A cross border park in the area is on the table.

### **Ethnobotany**

One of the more unusual traditional food sources is found in the western parts of the KCE where seeds are collected from the underground granaries of certain species of ant. The seeds are winnowed in a flat wooden bowl and then prepared as porridge or used in beer-brewing. Seeds of *Stipagrotis* and *Monsonia* species are harvested (Steyn & Du Pisani 1985).

### **References**

Agro-Ecological Zoning Programme. 1996-ongoing. Directorate of Agricultural Research and Training, Ministry of Agriculture, Water and Rural Development, Windhoek.

Becker, T. 2002. Zur Phytogeographie des Kaokolandes. In: Bollig, M., Brunotte, E. & Becker, T. (eds). Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia. Pp. 69–74. *Kölner Geographische Arbeiten 77*, Köln.

Becker, T. & Jürgens, N. 2000. Vegetation along climate gradients in Kaokoland, North-West Namibia. *Phytocoenologia* 30: 543–565.

Bollig, M., Brunotte, E. & Becker, T. 2002. Der Sonderforschungsbereich 389 und die Schwerpunktregion “Kaokoland” Perspektiven und forschungshistorische Bedingungen. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Kaokoland - Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semi-ariden Nordwesten Namibias*. Pp. 1–12. *Kölner Geographische Arbeiten 77*, Köln.

Brunotte, E. & Sander, H. 2000. Loess accumulation and soil formation in Kaokoland (Northern Namibia) as indicators of Quarternary climatic change. In: Kröpelin, S. & Petit-Maire, N. (eds). *Global and Planetary Change, Special Volume "Paleomonsoon Variations and Global Change during the Late Quaternary"*. *Global & Planetary Change* 26: 67–75.

Brunotte, E., Eichhorn, B. & Sander, H. 2002. Quarternary climate change in North Western Namibia: Sedimentologic, pedologic and archaeobotanic evidence. *Palaeoecology of Africa* 39.

- Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.
- De Carvalho, H. & Alves, P. 1990. Grabbro-Anorthosite Complex of SW Angola/NW Namibia. Notes about the general geology. An essay of genetic interpretation. *Commun. IICT. Sér. Ciênc. Da Rerra 2*.
- Dombo, A., da Costa, E. & Neto, G. 2002. Angola. In: Golding, J.S. (ed.). *Southern African Red Data Lists*. Southern African Botanical Diversity Network Report 14: 8–11. SABONET, Pretoria.
- Drüppel, K. & Okrusch, M. 2000. Petrology and geochemistry of anorthositic rocks of the Kunene Intrusive Complex, NW Namibia. *Geoluanda 2000 abstracts* 49–50.
- Drüppel, K., Brandt, S. & Okrusch, M. 2000. Evolution of the anorthositic Kunene Intrusive Complex and the metamorphic rocks of the Epupa Complex, NW Namibia: Evidence for cogenetic formation during proterozoic crustal extension? *Geoluanda 2000 abstracts* 47–48.
- Hachfeld, B. 1996. Vegetationsanalytische Transektanalyse in der noerdlichen Zentralen Namib. Diplomarbeit, Universitaet Hamburg, Hamburg.
- Huntley, B.J. 1974. Outlines of Wildlife Conservation in Angola. *Journal of South African Wildlife Management Association* 4: 157–166.
- Irish, J. 2002. Summit climate of Namibian mounatins. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Irish, J. 2003. Namibian Mountains: bioiversity potential based on topography. 2. Namib Mountains. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Jacobson, P.J., Jacobson, K.M. & Seely, M.K. 1995. *Ephemeral Rivers and their catchments*. Desert Research Foundation of Namibia.
- Jankowitz, W.J., Van Rooyen, M.W., Shaw, D., Kaumba, J.S. & Van Rooyen, N. 2008. Mysterious circles in the Namib Desert. *South African Journal of Botany* 74: 332–334.
- Malan, J.S. & Owen Smith, G.L. 1974. The ethnobotany of Kaokoland. *Cimbebasia* (B)2: 131–178.

- Martin, H. 1961. The hypothesis of continental drift in the light of recent advances of geological knowledge in Brazil and in South West Africa. *The Geological Society of South Africa* 64 (Alex L. du Toit Memorial lectures 7): 1–47.
- Martin, H. 1965. *The precambrian geology of South West Africa and Namaqualand*. Rustica Press, Wynberg.
- Matos, G.C. 1970. A vegetacao do Parque Nacional do Ohna. *Boletum da Sociedade Brottenana* 2: 245–247.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, A. 2002. *Atlas of Namibia: A portrait of the land and it's people*. David Phillip Publishers, Cape Town.
- Miller, R. McG. 2000. Geology of the Brandberg Massif, Namibia and its environs. In Kirk-Spriggs, A.H. & Marais, E. Biodiversity of the Brandberg Massif, Namibia. *Cimbebasia* 9: 17–38.
- Miller, R. McG. 2002. Simplified geological decriptions of Namibia's Mountains. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Olszewski, J.D.S. 2000. Brandberg climatic considerations. In: Kirk-Spriggs, A.H. & Marais, E. (eds). Biodiversity of the Brandberg Massif, Namibia. *Cimbebasia* 9: 39–48.
- Robinson, E.R. 1975–77. Phytogeography of the Namib Desert of South West Africa and its significance to discussions of the age and uniqueness of the desert. *Palaeoecology of Africa* 67–74.
- Robinson, E.R. 1977. Phytosociology of the Namib Desert Park, SWA. Unpublished. MSc Thesis, University of Natal, Pietermaritzburg.
- Sander, H. & Becker, T. 2002. Klimatologie des Kaokolandes. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 57–68. Kölner Geographische Arbeiten 77, Köln.
- Steyn, H.P. & Du Pisani, E. 1985. Grass-seeds, game and goats: An overview of Dama subsistence. *SWA Scientific Society Journal* 39: 37–52.

Van Rooyen, M.W., Theron, G.K., van Rooyen, N., Jankowitz, W.J. & Matthews, W.S. 2004. Mysterious circles in the Namib desert: review of hypotheses on their origin. *Journal of Arid Environments* 57: 467–485.

Viljoen, P.J. 1980. Veldtypes verspreiding van die groter soogdiere en enkele aspekte van die ekologie van Kaokoland. Unpublished. M.Sc. thesis, University of Pretoria, Pretoria.

Werger, M.J.A. (ed.). 1978. *Biogeography and ecology of southern Africa*. Junk, The Hague.

White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.

Wittneben, M. 2003. Vegetation on Brandberg Mountain, Namibia 2000. Unpublished. Diploma Thesis, University of Bremen, Bremen.



An undescrbed *Ammocharis* species in the Welwitschia-desert Group and it's locality, just south of the Swakop River in Namibia

## **Chapter 10**

### **Conclusions**

## Conclusions

Sir Joseph Dalton Hooker wrote: “of all the branches of botany there is none whose elucidation demands so much preparatory study or so extensive an acquaintance with plants and their affinities, as that of their phytogeographic distributions” (Polunin 1960).

These words, written over a century ago, remain appropriate today. They also go a long way in explaining why two seemingly separate sections make up this study and the difficulties encountered in systematically presenting a study of this nature. This final chapter draws together the findings of the previous chapters that cover the wide range of topics referred to by Hooker, and considers what this wide range of information enabled us to conclude about the Kaokoveld Centre of Endemism.

Firstly the area was delimited by numerical analysis and this showed conclusively that the Kaokoveld Centre of Endemism (KCE) consists of a distinctive complement of species with congruent distribution patterns (i.e. floristic elements). Some species lie marginally outside the core area and were defined as near-endemic KCE species.

Secondly the flora of the Kaokoveld Centre of Endemism (KCE) was shown to differ from that of surrounding regions in terms of taxonomic composition, as well as in its affinities and origins. In addition the floristic elements within the KCE were also separated into identified Groups that occupy distinct regions with different histories. The Kaoko Group is the most speciose, but the *Welwitschia*-desert Group is the most unique and considerably older, while the flora of the upper parts of the Brandberg Mountain is more closely related to a group of species associated with highlands and may also occur eastwards to the Highveld of South Africa. These distinct differences mean that certain issues, such as the age and origin of the flora of the KCE, must be seen as three-fold and cannot be generalized.

Because of the uncertainties with regard to many aspects of the flora, especially that in Angola, the results are regarded as exploratory at present, rather than definitive. However, there is sufficient data to say with confidence that the Kaokoveld Centre of Endemism is an area with a high concentration of endemic species that is based on actual distribution patterns of elements. It is not necessarily the richest in species, but the diversity of taxa, forms and adaptations to the harsh environment is obvious. Many of the endemics are localised and rare with specific habitat

preferences, but no particular life or growth forms dominate. It also includes the full distribution ranges of *Welwitschia mirabilis*, one of the most intriguing plants in the world.

The study showed that numerical analysis is useful in delimiting a biogeographically important area, but that it cannot provide any causal factors. Further investigation is needed for this facet. It would appear that the smaller the area and the more sparsely populated, the more accurate and detailed the information needs to be. For this reason, with the limited number of taxa per unit area in an arid environment such as this, it is recommended that such analyses be based on the taxa and at least one additional feature, such as altitude or membership of a floristic Group.

Molecular evidence contributed to understanding the age and origins of the Welwitschia-desert Group, but there remains a marked lack of appropriate data from phylogenies and palaeo-environmental studies for in the areas covered by the Kaoko group. This obviously hinders the formulation of hypothesis about the age of the flora, which must then rely on evidence from the extra-regional distribution patterns of taxa.

Mapped floristic Groups, based on recurrent patterns of plant distribution by shared species, is another visual presentation of useful information on the flora of Namibia. This is the first attempt at organizing species into groups based on coinciding distribution ranges with similar ecological tolerances, evolutionary histories or both for Namibia. It can serve as a basis, not only for plant biological and conservation studies, but also for studies on all other biological groups and help to clarify natural areas. It provides a framework for evaluation of climate change models, palaeo-environmental studies and potentially many others.

Detection of Centres of Endemism is essential for the formulation of conservation policies and it is essential that the complete flora of the Kaokoveld receive conservation attention. A World Heritage Site at Twyfelfontien lies within the KCE, along with another potentially vital site, the Brandberg Mountain. A Transfronteir Park is being planned for part of the KCE and it is being considered to use the Kunene River for a hydro electric scheme. There is a therefore an urgent need to reassess conservation priorities, including Red Data assessments, rarity (Orange lists of Victor & Keith 2004), and identifying Important Plant areas (Radford 2004). Despite falling within the tropics, the Kaokoveld is an arid area and the human inhabitants depend mainly on live-stock farming. They are faced with regular droughts, an increasing human population growth and ever-increasing pressure from tourism in the area. In combination with a diverse geology and topography, all of these factors impact on plant distribution patterns.



The determination of species distribution patterns is a starting point for all biogeographic analysis. This profile needs to be followed by detailed autecological studies of individual species and habitats. More complete listing of species within specific areas and the Groups is also necessary. This will in future enable statistical analyses to better gauge the biological significance of smaller areas within the Centre.

## **References**

Polunin, N. 1960. *Introduction to Plant Geography*. Longmans, London.

Radford, E. 2004. Important plant areas – a practical route to target 5. *Plant Talk* 38: 32–33.

Victor, J.E. & Keith, M. 2004. Orange Lists: A safety net for biodiversity in South Africa. *South African Journal of Science* 100: 139–140.

# Chapter 11

## References

- Acocks, J.P.H. 1953. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa* 28: 1–192.
- Adamson, R.S. 1958. The Cape as an ancient African flora. *The advancement of Science* 58: 1–10.
- African Flowering Plants Database. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, "Retrieved 2007/2008", from <<http://www.ville-ge.ch/cjb/bd/africa/index.php>>.
- Agro-Ecological Zoning Programme. 1996-ongoing. Directorate of Agricultural Research and Training, Ministry of Agriculture, Water and Rural Development, Windhoek.
- Albrecht, M., Berke, B., Eichhorn, B., Frank, T., Kuper, R., Prill, S., Vogelsang, R. & Wenzel, S. 2001. Oruwanje 95/1: A late Holocene stratigraphy in north western Namibia. *Cimbebasia* 17: 1–22.
- Anderberg, A. 1985. A new species of *Pegolettia* (Compositae – Inulae) from Namibia. *Nordic Journal of Botany* 5: 57–59.
- Archer, C. & Craven, P. 2004. Cyperaceae in Namibia. *SABONET News* 9: 18–28.
- Atlas for Southern Africa. 2002. Dynamic Atlas Resource CD. FAO-GTOS and SKE Inc.
- Atlas of Namibia Project. 2002. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek. <http://www.dea.met.gov.na/>.
- Avery, D.M. 1993. Last interglacial and Holocene altithermal environments in South Africa and Namibia: Micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101: 221–228.
- Balkwill, M.-J. & Balkwill, K. 1998. A preliminary analysis of distribution patterns in a large, pantropical genus, *Barleria* L. (Acanthaceae). *Journal of Biogeography* 25: 95–110.
- Barnard, P. (ed.) 1998. *Biological diversity in Namibia: A country study*. The Namibian National Biodiversity Task Force, Windhoek.

- Becker, T. 2002. Zur Phytogeographie des Kaokolandes. In: Bollig, M., Brunotte, E. & Becker, T. (eds), *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 69–74. *Kölner Geographische Arbeiten* 77, Köln.
- Becker, T. & Jürgens, N. 2000: Vegetation along climate gradients in Kaokoland, North-West Namibia. *Phytocoenologia* 30: 543–565.
- Beentje, H.J. 1994. Regional overview: Africa. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 101–116. Oxford University Press, Oxford.
- Beentje, H.J. 1996. Centres of plant diversity in Africa. In: Van der Maesen, L.J.G., van den Burgt, M. & van Medebach de Rooy, J.M. (eds), *The biodiversity of African plants*. Pp. 101–109. Kluwer Academic Publishers, Dordrecht.
- Beier, B.-A., Chase, M.W. & Thulin, M.P. 2003. Phylogenetic relationships and taxonomy of subfamily Zygophylloideae (Zygophyllaceae) based on molecular and morphological data. *Plant Systematics and Evolution* 240: 11–39.
- Bellstedt, D.U., van Zyl, L., Marais, E.M., Bytebier, B.L.G., de Villiers, C.A., Makwarela, A.M. & Dreyer, L.L. 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three chloroplast regions. *Molecular Phylogenetics and Evolution* 47: 932–949.
- Besler, H. 1977. Untersuchungen in der Dünen - Namib (Südwestafrika). *Journal of the SWA Scientific Society* 31: 33–64.
- Besler, H. 1991. Der Namib Erg: Älteste Wüste oder älteste Dünen? *Geomethodica* 16: 93–122.
- Bollig, M., Brunotte, E. & Becker, T. 2002. Der Sonderforschungsbereich 389 und die Schwerpunktregion "Kaokoland" Perspektiven und forschungshistorische Bedingungen. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Kaokoland - Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semi-ariden Nordwesten Namibias*. Pp. 1–12. Kölner Geographische Arbeiten 77, Köln.
- Born, J., Linder, H.P. & Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147–162.
- Bourke, M.C., Child, A. & Stokes, S. 2003. Optical age estimates for hyperarid fluvial deposits at Homeb, Namibia. *Quaternary Science Reviews* 22: 1099–1103.
- Bredenkamp, C.L. & Van Wyk, A.E. 2006. Phytogeography of *Passerina* (Thymelaeaceae). *Bothalia* 36: 191–199.
- Bremer, K. 1978. The genus *Leysera* (Compositae). *Botaniska Notiser* 131: 369–383.

- Brook, A., Cowart, J.B. & Marais, E. 1996. Wet and dry periods in the southern African summer rainfall zone during the last 300 kyr from speleothem, tufa and sand dune age data. *Palaeoecology of Africa* 24: 147–158.
- Brook, A., Marais, E. & Cowart, J.B. 1999. Evidence of wetter and drier conditions in Namibia from tufas and submerged speleothems. *Cimbebasia* 15: 29–39.
- Brook, A., Marais, E., Srivastava, P. & Jordan, T. 2007. Timing of lake-level changes in Etosha Pan, Namibia, since the middle Holocene from OSL ages of relict shorelines in the Okondeka region. *Quaternary International* 175: 29–40.
- Brook, A., Srivastava, P. & Marais, E. 2006. Characteristics and OSL minimum ages of relict fluvial deposits near Sossus Vlei, Tsauchab River, Namibia, and a regional climate record for the last 30 ka. *Journal of Quaternary Science* 21: 347–362.
- Brown, J.H. & Lomolino, M.V. 1998. *Biogeography*. 2nd edition. Sinauer Associates, Sunderland.
- Brunotte, E. & Sander, H. 2000. Loess accumulation and soil formation in Kaokoland (Northern Namibia) as indicators of Quaternary climatic change. In: Kröpelin, S. & Petit-Maire, N. (eds). *Global and Planetary Change, Special Volume "Paleomonsoon Variations and Global Change during the Late Quaternary"*. *Global & Planetary Change* 26: 67–75.
- Brunotte, E., Eichhorn, B. & Sander, H. 2002. Quaternary climate change in North Western Namibia: Sedimentologic, pedologic and archaeobotanic evidence. *Palaeoecology of Africa* 39.
- Bruyns, P.V. 2000. Phylogeny and biogeography of the Stapeliads 2. *Biogeography. Plant Systematics and Evolution* 221: 227–244.
- Bruyns, P.V. 2005. *Stapeliads of Southern Africa and Madagascar* 1 & II. Umdaus Press, Hatfield.
- Bruyns, P.V. 2007. Apocynaceae. A new species of *Huernia* (Asclepiadoideae–Ceropegieae) from Southern Angola. *Bothalia* 37: 23–56.
- Bruyns, P.V. 2008. Notes on African plants Apocynaceae: A new species of *Huernia* (Asclepiadoideae–Ceropegieae) from Angola. *Bothalia* 38: 83–85.
- Bruyns, P.V., Mapaya, R.J. & Hedderson, T. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and psbA-trnH sequence data. *Taxon* 55: 397–420.
- Burgess, N.D., D'Amico Hales, J., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. & Newman, K. 2004. *The terrestrial ecoregions of Africa and Madagascar: A conservation assessment*. Island Press, Washington, D.C.

- Burke, A. 2002. Implementation strategy for Sperrgebiet Conservation Planning Study. Unpublished Draft. November 2002. Conservation International and Ministry of Environment and Tourism, Windhoek.
- Burke, A. 2003. How special are Etendeka mesas? Flora and elevation gradients in an arid landscape in north-west Namibia. *Journal of Arid Environments* 55: 747–764.
- Burke, A. 2005. Vegetation types of mountain tops in Damaraland. *Biodiversity and Conservation* 14: 1487–1506.
- Burke, A. & Strohbach, B.J. 2000. Review: Vegetation studies in Namibia. *Dinteria* 26: 1–24.
- Carr, M.J., Carr, A.C., Jacobsen, L. & Vogel, U. 1976. Radiocarbon dates from the Zerrissene Mountain open station settlement complex. *South African Journal of Science* 72: 251–252.
- Carrión, J.S., Scott, L. & Marais, E. 2006. Environmental implications of pollen spectra from bat droppings and potential for paleoenvironmental reconstruction. *Cimbebasia* 14: 175–186.
- Caujape-Castells, J., Jansen, R.K., Membrives, N., Pedrola-Monfort, J., Montserrat, J.M. & Ardanuy, A. 2001. Historical biogeography of *Androcymbium* Willd. (Colchicaceae) in Africa: Evidence from cpDNA RFLPs. *Botanical Journal of the Linnean Society* 136: 379–392.
- Clarke, N.V. & Mannheimer, C.A. 1999. Cyperaceae of Namibia – an illustrated key. *Occasional Contributions* 1. National Botanical Research Institute, Windhoek.
- Coates Palgrave, M. 2002. *Keith Coates Palgrave Trees of Southern Africa*. Edition 3. Struik, Cape Town.
- Coe, M.J. & Skinner, J.D. 1993. Connections, disjunctions and endemism in the eastern and southern African mammal faunas. *Transactions of the Royal Society of South Africa* 48: 233–255.
- Coetzee, C.G. 1969. The distribution of mammals in the Namib Desert and adjacent inland escarpment. *Scientific Papers of the Namib Desert Research Station* 40: 23–36.
- Coetzee, C.G. 1983. An analysis of the distribution patterns of the Namibian terrestrial mammals (bats excluded). *Annalen van de Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen* 237: 63–73.
- Conspectus Florae Angolense* (various editorial teams). 1937–1970. Centro de Botânica, Instituto de Investigação Científica Tropical, Lisboa.
- Costa, E., Martins, T. & Monteiro, F. 2004. A checklist of Angola grasses – Checklist das Poaceae de Angola. *Southern African Botanical Diversity Network Report* 28. SABONET, Pretoria.

Cowling, R.M., Rundel, P.W., Desmet, P.G. & Esler, K.J. 1998. Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons. *Diversity and Distributions* 4: 27–36.

Craven, P. 2001. *Checklist: Kaokoveld*. Unpublished. National Herbarium of Namibia, National Botanical Research Institute, Windhoek.

Craven, P. 2002a. Plant species diversity in the Kaokoveld, Namibia. In: Bollig, M., Brunotte, E. & Becker, T. (eds), *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 75–80. *Kölner Geographische Arbeiten* 77, Köln.

Craven, P. 2002b. *Phytogeography of the Namibian flora: A taxon approach*. Unpublished. MSc thesis, University of Stellenbosch, Stellenbosch.

Craven, P. 2005. Centres of plant endemism and diversity: Namibia. *SABONET news* 9: 24–44.

Craven, P. 2009. Chapter 3, this volume. Plant geography in Namibia.

Craven, P. 2009. Chapter 4, this volume. Phytogeographical aspects of the flora of Namibia.

Craven, P. 2009. Chapter 5, this volume. Natural floristic areas of Namibia.

Craven, P. 2009. Chapter 6, this volume. Demarcating the Kaokoveld Centre of Endemism: A numerical approach.

Craven, P. 2009. Chapter 7, this volume. Floristic and environmental analysis of the Kaokoveld Centre of Endemism.

Craven, P. 2009. Chapter 8, this volume. Flora of the Kaokoveld Centre of Endemism.

Craven, P. 2009. Chapter 9, this volume. The endemic seed plants of the Kaokoveld Centre of Endemism

Craven, P. & Craven, D. 2000. The flora of the Brandberg, Namibia. In: Kirk-Sprigs, A.H. & Marais, E. (eds). *Biodiversity of the Brandberg Massif, Namibia*. *Cimbebasia* 9: 49–67.

Craven, P. & Kolberg, H. on-going. DB Index of plant species for Namibia and surrounds.

Craven, P. & Maggs, G.L 1993. *Checklist: Kaokoveld*. Unpublished. National Botanical Research Institute, Windhoek.

Craven, P. & Vorster, P.V. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.

- Crisci, J.V. 2001. The voice of historical biogeography. *Journal of Biogeography* 28: 157–168.
- Croizat, L. 1994. Pacific basin biogeography. Marginal notes to a symposium. *Kirkia* 15: 157–246.
- Cron, G.V., Balkwill, K. & Knox, E.B. 2008. Phylogenetic evidence for the generic circumscription of *Cineraria* L. (Asteraceae-Senecioneae). *Taxon* 57: 779–798.
- Curtis, B.A. & Mannheimer, C.A. 2005. *Tree Atlas of Namibia*. National Botanical Research Institute, Windhoek.
- De Carvalho, H. & Alves, P. 1990. Grabbro-Anorthosite Complex of SW Angola/NW Namibia. Notes about the general geology. An essay of genetic interpretation. *Commun. IICT. Sér. Ciênc. Da Rerra* 2.
- De Melo, N.F., Guerra, M., Benko-Iseppon, A.M. & de Menezes, N.L. 1997. Cytogenetics and cytotaxonomy of Velloziaceae. *Plant Systematics and Evolution* 204: 257–273.
- Deacon, J. & Lancaster, N. 1988. *Late Quarternary Palaeoenvironments of Southern Africa*. Clarendon Press, Oxford.
- De-Zhi, F., Yong, Y. & Guang-Hua, Z. 2004. A new scheme of classification of living Gymnosperms at family level. *Kew Bulletin* 59: 111–116.
- Dilcher, D.L., Bernardes-de-Oliveira, M.E., Pons, D. & Lott, T.A. 2005. Welwitschiaceae from the Lower Cretaceous of northeastern Brazil. *American Journal of Botany* 92: 1294–1310.
- DIVA GIS 2007. A Geographical Information System for the Analysis of Biodiversity data. International Potato Center (CIP), [www.cipotato.ORG](http://www.cipotato.ORG)
- Dombo, A., da Costa, E. & Neto, G. 2002. Angola. In: Golding, J.S. (ed.). *Southern African Red Data Lists*. Southern African Botanical Diversity Network Report 14: 8–11. SABONET, Pretoria.
- Drüppel, K. & Okrusch, M. 2000. Petrology and geochemistry of anorthositic rocks of the Kunene Intrusive Complex, NW Namibia. *Geoluanda 2000 abstracts* 49–50.
- Drüppel, K., Brandt, S. & Okrusch, M. 2000. Evolution of the anorthositic Kunene Intrusive Complex and the metamorphic rocks of the Epupa Complex, NW Namibia: Evidence for cogenetic formation during proterozoic crustal extension? *Geoluanda 2000 abstracts* 47–48.
- Du Pisani, A.L. 2001. The idiosyncrasies of Namibian rainfall. *Agricola* 2001: 28–32.
- Dupont, L. M. 2006. Late Pliocene vegetation and climate in Namibia (southern Africa) derived from palynology of ODP Site 1082. *Geochemistry, Geophysics, Geosystems* 7: 1–15.

- Dupont, L.M. & Behling, H. 2006. Land-sea linkages during deglaciation: High resolution records from the eastern Atlantic off the coast of Namibia and Angola (ODP Site 1078). *Quaternary International* 148: 19–28
- Dupont, L.M. & Wyputta, U. 2003. Reconstructing pathways of Aeolian pollen transport to the marine sediments along the coastline of South West Africa. *Quaternary Science Review* 22: 157–174.
- Dupont, L.M., Behling, H., Jahns, S., Marret, F. & Kim, J-H. 2007. Variability in glacial and Holocene marine pollen records offshore from west southern Africa. *Vegetation History and Archaeobotany* 16: 87–100.
- Dupont, L.M., Donner, B., Vidal, L., Pérez, E.M. & Wefer, G. 2005. Linking desert evolution and coastal upwelling: Pliocene climate change in Namibia. *Geology* 33: 461–464.
- Dupont, L.M., Kim, J.-H., Schneider, R.R. & Shi, N. 2004. Southwestern African climate independent of Atlantic sea surface temperatures during the Younger Dryas. *Quaternary Research* 61: 318–324.
- Ebach, M.C. 2004. Forum on biogeography: Introduction. *Taxon* 53: 889–891.
- Ebach, M.C., Morrone, J.J., Parenti, L.R. & Vilorio, A.L. 2008. International Code of Area Nomenclature. *Journal of Biogeography* 35: 1153–1157.
- Edwards, D. & Leistner, O.A. 1971. A degree reference system for citing biological records in South Africa. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 501–509.
- Edwards, S., Tadesse, M., Demissew, S. & Hedberg, I. (eds). 2000. *Flora of Ethiopia and Eritrea* 2 Addis Ababa, Ethiopia.
- Eggle, U. 2001. *Illustrated Handbook of Succulent Plants: Monocotyledons*. Springer, Berlin.
- Eichhorn, B. & Jürgens, N. 2003. The contribution of charcoal analysis to the late Pleistocene and Holocene vegetation history of north-western Namibia. In: Neumann, K., Butler, A. & Kahlheber, S. (eds). *Progress in African archaeobotany*. Africa Praehistorica 15: 92–101. Heinrich-Barth-Institut, Cologne.
- Eichhorn, B. 2004. Anthrakologische Untersuchungen zur Vegetationsgeschichte des Kaokolandes, Nordwest-Namibia. PhD dissertation, University of Cologne, Cologne.
- Eitel, B. & Zöllner, L. 1996. Soils and sediments in the basin of Dieprivier-Uitskot (Khorixas District, Namibia): Age, geomorphic and sedimentological investigation, paleoclimatic interpretation. *Palaeoecology of Africa* 24: 159–201.



- Eitel, B., Blümel, W.D. & Hüser, K. 1998. River silt terraces at the eastern margin of the Namib Desert (NW/Namibia): Genesis and paleoclimatic evidence. *Zeitblät für Geologie und Paläontologie* 1: 243–254.
- Eitel, B., Blümel, W.D. & Hüser, K. 1999. Der Uniab-Lehm: Relikt feuchttropischer Tertiärklimate in der Nördlichen Namib (Skelettküste/Namibia). *Die Erde* 130: 17–27.
- Eitel, B., Blümel, W.D. & Hüser, K. 2002. Environmental transitions between 22 ka and 8 ka in monsoonally influenced Namibia - a preliminary chronology. *Zeitschrift für Geomorphologie* 126: 31–57.
- Eitel, B., Blümel, W.D., Hüser, K. & Mauz, B. 2001. Dust and loessic alluvial deposits in Northwestern Namibia (Damaraland, Kaokoveld): sedimentology and palaeoclimatic evidence based on luminescence data. *Quaternary International* 76/77: 57–65.
- Eitel, B., Kadereit, A., Blümel, W.D., Hüser, K. & Kromer, K. 2005. The Amspoort silts, northern Namib Desert (Namibia): Formation, age and palaeoclimatic evidence of river-end deposits. *Geomorphology* 64: 299–314.
- Ellis, R.P., Vogel, J.C. & Fuls, A. 1980. Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. *South African Journal of Science* 76: 307–314.
- Endrödy-Younga, S. 1982. The evidence of coleoptera in dating the Namib Desert re-examined. *Palaeoecology of Africa* 15: 217–223.
- ESRI. 2000. *ArcView 3.2a Software*. Environmental Systems Research Institute, Redlands, USA.
- Exell, A.W. & Gonçalves, M.L. 1973. A statistical analysis of a sample of the flora of Angola. *Garcia de Orta, Ser.Bot.* 1: 105–128.
- Figueiredo, E. 2008. The Rubiaceae of Angola. *Botanical Journal of the Linnean Society* 156: 537–638.
- Flora of southern Africa* (various editorial teams). 1963–ongoing. National Botanical Institute, Pretoria.
- Flora Zambesiaca* (various editorial teams). 1960–ongoing. Crown Agents for Overseas Development, London.
- Friis, I. 1986. Ethiopia in regional phytogeography. *Symbolae Botanicae Upsaliensis* 26: 68–85.
- Gauch, H.G. & Whittaker, R.H. 1981. Hierarchical classification of community data. *Journal of Ecology* 69: 537–557.

- Gerbaulet, M. 1992. Die Gattung *Anacampseros* L. (Portulacaceae). 1. Untersuchungen zur Systematik. 2. Untersuchungen zur Biographie. *Botanische Jahrbücher* 113: 477–564, 565–576.
- Germishuizen, G. & Meyer, N.L. (eds). 2003. Plants of southern Africa: an annotated checklist. *Strelitzia* 14. National Botanical Institute, Pretoria.
- Gerstel, D.U., Burns, J.A. & Burk, L.G. 1979. Interspecific hybridisations with an African tobacco, *Nicotiana africana* Merxm. *The Journal of Heredity* 70: 342–344.
- Gibbs Russell, G.E. 1986. Significance of different centres of diversity in subfamilies of Poaceae in southern Africa. *Palaeoecology of Africa* 17: 183–191.
- Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4: 5–114.
- Giess, W. 1989. *Bibliography of South West African Botany*. South West African Scientific Society, Windhoek.
- Gil-Romera, G., Scott, L., Marais, E. & Brook, G.A. 2006. Middle- to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen. *The Holocene* 16: 1073–1084.
- Gil-Romera, G., Scott, L., Marais, E. & Brook, G.A. 2007. Late Holocene environmental change in the northwestern Namib Desert Margin: New fossil pollen evidence from hyrax middens. *Palaeogeography, Paleoclimatology, Palaeoecology* 249: 1–17.
- Goldblatt, P. & Manning, J. 1998. *Gladiolus in southern Africa*. Fernwood Press, Vlaeberg.
- Goldblatt, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships and origins. *Annals of the Missouri Botanic Garden* 65: 369–436.
- Goldblatt, P. 1986. The Moraeas of Southern Africa. *Annals of Kirstenbosch Gardens*. Volume 14.
- Goldblatt, P. 1990. Systematics of *Lapeirousia* (Iridaceae-Ixioideae) in tropical Africa. *Annals of the Missouri Botanic Garden* 77: 430–484.
- Good, R.D. 1974. *The geography of flowering plants*. Wiley, New York.
- Goodspeed, T.H. 1954. The genus *Nicotiana*. *Chronicles of Botany* 16: 1–536.
- Gugerli, F., Sperisen, C., Büchler, U., Brunner, I., Brodbeck, S., Palmer, J.D. & Qiu, Y.-L. 2001. The evolutionary split of Pinaceae from other conifers: Evidence from an intron loss and a multigene phylogeny. *Molecular Phylogenetics and Evolution* 21: 167–175.

- Haacke, W.D. 1982. Distribution patterns of reptiles as indicators of geomorphological events in the Namib Desert. *Palaeoecology of Africa* 15: 225–226.
- Hachfeld, B. 1996. Vegetationsanalytische Transektanalyse in der noerdlichen Zentralen Namib. Diplomarbeit, Universitaet Hamburg, Hamburg.
- Hartmann, H.E.K. 1964. On the phytogeography and evolution of Mesembryanthea (Aizoaceae). In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the IIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1165–1189. National Herbarium and Botanic Gardens of Malawi, Zomba.
- Hedberg, O. 1954. A pollen-analytical reconnaissance in Tropical East Africa. *Oikos* 5: 137–166.
- Heine, K. & Heine, J.T. 2002. A paleohydrologic reinterpretation of Homeb Silts, Kuiseb River, Central Namib Desert (Namibia) and paleoclimatic implications. *Catena* 48: 107–130.
- Heine, K. 1992. On the ages of humid Late Quaternary phases in southern African arid areas (Namibia, Botswana). *Palaeoecology of Africa* 23: 149–164.
- Heine, K. 1998. Climate change over the past 135,000 years in the Namib Desert (Namibia) derived from proxy data. *Palaeoecology of Africa* 25: 171–198.
- Heine, K. 2005. Holocene climate of Namibia: A review based on geoarchives. *African Study Monographs, Supplement 30*. 119: 33.
- Heine, K. & Walter, R. 1996. Gypcretes of the central Namib Desert, Namibia. *Palaeoecology in Africa* 24: 173–201.
- Hill, M.O. 1979. TWINSpan - A FORTRAN program for arranging data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*. Cornell University. Ithaca, New York.
- Hilliard, O.M. 1994. *The Manuleae. A tribe of Scrophulariaceae*. Edinburgh University Press, Edinburgh.
- Hilton-Taylor, C. 1994a. Centres of plant diversity: Karoo-Namib Region: Kaokoveld. In: Davis, S.D. & Heywood, V.H. (eds). *Centres of Plant Diversity: A guide and strategy for their conservation*. Pp. 201–203. Oxford University Press, Oxford.
- Hilton-Taylor, C. 1994b. Centres of plant diversity: Karoo-Namib region: Western Cape domain (Succulent Karoo). In: Davis, S.D. & Heywood, V.H. (eds). *Centres of plant diversity: A guide and strategy for their conservation*. Pp. 204–217. Oxford University Press, Oxford.
- Holm, E. 1990. Notes on faunas bordering on the Namib Desert. In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 55–60. Transvaal Museum Pretoria.

- Holm, E. & Scholtz, C.H. 1983. Zoogeographical delimitation of the Kalahari subregion based on excluded species. *Journal of Arid environments* 8: 165–169.
- Huntley, B.J. 1974. Outlines of Wildlife Conservation in Angola. *Journal of South African Wildlife Management Association* 4: 157–166.
- Ickert-Bond, S.M. & Wojciechowski, M.F. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): Evidence from nuclear and chloroplast DNA sequence data. *Systematic Botany* 29: 834–849.
- Ihlenfeldt, H.-D. 1994. Phytogeography of Pedaliaceae R.Br. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the XIIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1063–1075. National Herbarium and Botanic Gardens of Malawi, Zomba.
- Ihlenfeldt, H.-D. 1967. Über die Abrensung und die natürliche Gliederung der Pedaliaceae R.Br. *Mitteilungen aus dem Institut für Allgemeine Botanik, Hamburg* 12: 43–28.
- Irish, J. 1990. Namib biogeography, as exemplified mainly by Lepismatidae (Thysanura: Insecta). In: Seely, M.K. *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 61–66.
- Irish, J. 1994. The biomes of Namibia, as determined by objective categorisation. *Research of the National Museum, Bloemfontein* 10: 549–592.
- Irish, J. 2002. Summit climate of Namibian mountains. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Irish, J. 2003. Namibian Mountains: bioiversity potential based on topography. 2. Namib Mountains. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Jacobson, K.M. & Lester, E. 2003. A first assessment of genetic variation in *Welwitschia mirabilis* Hook. *Journal of Heredity* 94: 212–217.
- Jacobson, P.J., Jacobson, K.M. & Seely, M.K. 1995. *Ephemeral Rivers and their catchments*. Desert Research Foundation of Namibia.
- Jankowitz, W.J., Van Rooyen, M.W., Shaw, D., Kaumba, J.S. & Van Rooyen, N. 2008. Mysterious circles in the Namib Desert. *South African Journal of Botany* 74: 332–334.
- Jürgens, N. 1991. A new approach to the Namib region. I. Phytogeographic subdivision. *Vegetatio* 97: 21–38.

- Jürgens, N. 1992. Vegetation der Namib. Ein Beitrag zur ökologische Gliederung, Phytochorologie und Florengeschichte einer afrikanischen Trockengebiet. Unpublished. "Habilitationsschrift" for the University of Hamburg, Hamburg.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495–514.
- Kent, M. & Coker, P. 1996. *Vegetation description and analysis*. John Wiley & Sons. Chichester.
- Kers, L.E. 1967. The distribution of *Welwitschia mirabilis* Hook.f. *Svensk Botanisk Tidskrift* 61: 97–125.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1–10.
- Kirkbride, J.H. 1994. Revision of *Cucumella* (Cucurbitaceae, Cucurbitoideae, Melothrieae, Cucumerinae). *Brittonia* 46: 161–186.
- Klak, C., Bruyns, P.V. & Hedderson, T.A.J. 2007. A phylogeny and new classification for the Mesembryanthemoideae (Aizoaceae). *Taxon* 56: 737–756.
- Klak, C., Reeves, G. & Hedderson, T. 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* 427: 63–65.
- Knapp, S., Chase, M.W. & Clarkson, J.J. 2004. Nomenclatural changes and a new sectional classification in *Nicotiana* (Solanaceae). *Taxon* 53: 73–82.
- Knight, R.S. & Siegfried, W.R. 1982. Distribution and evolution of aril-bearing trees in southern Africa. *South African Journal of Botany* 1: 117–123.
- Knoll, A.H. 1983. Africa and Precambrian biological evolution. *Bothalia* 14: 329–336.
- Lancaster, N. 1984. Paleoenvironments of the Tsondeb valley, central Namib Desert. *Paleoecology of Africa*. 16: 411–419.
- Lancaster, N. 2002. How dry was dry? Late Pleistocene paleoclimates in the Namib Desert. *Quaternary Science Reviews* 21: 91–107.
- Lawesson, J.E. & Skov, F. 2002. The phytogeography of Denmark revisited. *Plant Ecology* 158: 113–122.
- Lawrence, G.H.M. 1971. *Taxonomy of vascular plants*. Macmillan Company, New York.

- Lebrun, J.-P. & Stork, A.L. 2003. *Tropical African flowering plants. Ecology and distribution 1, Annonaceae – Balanitaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.
- Lebrun, J.-P. & Stork, A.L. 2006. *Tropical African Flowering plants. Ecology and distribution 2, Euphorbiaceae – Dichapetalaceae*. Des Conservatoire at Jardin Botaniques Genève, Ville de Genève.
- Levyns, M.R. 1964. Migrations and origin of the Cape Flora. *Transactions of the Royal Society of South Africa* 37: 85–107.
- Lewis, G., Schrire, B., Mackinder, B. & Lock, M. 2005. *Legumes of the World*. The Royal Botanic Gardens, Kew.
- Linder, H.P. 1998. Numerical analyses of African plant distribution patterns. In: Huxley, C.R., Lock, J.M. & Cutler, D.F. (eds). *Chorology, taxonomy and ecology of the floras of Africa and Madagascar*. Pp. 67–86. Royal Botanic Gardens, Kew.
- Linder, H.P. 2001. On areas of endemism, with an example from the African Restionaceae. *Systematic Biology* 50: 892–912.
- Linder, H.P. 2003. The radiation of the Cape flora, southern Africa. *Biological Review* 78: 597–638.
- Linder, H.P., Lovett, J.C., Mutke, J., Barthlott, W., Jürgens, N., Rebelo, T. & Küper, W. 2005. A numerical re-evaluation of the sub-Saharan phytochoria. *Biologiske Skrifter* 55: 229–252.
- Linder, H.P., Meadows, M.E. & Cowling, R.M. 1992. History of the Cape flora. In: Cowling, R.M. (ed.). *The ecology of fynbos. Nutrients, fire and diversity* 5. Pp. 113–134. Oxford University Press, Oxford.
- Little, R.J. & Jones, C.E. 1980. *A dictionary of Botany*. Van Nostrand Reinhold, New York.
- Maggs, G.L. 1998. Plant diversity in Namibia. In: Barnard, P. (ed.). *Biological diversity in Namibia: A country study*. Pp. 116–122. The Namibian National Biodiversity Task Force, Windhoek.
- Maggs-Kolling, G.L. 1999. Namibia – a watermelon wonderland. *Spotlight on Agriculture* 16. January 1999.
- Major, J. 1988. Endemism: A botanical perspective. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 117–146. Chapman & Hall, London.
- Malan, J.S. & Owen Smith, G.L. 1974. The ethnobotany of Kaokoland. *Cimbebasia* (B)2: 131–178.

- Manktelow, M. 1996. *Phaulopsis* (Acanthaceae) – a monograph. *Symbolae Botanicae Upsaliensis* 31: 1–184.
- Manktelow, M. 2000. The filament curtain: A structure important to systematics and pollination biology in the Acanthaceae. *Botanical Journal of the Linnean Society* 133: 129–160.
- Manning, J.C., Forest, F. & Mannheimer, C.A. 2005. *Eremiolirion*, a new genus of southern African Tecophilaeaceae, and taxonomic notes on *Cyanella alba*. *Bothalia* 35: 115–120.
- Marlow, J.R., Lange, C.B., Wefer, G. & Rosell-Mele, A. 2000. Upwelling intensification as part of the Pliocene-Pleistocene climate transition. *Science* 290: 2288–2291.
- Martin, H. 1961. The hypothesis of continental drift in the light of recent advances of geological knowledge in Brazil and in South West Africa. *The Geological Society of South Africa* 64 (Alex L. du Toit Memorial lectures 7): 1–47.
- Martin, H. 1965. *The precambrian geology of South West Africa and Namaqualand*. Rustica Press, Wynberg.
- Matos, G.C. 1970. A vegetacao do Parque Nacional do Ohna. *Boletum da Sociedade Brottenana* 2: 245–247.
- Matthews, W.S., Van Wyk, A.E. & Bredenkamp, G.J. 1993. Endemic flora of the north-eastern Transvaal escarpment, South Africa. *Biological Conservation* 63: 83–94.
- McLaughlin, S.P. 1989. Natural floristic areas of the western United States. *Journal of Biogeography* 16: 239–248.
- McLaughlin, S.P. 1992. Are floristic areas hierahically arranged? *Journal of Biogeography* 19: 21–32.
- McLaughlin, S.P. 1994. Floristic plant geography: The classification of floristic areas and elements. *Progress in Physical Geography* 18: 185–208.
- Meester, J. 1965. The origins of the southern African mammal fauna. *Zoologica Africana* 1: 87–93.
- Meeuse, A. 1960. Verbenaceae. *Priva auricocca*. *Bothalia* 7: 424–5.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, A. 2002. *Atlas of Namibia: A portrait of the land and it's people*. David Phillip Publishers, Cape Town.

- Merxmüller, H. & Buttler, K.P. 1975. *Nicotiana* in der Afrikanischen Namib – ein pflanzengeographisches Rätsel. *Mitteilungen aus der Botanischen Staatssammlung, München* 12: 91–104.
- Merxmüller, H. (ed.) 1966–1972. *Prodromus eine Flora von Südwestafrika*. Cramer Verlag, Lehre.
- Meyer, P.G. 1973. Neue und wenig bekannte Acanthaceen aus dem Kaokoveld (SWA). *Mitteilungen aus der Botanischen Staatssammlung, München*. 11: 101–103.
- Midgley, G., Hughes, G., Thuiller, G., Drew, G. & Foden, W. 2005. Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function. Report for *Namibian National Biodiversity Programme*.
- Miller, R. McG. 2000. Geology of the Brandberg Massif, Namibia and its environs. In Kirk-Spriggs, A.H. & Marais, E. Biodiversity of the Brandberg Massif, Namibia. *Cimbebasia* 9: 17–38.
- Miller, R. McG. 2002. Simplified geological descriptions of Namibia's Mountains. Unpublished. Report for the Mountain Ecosystem Group of the Namibian National Biodiversity Task Force.
- Mittermeier, R. & Mittermeier, C. 2001. Hope for Nature's greatest treasures. *Africa Geographic Biodiversity Hotspots* 30–37.
- Mittermeier, R.A., Myers, N., & Thomsen, J.B. 1998. Biodiversity Hotspots and Major Wilderness Areas: Approaches to setting conservation priorities. *Conservation Biology* 12: 516–520.
- Mittermeier, R.A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., Lamoreux, J. & Da Fonseca, G.A.B. (eds). 2004. *Hotspots revisited: earth's biologically richest and most threatened terrestrial ecoregions*. Cemex & Conservation International, Washington.
- Moreno Saiz, J.C., Castro Parga, J. & Sainz Ollero, H. 1998. Numerical analysis of distributions of Iberian and Balearic endemic monocotyledons. *Journal of Biogeography* 25: 179–194.
- Myers, A.A. & Giller, P.S. (eds). 1988. *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Chapman and Hall, London.
- Myers, A.A. & Giller, P.S. 1988. Process, pattern, and scale in biogeography. In: *Analytical biogeography*. Myers, A.A. & Giller, P.S. (eds). Pp. 3–12 Chapman & Hall, London.
- Nickerson, J. & Drouin, G. 2004. The sequence of the largest subunit of RNA polymerase II is a useful marker for inferring seed plant phylogeny. *Molecular Phylogenetics and Evolution* 31: 403–415.
- Nimis, P.L., Malyshev, L.I., Bolognini, G. & Friesen, N. 1998. A multivariate phytogeographic analysis of plant diversity in the Putorana Plateau (Northern Siberia). *Opera Botanica* 136: 1–72.



- Nordenstam, B. 1969. Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica* 23: 7–75.
- Nordenstam, B. 1974. The flora of the Brandberg. *Dinteria* 11: 3–67.
- Nordenstam, B. 1982. A monograph of the genus *Ornithoglossum* (Liliaceae). *Opera Botanica* 64: 1–51.
- Olson, D.M. & Dinerstein, E. 2002. The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanic Garden* 89: 199–224.
- Olszewski, J.D.S. 2000. Brandberg climatic considerations. In: Kirk-Spriggs, A.H. & Marais, E. (eds). Biodiversity of the Brandberg Massif, Namibia. *Cimbebasia* 9: 39–48.
- Ortiz, A. 2000. A phylogenetic analysis of *Dicoma* Cass. and related genera (Asteraceae: Cichorioideae: Mutisieae) based on morphological and anatomic characters. *Annals of Missouri Botanic Garden* 87: 459–481.
- Ortiz, S. & Netnou, N.C. 2005. A new species of *Dicoma* (Asteraceae, Mutisieae) from South Africa. *Botanical Journal of the Linnean Society* 147: 509–513.
- Ortiz, S. & Pulgar, I. 2002. A new species of *Dicoma* Cass. (Asteraceae: Mutisieae) from Namibia. *Botanical Journal of the Linnean Society* 139: 317–322.
- Otieno, D.F., Balkwill, K., Paton, A.J. & Savolainen, V. 2006. A reassessment of *Hemizygia* and *Syncolostemon* (Ocimeae—Lamiaceae). *Taxon* 55 : 941–958.
- Parenti, L. R. & Humphries, C. J. 2004. Historical biogeography, the natural science. *Taxon* 53: 899–903.
- Paton, A.J., Harley, M.M., Harley, R.M. & Weeks, S. 1994. A revision of *Endostemon* (Labiatae). *Kew Bulletin* 49: 673–716.
- Pedersen, B. 1990. Distributional patterns of vascular plants in Fennoscandia: A numerical approach. *Nordic Journal of Botany* 10: 163–189.
- Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Peterson, A.T. & Watson, D.M. 1998. Problems with areal definitions of endemism: The effect of spatial scaling. *Diversity and Distributions* 4: 189–194.

- Pickford, M. 2000. Neogene and Quaternary vertebrate biochronology of the Sperrgebiet and Otavi Mountainland, Namibia. *Communications of Geological Survey, Namibia* 12: 359–365.
- Polhill, R.M. 1982. *Crotalaria in Africa and Madagascar*. Balkema, Rotterdam.
- Polunin, N. 1960. *Introduction to Plant Geography*. Longmans, London.
- Posadas, P. & Donato, M. 2007. Everything you always wanted to know about historical biogeography, but were afraid to ask: A preliminary overview based on papers published in Journal of Biogeography 2005–2006. *Biogeografía* 2: 1–6.
- Poynton, J.C. 1962. Patterns in the distribution of Southern African amphibia. *Annals of the Cape Provincial Museum* 2: 252–272.
- Poynton, J.C. 1986. Historical biogeography: Theme and south African variations. *Palaeoecology of Africa* 17: 139–153.
- Poynton, J.C. 1995. The arid corridor distribution in Africa: A search for instances among the amphibians. *Madoqua* 19: 45–48.
- Prendini, L. 2001. Phylogeny of *Parabuthus* (Scorpiones, Buthidae). *Zoologica Scripta* 30: 13–35.
- Prendini, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109–186.
- Radford, E. 2004. Important plant areas – a practical route to target 5. *Plant Talk* 38: 32–33.
- Range, P. 1932–38. Die Flora des Namalandes I–XIII, *Feddes Repertorium* 1–13.
- Rennie, J.V.L. 1936. On the flora of a high mountain in SWA. *Transactions of the Royal Society of South Africa* 259–263.
- Retief, E. & Van Wyk, A.E. 2008. The genus *Wellstedia* (Boraginaceae: Wellstedioideae) in southern Africa. *Bothalia* 38: 57–63.
- Richardson, I.B.K. 1978. Endemic taxa and the taxonomist. In: Street, H.E. (ed.), *Essays in plant taxonomy*. Pp. 245–262. Academic Press, London.
- Robinson, E.R. 1975–77. Phytogeography of the Namib Desert of South West Africa and its significance to discussions of the age and uniqueness of the desert. *Palaeoecology of Africa* 67–74.
- Robinson, E.R. 1977. Phytosociology of the Namib Desert Park, SWA. Unpublished. MSc Thesis, University of Natal, Pietermaritzburg.

- Rosen, B.R. 1988. Biogeographic patterns: A perceptual overview. In: Myers, A.A. & Giller, P.S. (eds). *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. Pp. 23–55. Chapman & Hall, London.
- Ross, J.H. 1981. An analysis of the African *Acacia* species: Their distribution, possible origins and relationships. *Bothalia* 13: 389–413.
- Russell, S. & van Rooy, J. 1986. Biogeographical relationships of the Namibian Bryoflora. In: Deacon, H.J. (ed). *Proceedings of the South African Society for Quaternary Research*. Stellenbosch 1985. *Palaeoecology of Africa* 17: 201–203.
- Rust, U. & Vogel 1988. Late Quaternary environments in the northern Namib Desert as evidenced by fluvial landforms. *Palaeoecology of Africa* 19: 127–137.
- Rust, U. 1984. Geomorphic evidence of Quaternary environmental changes in Etosha, South West Africa/Namibia. In: Vogel, J.C. (ed.). *Late Cainozoic Palaeoclimates of the Southern Hemisphere*. Pp. 279–286. Balkema, Rotterdam.
- Rust, U. 1987. Geomorphologische Forschungen im Südwestafrikanischen Kaokoveld zum Angeblichen Vollariden Quartären Kernraum der Namibwüste. *Erdkunde* 41: 118–133.
- Rust, U. 1999. River-end deposits along the Hoanib River, northern Namib: Archives of Late Holocene climatic variation on a subregional scale. *South African Journal of Science* 95: 205–208.
- Rust, U., Schmidt, H.H. & Dietz, K.R. 1984. Palaeoenvironments of the present day arid south western Africa 30 000-5 000 BP: Results and problems. *Palaeoecology of Africa* 16: 142–174.
- Rydin, C., Källersjö, M. & Friis, E.M. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast dna: Conflicting data, rooting problems, and the monophyly of conifers. *International Journal Plant Science* 163: 197–214.
- Ryding, O. 1986. The genus *Aeollanthus* s. lat. (Labiatae). *Symbolae Botanicae Upsaliensis* 26: 1–152.
- Sander, H. & Becker, T. 2002. Klimatologie des Kaokolandes. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semiariden Nordwest Namibia*. Pp. 57–68. Kölner Geographische Arbeiten 77, Köln.
- Schrire, B.D., Lavin, M. & Lewis, G.P. 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. *Biologische skrifter* 55: 375–422.
- Schrire, B.D., Lavin, M., Barker, N.P. & Forest, F. Phylogeny of the tribe Indigofereae (Leguminosae-Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments. *American Journal of Botany* (in press).

Schrire, B.D., Lavin, M., Barker, N.P., Cortes-Burns, H., Von Senger, I. & Kim, J.-H. 2003. Towards a phylogeny of *Indigofera* (Leguminosae-Papilionoideae): Identification of major clades and relative ages. In: Klitgaard, B.B. & Bruneau, A. (eds). *Advances in Legume Systematics 10 Higher Level Systematics*. Pp. 269–302. Royal Botanic Gardens, Kew.

Scott, L. 1996. Palynology of Hyrax Middens: 2000 years of palaeoenvironmental history in Namibia. *Quaternary International* 33: 73–79.

Scott, L., Cooremans, B., De Wet, J.S. & Vogel, U. 1991. Holocene environmental changes in Namibia inferred from pollen analysis of swamp and lake deposits. *The Holocene* 1: 8–13.

Scott, L., Marais, E. & Brook, G.A. 2004. Fossil hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert. *Journal of Quaternary Science* 19: 1–4.

Segalen, L., Renard, M., Lee-Thorp, J. A., Senut, B., Pickford, M. 2004. Emergence of the Namib Desert during the Neogene, and correlations with global palaeoclimate changes. *American Geophysical Union, Fall Meeting 2004*, abstract #PP51B-1337.

Sheahan, M.C. & Chase, M.W. 2000. Phylogenetic relationships within Zygophyllaceae based on DNA sequences of three regions, with special emphasis on Zygophylloideae. *Systematic Botany* 25: 371–384.

Shi, N. & Dupont, L.M. 1997. Vegetation and climatic history of southwest Africa: A marine palynological record of the last 300,000 years. *Vegetation History and Archaeobotany* 6: 117–131.

Shi, N., Dupont, L.M., Beug, H.-J. & Schneider, R. 1998. Vegetation and climatic changes during the last 21,000 years in south west Africa based on a marine pollen record. *Vegetation History and Archaeobotany* 7: 127–140.

Shi, N., Dupont, L.M., Beug, H.-J. & Schneider, R. 2000. Correlation between vegetation in southwestern Africa and Oceanic upwelling in the past 21,000 years. *Quaternary Research* 54: 72–80.

Shi, N., Schneider, R., Beug, H.-J. & Dupont, L.M. 2001. Southeast trade wind variations during the last 135 kyr: Evidence from pollen spectra in eastern South Atlantic sediments. *Earth and Planetary Science Letters* 187: 31–321.

Shortridge, G.C. 1934. *The mammals of South West Africa*. Heineman, London.

Siesser, W.G. 1978. Aridification of the Namib Desert: Evidence from oceanic cores. In: Van Zinderen Bakker, E.M. (ed.) *Antarctic glacial history and world palaeoenvironments*. Pp. 105–113. Balkema, Rotterdam.

- Siesser, W.G. 1980. Late Miocene origin of the Benguela upwelling system of northern Namibia. *Science* 208: 283–285.
- Simmons, R.E. 1998. Areas of high species endemism. In: Barnard, P. (ed.). *Biological diversity in Namibia: A country study*. Pp. 72–74. The Namibian National Biodiversity Task Force, Windhoek.
- Simmons, R.E., Griffen, M., Griffen, R.E., Marais, E. & Kolberg, H. 1998. Endemism in Namibia: Patterns, processes and predictions. *Biodiversity and Conservation* 7: 513–530.
- SKEP (Succulent Karoo Ecosystem Planning Strategy). 2002. Conservation International, Cape Town. [www.cepf.net](http://www.cepf.net).
- Smith, T. 2004. Important plant areas (IPAs) in southern Africa. *SABONET News* 9: 73.
- Soares, M., Abreu, J., Nunes, H., Silveira, P., Schrire, B. & Figueiredo, E. 2007. The Leguminosae of Angola: Diversity and endemism. *Systematics and geography of plants* 77: 141–212.
- Sole, C.L., Scholtz, C.H. & Bastos, A.D.S. 2005. Phylogeography of the Namib Desert dung beetles *Scarabaeus* (Pachysoma) MacLeay (Coleoptera: Scarabaeidae). *Journal of Biogeography* 32: 75–84.
- Srivastava, P., Brook, A. & Marais, E. 2005. Depositional environment and luminescence chronology of the Hoarusib River Clay Castles sediments, northern Namib Desert, Namibia. *Catena* 59: 187–204.
- Srivastava, P., Brook, A. & Marais, E. 2004. A record of fluvial aggradation in the Northern Namib Desert during the Late Quaternary. *Zeitschrift für Geomorphologie* 133: 1–18.
- Srivastava, P., Brook, A., Marais, E., Morthekai, P. & Singhvi, A.K. 2006. Depositional environment and single aliquot and single grain OSL chronology of the Homeb silt deposits, Kuiseb River, Namibia. *Quaternary Research* 65: 478–91.
- Steenkamp, Y., van Wyk, A.E., Smith, G.F. & Steyn, H. 2005. Floristic endemism in southern Africa: A numerical classification at generic level. *Biologiske skrifter* 55: 253–271.
- Stengel, I. & Leser, H., 2004. Late Quaternary valley-fill terraces and palaeoenvironments of the Huns River, Southern Namibia. *Die Erde* 135: 129–149.
- Stengel, I. 2000. Fossil landslides in the Schwarzrand, Huib and Huns escarpment areas – a contribution to the Quaternary morpostratigraphy of southern Namibia. *Palaeoecology of Africa* 27: 221–238.
- Steyn, H.P. & Du Pisani, E. 1985. Grass-seeds, game and goats: An overview of Dama subsistence. *SWA Scientific Society Journal* 39: 37–52.

- Stott, P. 1981. *Historical plant geography. An introduction*. George Allen & Unwin, London.
- Strohbach, B.J. & Strohbach, M.M. 2004. An annotated plant species list for Mile 46 LDC and surrounding area in central Kavango, Namibia, with some notes on species diversity. *Dinteria* 29: 55–78.
- Swanepoel, W. 2007a. *Ceraria kaokoensis*, a new species from Namibia, with notes on gynodioecy in the genus. *Bothalia* 37: 202–206.
- Swanepoel, W. 2007b. *Commiphora kuneneana*, a new species from the Kaokoveld, Namibia. *Bothalia* 37: 40–48.
- Swanepoel, W. 2008a. *Ceraria kuneneana* (Didiereaceae/Portulacaceae), a new species from the Kaokoveld, Namibia. *South African Journal of Botany* 74: 71–75.
- Swanepoel, W. 2008b. *Commiphora otjihipana* (Burseraceae), a new species from the Kaokoveld, Namibia. *South African Journal of Botany* 74: 623–628.
- Takhtajan, A. 1986. *Floristic regions of the world*. University of California Press, Berkeley.
- Teller, J.T., Rutter, N.W. & Lancaster, N. 1990. Sedimentology and palaeohydrology of late Quarternary lake deposits in the northern Namib Sand Sea, Namibia. *Quaternary Science Reviews* 9: 343–364.
- Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C. & Woodward, F.I. 2006. Endemic species and ecosystem vulnerability to climate change in Namibia. *Global Change Biology* 12: 759–776.
- Thulin, M. & Johansson, A.N.B. 1996. Taxonomy and biogeography of the anomalous genus *Wellstedtia*. In: Van der Maesen, L.J.G., van den Burgt, M. & van Medebach de Rooy, J.M. (eds). *The Biodiversity of African Plants*. Pp. 73–86. Kluwer Academic Publishers, Dordrecht.
- Thulin, M. 1994. Aspects of disjunct distributions and endemism in the arid parts of the Horn of Africa, particularly Somalia. In: Seyani, J.H. & Chikuni, A.C. (eds). *Proceedings of the XIIIth plenary meeting of AETFAT, Zomba, Malawi*. Pp. 1105–1119. National Herbarium and Botanic Gardens of Malawi, Zomba.
- Torquato, J.R. 1970. Origin and evolution of the Mocamedes Desert (Angola). *Boletim do Instituto de Investigacao Cientifica de Angola* 7: 29–38.
- UNEP. 2003. Global strategy for plant conservation. Target 5: Important Plant Areas. Stakeholder consultation report. UNEP/CBD/GSPC/Target 5. Durban.

- Van Jaarsveld, E.J. & Van Wyk, A.E. 2005. *Aeollanthus rydingianus*, a new species from northern Namibia and southern Angola. *Bothalia* 35: 157–173.
- Van Jaarsveld, E.J. & van Wyk, A.E. 2006. *Pelargonium vanderwaltii*, a new cliff-dwelling species from the Otjihipa Mountains, Northern Namibia. *Aloe* 43: 32–34.
- Van Jaarsveld, E.J. & Van Wyk, A.E. 2007. *Dewinteria*, a new semisucculent, cliff dwelling genus endemic to the Kaokoveld, Namibia. *Bothalia* 37: 198–201.
- Van Jaarsveld, E.J., Swanepoel, W. & van Wyk, A.E. 2006. *Aloe kaokoensis*, a new species from the Kaokoveld, Northwestern Namibia. *Bothalia* 36: 75–77.
- Van Rooy, J. 2000. Diversity and phytogeography of the moss flora of southern Africa. PhD thesis University of Pretoria, Pretoria.
- Van Rooyen, M.W., Theron, G.K., van Rooyen, N., Jankowitz, W.J. & Matthews, W.S. 2004. Mysterious circles in the Namib desert: review of hypotheses on their origin. *Journal of Arid Environments* 57: 467–485.
- Van Wyk, A.E. & Smith, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Pretoria.
- Van Wyk, B-E. 1991. A synopsis of the genus *Lotononis* (Fabaceae: Crotalariaeae). *Contributions from the Bolus Herbarium* 14: 1–292.
- Van Wyk, B.-E. & Kolberg, H. 2008. A new species of *Lotononis* section *Oxydium* (Fabaceae, Crotalariaeae). *South African Journal of Botany* 74: 750–752.
- Van Zinderen Bakker, E.M. 1975. The origin and palaeoenvironment of the Namib Desert biome. *Journal of Biogeography* 2: 65–73.
- Van Zinderen Bakker, E.M. 1984a. Aridity along the Namibian coast. *Palaeoecology of Africa* 16: 149–160.
- Van Zinderen Bakker, E.M. 1984b. A late- and post-glacial pollen record from the Namib Desert. *Palaeoecology of Africa* 16: 421–427.
- Van Zinderen Bakker, E.M. 1984c. Palynological evidence for Late Cenozoic arid conditions along the Namibia coast from Holes 532 and 530A, LEG 75, Deep Sea Drilling Project. Initial Reports of the Deep Sea Drilling Project LXXV, 763–768.
- Van Zinderen Bakker, E.M. & Müller, M. 1987. Pollen studies in the Namib Desert. *Pollen and Spores* 29: 185–206.

- Van Zinderen Bakker, E.M. Snr. 1983. The late Quaternary history of climate and vegetation in East and Southern Africa. *Bothalia* 14: 369–375.
- Van Zyl, L. 2000. A systematic revision of *Zygophyllum* (Zygophyllaceae) in the southern African region. Unpublished. PhD thesis. University of Stellenbosch, Stellenbosch.
- Venter, H.J.T. 1983. Phytogeography and interspecies relationships in *Monsonia* (Geraniaceae). *Bothalia* 14: 865–869.
- Venter, H.J.T., Kotze, J.D.S. & Verhoeven, R.L. 1990. A taxonomic revision of *Ectadium* (Periplocaceae). *South African Journal of Botany* 56: 113–124.
- Verhoeven, R.L. & Venter, H.J.T. 1996. *Raphionacme haeneliae* (Periplocaceae), a new species from the Namib Desert, Namibia. *South African Journal of Botany* 62: 316–320.
- Victor, J.E. & Keith, M. 2004. Orange Lists: A safety net for biodiversity in South Africa. *South African Journal of Science* 100: 139–140.
- Viljoen, P.J. 1980. Veldtipes verspreiding van die groter soogdiere en enkele aspekte van die ekologie van Kaokoland. Unpublished. M.Sc. thesis, University of Pretoria, Pretoria.
- Vogel, J.C. & Rust, U. 1987. Environmental changes in the Kaokoland Namib Desert during the present millennium. *Madoqua* 15: 5–16.
- Vogel, J.C. 1983. Isotopic evidence for the past climates and vegetation of southern Africa. *Bothalia* 14: 391–394.
- Vogel, J.C. 1989. Evidence for the past climatic change in the Namib Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70: 355–366.
- Vogel, J.C. 2003. The age of dead trees at Sossus and Tsondab Vleis, Namib Desert, Namibia. *Cimbebasia* 18: 247–251.
- Vogel, J.C., Fuls, A. & Ellis, R.P. 1978. The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science* 74: 209–215.
- Vogelsang, R. 2002. Migration oder Diffusion? – Frühe Viehhaltung im Kaokoland. In: Bollig, M., Brunotte, E. & Becker, T. (eds). *Kaokoland - Interdisziplinäre Perspektiven zu Kultur- und Landschaftswandel im ariden und semi-ariden Nordwesten Namibias*. Pp. 137–144. Kölner Geographische Arbeiten 77, Köln.
- Vogelsang, R., Eichhorn, B & Richter, J. 2002. Holocene human occupation and vegetation history in northern Namibia. *Die Erde* 133: 113–132.



- Volk, O. H. 1966. Die Florengebiete von Südwestafrika. *Journal of the South West African Scientific Society* 20: 25–58.
- Volk, O.H. 1964. Die afro-meridionale-occidentale Floren-Region in Südwestafrika. *Beiträge zur Phytologie zu Ehren Prof. H. Walters 65 Geburtstages*. Ulmer, Stuttgart.
- Von Willert, D.J., Armbruster, N., Drees, T. & Zaborowski, M. 2005. *Welwitschia mirabilis*: CAM or not CAM – what is the answer? *Functional Plant Biology* 32: 389–395.
- Walter, H. 1983. The Namib Desert. In: Evenari, M., Noy-Meir, I. & Goodaall, D.W. (eds). *Ecosystems of the world 12B. Hot deserts and arid shrublands*. Pp. 245–282. Elsevier, Amsterdam.
- Walter, H. S. 2004. Understanding places and organisms in a changing world. *Taxon* 53: 905–910.
- Ward, J.D. & Corbett, I. 1990. Towards the age of the Namib. In: Seely, M.K. (ed.). *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph 7: 17–26. Transvaal Museum, Pretoria.
- Weimarck, H. 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Acta University Lund* 3: 5–143.
- Werger, M.J.A. (ed.). 1978. *Biogeography and ecology of southern Africa*. Junk, The Hague.
- Werger, M.J.A. 1983. Vegetational geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa. *Bothalia* 14: 405–410.
- White, F. 1965. The savanna woodlands of the Zambezan and Sudanian Domains. An ecological and phytogeographical comparison. *Webbia* 19: 651–681.
- White, F. 1971. The taxonomic and ecological basis of chorology. *Mitteilungen aus der Botanischen Staatssammlung, München* 10: 91–112.
- White, F. 1976. The vegetation of Africa - the history of a completed project. *Boissiera* 24: 659–666.
- White, F. 1978. The afromontane region. In: Werger, W.J.A. *Biogeography and ecology of southern Africa*. Pp. 463–513. Junk, The Hague.
- White, F. 1983. *The vegetation of Africa: A Descriptive Memoir to accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa*. United Nations Educational Scientific Cultural Organization, Paris.

- White, F. 1990. *Ptaeroxylon obliquum* (Ptaeroxylaceae), some other disjuncts and the Quarternary history of African vegetation. *Bulletin du Museum National d'Histoire Naturelle Section B. Adansonia* 2: 139–185.
- Wittneben, M. 2003. Vegetation on Brandberg Mountain, Namibia 2000. Unpublished. Diploma Thesis, University of Bremen, Bremen.
- Wolfe, J.A. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanic Garden* 62: 264–279.
- Won, H. & Renner, S.S. 2003. Horizontal gene transfer from flowering plants to *Gnetum*. *Proceedings of the National Academy of Science, USA*. 100:10824–10829.
- Won, H. & Renner, S. 2005. The chloroplast *trnT-trnF* region in the seed plant lineage Gnetales. *Journal of Molecular Evolution* 61: 425–436.
- Won, H. & Renner, S.S. 2006. Dating dispersal and radiation in the Gymnosperm *Gnetum* (Gnetales)—Clock calibration when outgroup relationships are uncertain. *Systematic Biology* 55: 610–622.
- World Wildlife [http://www.worldwildlife.org/wildworld/profiles/terrestrial/at/at1310-\\_full.html](http://www.worldwildlife.org/wildworld/profiles/terrestrial/at/at1310-_full.html)
- WWF and IUCN. 1994. Centres of Plant Diversity. *A guide and strategy for their conservation*. Volume 1: Europe, Africa, South West Asia and the Middle East. IUCN Publications Unit, Cambridge, UK.