

**Systematics of *Hermannia* L. (Malvaceae):  
A Taxonomic Revision of the Genus.**

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## ***ABSTRACT***

*Hermannia*, commonly known as *dolls roses*, is a genus of plants predominantly found in South Africa. While four species occur within North and Central America and one species in Australia, most species are distributed across Africa from Cape Verde eastwards to Saudi Arabia, with the majority restricted to Southern Africa. The taxonomy of the genus is not well understood, species concepts are poorly defined, and there have not been any comprehensive studies on its phylogeny, distribution, diversity or ecology. With the limited knowledge of the genus prior to this thesis, it was not possible to assess how *Hermannia* has evolved and dispersed, nor to gauge its value as an indicator of diversity or climate change.

In this thesis, a study of the systematics of *Hermannia* is undertaken, utilizing molecular analysis of DNA samples obtained from plant material. Sequencing and phylogenetic analysis is undertaken for 141 species based primarily on the nuclear gene region ITS4-5m. The result is used to create a phylogenetic tree of a representative portion of the known species of *Hermannia*. The phylogenetic hypothesis is then used as a framework for analysing the locality and morphological information for each available accession. The principle outputs of these analyses include 1) a taxonomic framework for the genus, 2) distributions of clades within *Hermannia*, 3) molecular dating of the phylogeny, 4) reconstructions of ancestral states for a species included in the phylogeny for 13 characters, 5) maps of richness and diversity of *Hermannia*, 6) phytochoria for *Hermannia* and climatic modelling. In addition, a taxonomic treatment is provided for the subgenus *Mahernia* and a revised nomenclatural account for the subgenus *Hermannia*. Morphological characters for a selection of over 100 species of subgenus *Mahernia* are encoded and used to produce an electronic key.

Data from the molecular dating and reconstructions are analysed in order to address the origins of the genus, modes and directions of dispersal and morphological support for the molecular-based phylogeny. The locations of high richness and diversity are related to persistence and speciation of the genus and patterns of distribution. The phytochoria are compared to known vegetation types and subjected to bioclimatic and prediction modelling in order to identify climatic variables associated with the distributions of various clades and to predict alteration of their current ranges under predicted future climatic conditions.

The phylogenetic analysis confirms the monophyly of two subgenera that were initially proposed at generic level by Linnaeus, namely the widely distributed subgenus *Hermannia* containing approximately 127 species and subgenus *Mahernia* containing approximately 112 species. The newly proposed taxonomy consolidates more than 600 species names into some 250 species, and includes descriptions and depictions of close to 70 new species. The earliest split between clades within *Hermannia* is postulated to have occurred around 27 million years ago, with subsequent splits between 17 and 4.5 million years ago. Reconstruction of characters provides strong indirect support for the proposed phylogeny, unambiguous ancestral states for most characters, and reveals four clear synapomorphies. High levels of richness and diversity are found for a number of small regions across Southern Africa, with a concentration in the Cape Floral Region, despite the genus being almost absent from the mountains where most fynbos diversity resides. At a broad level, the cluster analysis of *Hermannia* displays similar boundaries to the biomes recently derived from a comprehensive assessment of species and environmental

factors for the Vegetation Map of South Africa (Vegmap), suggesting that *Hermannia* may be a good proxy for overall phylogeographic processes within Southern Africa. Analysis of the climatic envelope for each species shows that *Hermannia* is a genus primarily of species that occupy arid habitats, with subsequent adaptations to more moderate environments. Prediction of changes in distribution resulting from climate change models shows some generalized reaction patterns, with a shrinking of overall distribution for nearly all species. The section *Hermannia* is found to fit Linder's (2005) criteria for a Cape Clade, and provides independent support for the concept of a Greater Cape Floristic Region (Born, Linder et al. 2007).

The results of this thesis provide a good general framework for species relationships within *Hermannia* on a molecular and morphological basis, patterns of distribution for its newly defined clades, and an initial assessment of broader issues of diversity and climate change via analysis of the genus.

## *ACRONYMS*

- ADC – Association of Distribution to Climate – A simple numerical estimate defined as the proportion of a species that falls within a particular climatic type.
- ANOVA – Analysis of Variance.
- APG – Angiosperm Phylogeny Group.
- CCM3 – Community Climate Model 3.
- CEM – Climate Envelope Model.
- CFK – Cape Floristic Kingdom.
- CFR – Cape Floristic Region.
- DAR – Drakensberg Alpine Region.
- DELTA – Descriptive Language of Taxonomy – Software for species descriptions.
- DEM – Digital Elevation Model.
- FF – Foliage as Fruit – A hypothesis on plant palatability by Janzen (1984).
- GAM – General Additive Model.
- GPS – Global Positioning System.
- I.O.C.B. – Indian Ocean Coastal Belt – A vegetational region.
- IPNI – International Plant Names Index.
- LHS – Left hand side.
- LO-pattern – A pattern of ornamentation that appears to show "bright islands" at high focus (H) and that become dark at low focus (L), observed when using LO-analysis.
- MAP – Mean Annual Precipitation.
- Maxent – Maximum entropy – Software for modelling potential distributions.
- MM – Mechanistic Model.
- MS – Manuscript name, referring to a name that has not been validly published yet.
- Mya – Million Years Ago.
- Myr – Million Years
- ICN – International Code of Nomenclature – currently the Melbourne Code.
- IPNI – International Plant Naming Institute.
- PRECIS - Pretoria National Herbarium Computerised Information System.
- RHS – Right hand side.
- sect. – Section, A formal rank which lies between subgenus and subsectional level.
- SEM – Scanning Electron Microscope.
- Sp. – Species (singular - various or a particular unknown species).
- Spp. – Species (plural – applying to many species but not all).
- Subg. – Subgenus, A formal rank which lies between genus and section.
- subsect. – Subsection, a formal taxonomic rank between section and species.
- TNT – “Free analysis using New Technology” – software for phylogenetic analysis.
- QDS – Quarter Degree Square. A grid system that divides a degree of latitude and longitude into 16 QDSs annotated from AA in the top left corner, to DD in the bottom right.
- UCT – University of Cape Town.
- UPGMA - Unweighted Pair Group Method with Arithmetic mean, also known as average linkage method.



## *ACRONYMS OF HERBARIA*

The number in brackets represents the approximate number of types in the current nomenclature.

B - Botanischer Garten und Botanisches Museum Berlin-Dahlem (35).

BM - The Natural History Museum, London (9).

BOL – The Bolus Herbarium (39).

CGE - University of Cambridge (43).

COI – Department of Botany, University of Coimbra (3).

E - Royal Botanic Garden Edinburgh (93).

F – Field Museum of Natural History, Chicago (1).

FI - Museo di Storia Naturale dell'Università, Firenze (2).

FR - Herbarium Senckenbergianum (2).

GH - Harvard University (3).

GRA - Albany Museum, Grahamstown (5).

GZU - Karl-Franzens-Universität Graz (1).

HAL – Martin Luther University (42).

JE - Friedrich-Schiller-Universität, Jena (8).

K - Royal Botanic Gardens, Kew (60).

KW - National Academy of Sciences of Ukraine, Kiev (6).

LISC - Instituto de Investigação Científica Tropical (1).

LY - Université Claude Bernard, Lyon (20).

M - Botanische Staatssammlung München (54).

MO – Missouri Botanical Garden (5).

MPU - Université Montpellier 2 (10).

NH – Kwazulu-Natal Herbarium (8).

NY - New York Botanical Garden (2).

P - Muséum National d'Histoire Naturelle, Paris (15).

PH - Academy of Natural Sciences, Philadelphia (7).

PR – National Museum in Prague (13).

PRE –National Herbarium, Pretoria (60).

PRU – Schweickerdt Herbarium, University of Pretoria (8).

S - Swedish Museum of Natural History, Stockholm (69).

SAM – South African Museum (in Compton) (16).

SBT - Bergius Foundation, Stockholm (1).

TCD – Trinity College, Dublin (19).

UPS – Uppsala University (11).

US - Smithsonian Institution (2).

WAG - Wageningen University, Netherlands (3).

Z - Universität Zürich (50).

*“In this dry uncompromising district, grows one of the most beautiful little shrubs of the Bushman country. It was a Mahernia, not more than a foot in height, and covered with large scarlet bell-shaped flowers, elegantly turned downwards; the emblem of modesty united to beauty: chance having guided my steps to the only spot where it grew; nor was it ever afterwards, during my travels, met with again.”*

From Burchell's Travels, 1822.

Overleaf: A tantalising image suggesting that sunbirds may play a role in the pollination of some species: a malachite sunbird (*Nectarinia famosa*) visiting *H. amoena* in Namaqualand (by D. Hanson).



# 1. Introduction and background

## 1.1 *Hermannia*: A poorly-known genus rich in diversity and morphological variation

The genus *Hermannia* (including *Mahernia* L., treated here at subgeneric rank) comprises nearly 250 species, found primarily in Southern Africa but with disjunctions to Saudi Arabia, Cape Verde, southern North America, and Australia (Mabberley 2002). *Hermannia* species occur in every country in Southern Africa (Leistner 2000), every province in South Africa and in every centre of endemism (Rebelo and Siegfried 1990) within the Cape Floristic Region (CFR). *Hermannia* species occupy remarkably diverse habitats including the sea-spray zone on the West Coast of Southern Africa, the arid Karoo and Namibian deserts, the mesic summer rainfall mountains of the Drakensberg and the tropical regions of Kenya. In the present work the number of species occurring in the CFR is updated to 127 and worldwide to ca. 230. *Hermannia* is thus the sixth largest genus in the CFR (see Table 10.2, below). This thesis focuses on the Southern African species due to resource limitations.

### 1.1.1 Prior estimates of species numbers and representation of *Hermannia* species.

The most accurate estimate of species numbers within *Hermannia* is in *Seed Plants of Southern Africa* (Leistner 2000). It provides an estimate of the global number of species at 180 and differentiates the 11 strictly tropical African species from the 30 Southern African species that are shared with the tropics. *Hermannia* is split into 94 species of subgenus (denoted subg.) *Hermannia* and 68 species of subg. *Mahernia*. Other recent literature is however typically inaccurate and incomplete. Mabberley (2002) places the number of species at 100+, whilst both Shamsi (2010) working on the Egyptian Sterculiaceae, and Snijman (2013) who has edited the latest assessment of the Extra Cape Flora estimate there to be only 120 species. The most comprehensive conspectus of the Cape flora, *Cape Plants* (Goldblatt and Manning 2000), underestimates the number of species by around 30%. Electronic resources do no better at providing a consensus of species numbers: *Wikipedia* ([www.wikipedia.org](http://www.wikipedia.org), 2014) has a stub, *Tree of Life* ([www.tol.org](http://www.tol.org), 2014) has no entry for *Hermannia*, whilst in 2009 the *Encyclopaedia of Life* ([www.eol.org](http://www.eol.org)) represented only the American species. *Aluka* ([www.aluka.org](http://www.aluka.org)) the repository for African type specimens in 2009 had scans of 279 specimens and now has 1,455

(2014). The official record of all valid and past names is IPNI ([www.ipni.org](http://www.ipni.org), 2014), which acknowledges 431 species names used within *Hermannia* and 105 names within *Mahernia*.

In field guides the genus is typically sparsely represented (Table 1.1) and only the most common and widespread species are included. Furthermore, there is significant overlap of the species covered between guides. Approximately 20% of species have representative photographs or drawings but these are scattered across the literature.

As a vegetational component, the contribution of the genus *Hermannia* to the local flora is better acknowledged by regional inventories. In a survey of the south-eastern parts of South Africa, *Hermannia* is placed as the tenth, eighth equal and eighth most speciose genus, respectively, in the areas of i) Albany and Bathurst ii) Uitenhage and Port Elizabeth, and iii) George, Knysna and Humansdorp (Dyer 1937).

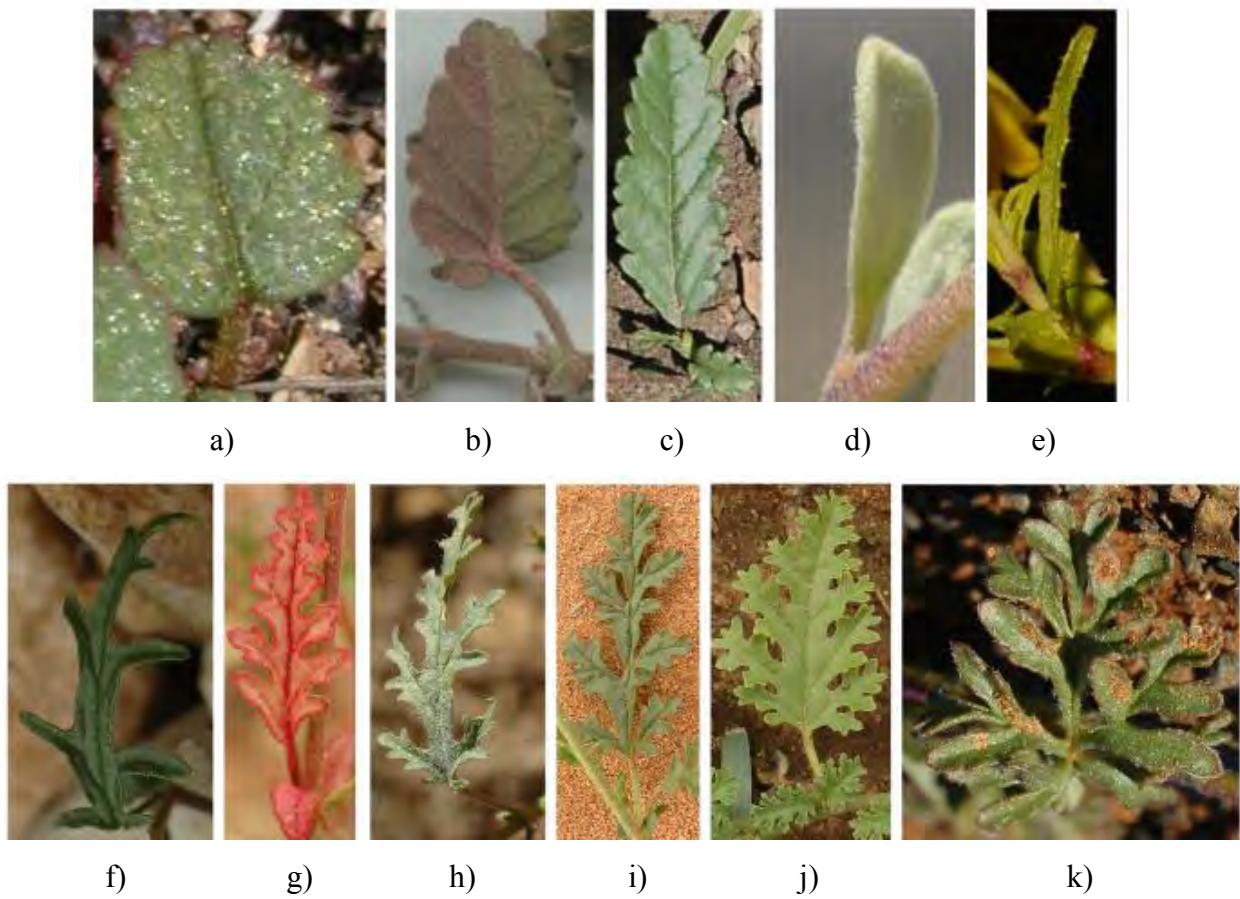
### **1.1.2 Morphological diversity.**

Given its extensive taxonomic and ecological diversity, it is no surprise that the genus also displays very extensive morphological diversity. A shrubby habit predominates in the genus, though creeping herbs, thick-stemmed bushes and annuals also occur. Leaves are diverse, varying in shape from suborbicular (Fig. 1.1a) to linear (Fig. 1.1e) and with dissection varying from entire (Fig. 1.1d) to tri-pinnatifid (Fig. 1.1j). Leaf length varies by more than an order of magnitude, from 4 mm long in desert environments, to over 125 mm long in the moist habitats of the Drakensberg. The vegetative parts vary tremendously in their indumentum from glabrous to densely stellate (Fig. 1.2).

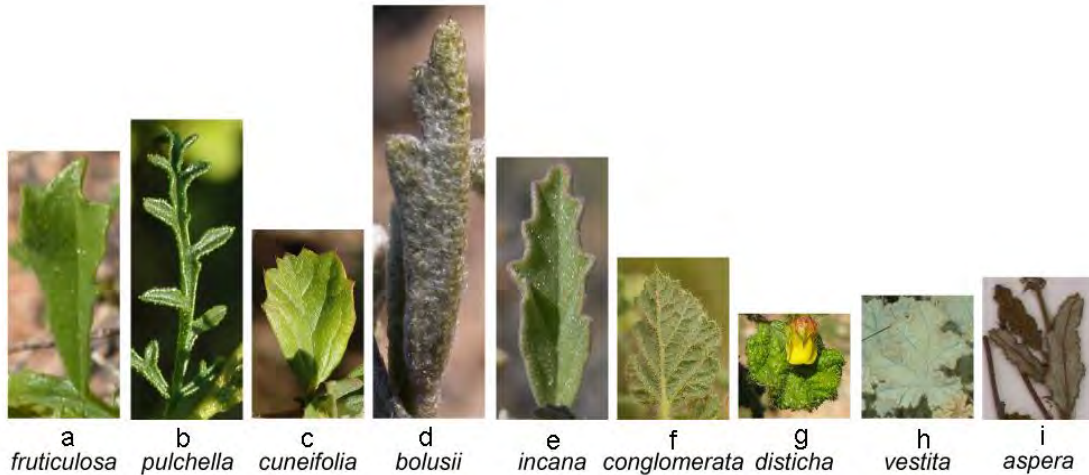
Table 1.1 Number of *Hermannia* species included in South African field guides.

<b>Title / Region</b>	<b>Citation</b>	<b># sp.</b>
Niewoudtville.	(Manning and Goldblatt 1997)	5
Namaqualand.	(Le Roux and Schelpe 1988)	5
Namaqualand and Clanwilliam.	(Le Roux and Schelpe 1981)	3
Mountain Flowers (Drakensberg and Lesotho).	(Pooley 2003)	4
West Coast.	(Manning and Goldblatt 1996)	8
Hottentots Holland to Hermanus.	(Burman and Bean 1985)	3
Outeniqua, Tsitsikamma and Eastern Little Karoo.	(Moriarty 1982)	5
Wild Flowers of the Northern Cape.	(Adams 1976)	4
Wild Flowers of the Table Mountain National Park.	(Trinder-Smith 2006)	7
Eastern Cape.	(Manning 2001)	7





**Fig. 1.1** Variation in leaf morphology within the subg. *Mahernia*. Progression of sub-entire leaves from broadly crenate and ovate to linear (a-e). Increasingly pinnatifid leaves that become palmatisect / pedate and ovate. a) *H. nana*; b) *H. cernua*; c) *H. sneebergensis*; d) *H. trifurca*; e) *H. glabripedicellata*; f) *H. dinkyflora*; g) *H. supplicans*; h) *H. imperialis*; i) *H. serpens*; j) *H. coriolis*; k) *H. pedata*.



**Fig. 1.2 Variation<sup>1</sup> in leaf texture in the genus *Hermannia*, in order of increasing density. a) viscid from deliquescent glands; b) sticky from sessile glands; c) sandpaperly from discoid stellate hairs; d) softly canescent from silvery scales; e) softly tomentose due to flattened stellate hairs; f) densely pubescent with thin radiating stellate hairs g) roughly pubescent due to few-rayed thick radiating stellate hairs; h) densely tomentose due to short-rayed stellate hairs; i) harshly scabrid due to tough stellate bristles. This species is also discolourous.**

In South Africa, *Hermannia* superficially resembles several other genera in the vegetative state, such as *Pelargonium*, *Stachys* and *Jamesbrittenia*, but has alternate leaves that lack scent when crushed. *Hermannia* is readily identifiable by the hanging flowers, the petals that are contorted in most species and the transversely expanded filaments. Flowers vary from broadly open to all but closed, with a pin-prick aperture providing pollinators with access to the meagre quantities of nectar held within (Fig. 1.3). Petals range from 4 mm to over 20 mm long. A typically green calyx encloses the base of the free petals. Within and opposite the petals, the five elongated stamens terminate filaments that usually have a transversely expanded portion. The expanded filaments provide the only robust character for dividing *Hermannia* into two subgenera, nearly equal in species number: The filament of subg. *Mahernia* is abruptly expanded and contracted beneath the base of the anther into a –eruciform filament<sup>2</sup>; whereas in subg. *Hermannia* the expanded portion of the filament overlaps the base of the anther.

<sup>1</sup> As texture is tangible rather than visual, and is difficult to represent by a images, readers are encouraged to experience the characters above by running their finger over specimens of these chosen species in a herbarium or viewing further images on the DVD.



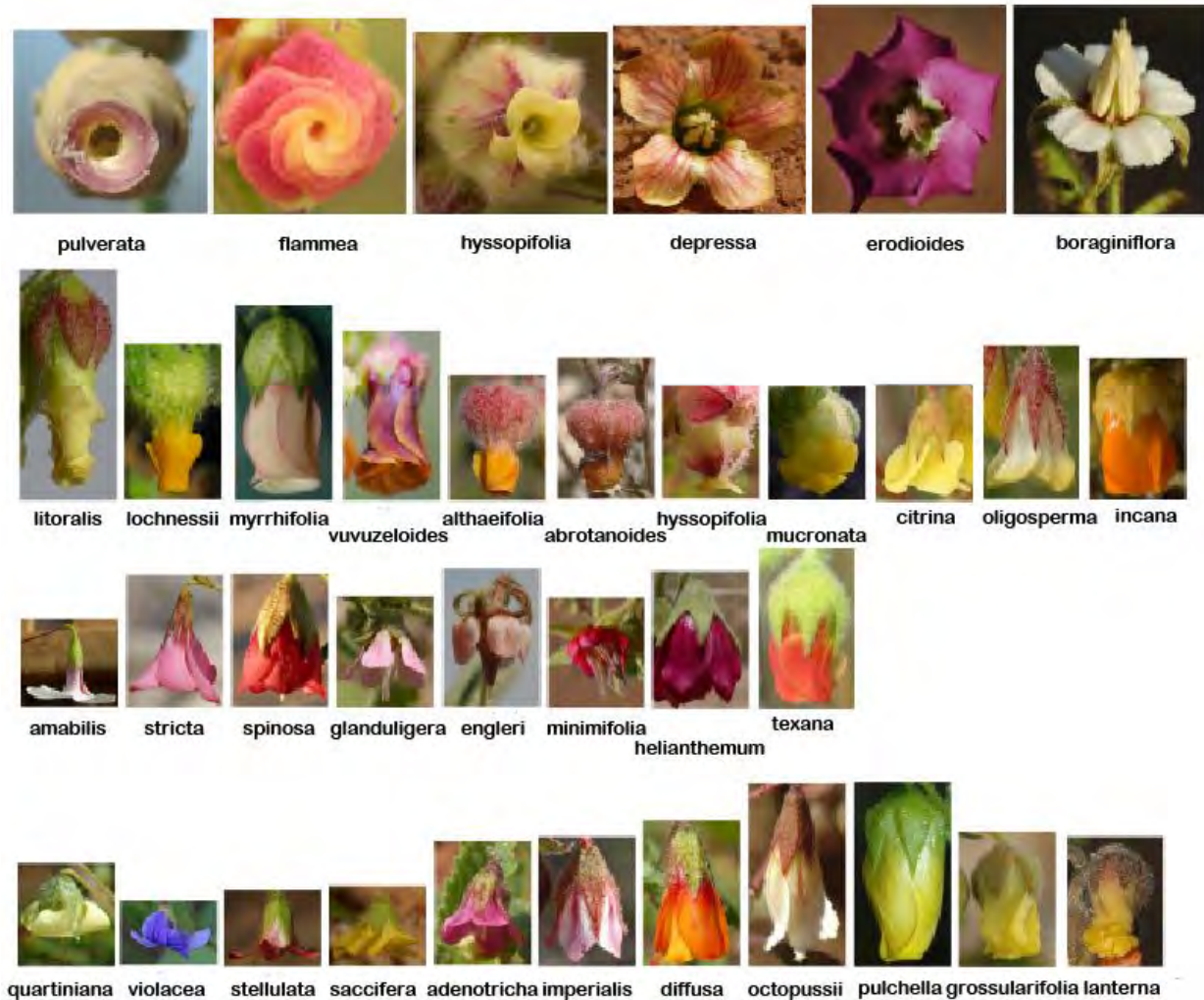


Fig. 1.3 Variation in flower shape in the genus *Hermannia*: Top row: ventral view of flowers showing narrowed apertures to open floral plans; 2<sup>nd</sup> row shows the variation in the subg. *Hermannia* from closed and tubular, to a more open flower; 3<sup>rd</sup> row shows the variation in the sect. *Acicarpus*, with tubular flowers to a more open plan. Note the longer anthers than petals in *H. engleri* and *H. minimifolia* that have been used to group species; Bottom row shows the variation in the subg. *Mahernia*, from reflexed petals to open to tubular petals.

### 1.1.3 Existing knowledge of useful and medicinal properties

As suggested by common names such as *pleisterbos* (plaster bush) and *agtdaegeneebossie* (eight day healing bush), several species of *Hermannia* have medicinal properties. *Hermannia* species have been used by a wide spectrum of people such as Europeans, Kwena, Tswana, Sotho, Xhosa, Zulu and the San (Essop, van Zyla et al. 2008). Ezzo et al. (2008) provide a concise list of uses of *Hermannia* species, namely for diarrhoea, fever and cough. It is applied topically for

burns, eczema and wounds. It is ingested as a diaphoretic (to induce sweating) and to combat heartburn, colic, haemorrhoids, convulsions and as an aromatic tea against syphilis. The Xhosa use a decoction of the root for dysuria (painful urination) and apply *H. depressa* as a post-circumcision anti-septic poultice (Letsie 2007). The San (Bushmen) in Botswana use the roots of *H. glanduligera* to burn decorative marks on their skin (Ellery and Ellery 1997). Further uses are compiled in *Medicinal and Poisonous Plants of Southern and Eastern Africa* (Watt and Breyer-Brandwijk 1962) and include the treatment of respiratory diseases, an aphrodisiac for bulls, to provide magical protection, for heartburn and for relieving flatulence in pregnant women. There is a geographically and phylogenetically independent usage of *Hermannia* within ‘Marehnia’, where the Mberere people of Kenya use the plant as shampoo (Kareru, Kenji et al. 2007) and in Tanzania, where soup is made from the root of *H. uhligii* (Brenan and Greenway 1949).

Recent pharmacological investigations have tested the reputed properties of twelve species of *Hermannia*. Essop et al. (2008) found that all twelve species had good free radical scavenging ability, promising antimicrobial activity and, with the exception of *H. cuneifolia*, moderate anti-inflammatory activity. *H. depressa* was found to be the most efficacious against bacteria when a suite of five Sterculiaceae were assessed (Reid, Jager et al. 2005). They suggest that this may explain its role in combating bacterially induced coughs, diarrhoea and stomach-ache.

Thus *Hermannia* provides numerous products of traditional, pharmacological and cosmetic usage. A taxonomic framework is helpful in exploiting known uses of existing species, while a phylogenetic tree is key to unlocking further potential in related species.

## **1.2 Taxonomy**

Stewart Hinsley has produced an annotated table on the history of the Malvaceae which is on his Malvaceae website (<http://www.malvaceae.info/Classification/history.html>, 2010). This web page has been adapted to form the basis for the following section, in which changes in taxonomic classification of *Hermannia* have been traced through time.

### **1.2.1 Taxonomic position of *Hermannia***

### 1.2.1.1 Linnaeus and the placement of *Hermannia* in the 18<sup>th</sup> century

Linnaeus (1753) placed *Hermannia* together with *Waltheria* and *Melochia* in the Class Monadelphia within Pentandria. A continuation of Linnaeus's *Species Plantarum* by Willdenow in 1797 continued this system, as did Thunberg (1823) in his *Flora Capensis*. However, as early as 1740, Van Royen was classifying *Hermannia* within the Malvaceae. This classification was followed by Adanson (1763) who added the genera *Dombeya* and *Byttneria* to the family. Jussieu (1789) transferred *Hermannia* and *Waltheria* to the Tiliaceae with the caveat "*Filiaceae dubiae*", indicating his doubt as to their position. This classification is followed by Desfontaines (1804).

De Necker (1790), in his "*Elementa Botanica*", presented a strikingly less modern classification than that of Adanson and Jussieu. He placed plants into 54 groups all having the suffix *\_phytum*'. Despite being named as genera, these groups correspond roughly to the rank of family. *\_Comizophytum*' includes most genera from Byttnerioideae with the exception of *Byttneria*, having *Hermannieae* as the core of the group. *\_Comizophytum*' also contains *Kleinhovia* and 19 other genera currently placed in several other families.

Jussieu (1789) was first to recognise the affinity between *Hermannia* and *Waltheria*, placing them in the family "*Filiaceae dubiae*". Baillon (1873) rather placed them together with *Melochia* in the tribe *Hermannieae* DC within the family Malvaceae.

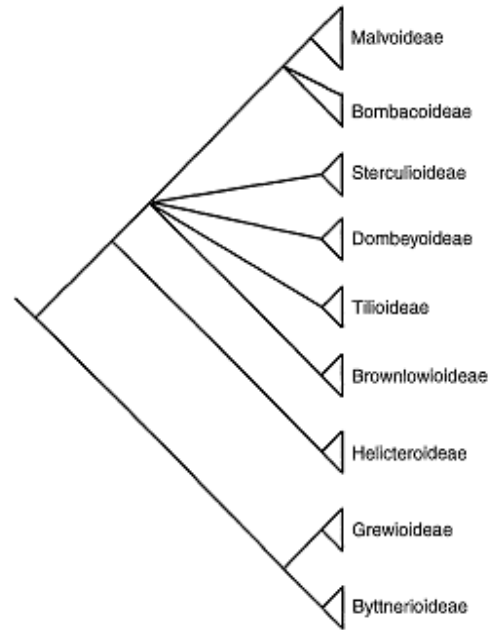
### 1.2.1.2 19<sup>th</sup> and 20<sup>th</sup> century taxonomy of the genus

The placement of *Hermannia* within Byttneriaceae is followed by some ten authors between de Necker (1790) and Grisebach (1864). Gay (1821), Desfontaines (1804) and Agardh (1858) considered *Hermannia* to be in the *Hermannieae*. Schumann (1895) further expanded the tribe to include *Dicarpidium*. Since Bentham & Hooker (1862) until very recently, *Hermannia* has been predominantly placed within the Sterculiaceae. Edlin (1935) was exceptional for this period in choosing to place *Hermannia* within the *Hermannieae*.

### 1.2.1.3 Contemporary taxonomy

In recent years however, since the cladistic analysis of Judd (1997), and the molecular work of the Angiosperm Phylogeny Group (APG 1998; APG 2003) and Bayer et al. (1999), *Hermannia* has generally been placed within the Malvaceae *s.l.* Bayer and Kubitzki (2003) further place *Hermannia* together with *Melochia*, *Dicarpidium* and *Waltheria* within the subfamily Byttnerioideae in the Tribe Hermannieae DC. This thus far appears to be the favoured position for *Hermannia*.

A molecular phylogeny by Whitlock et. al. (2001) shows *Hermannia* to be embedded within the monophyletic tribe Hermannieae. There are some nine subfamilies within the Malvaceae *s.l.*, of which *Hermannia* falls within the subfamily Byttnerioideae, recognised as being the sister group to the Grewioideae. Molecular techniques have been used to explore relationships within many of these subfamilies, i.e. Malvoideae (Tate, Fuertes et al. 2005), Bombacoideae (Baum, Smith et al. 2004), Sterculioideae (Wilkie, Clark et al. 2006) and the Byttnerioideae (Whitlock, Bayer et al. 2001) which included several members of the Grewioideae in the phylogeny (Fig. 1.4). However, despite Whitlock et. al. (2001) having good representative samples of the Byttnerioideae, resolution within the Hermannieae is lacking. At higher levels, Malvales Juss. ex Bercht & J. Presl (1820) has been found to be sister to the Brassicales (APG 2009; Worberg, Alford et al. 2009; Qiu, Li et al. 2010). A discussion of the position of *Hermannia* and its relatives within the Hermannieae follows.



**Fig. 1.4** The summary of the findings of Whitlock (2001) on the overall phylogeny of the Malvaceae s.l.

Molecular analyses based on the gene regions *ndhF* (Alverson, Whitlock et al. 1999) and combined analysis of *rbcL* and *atpB* (Bayer, Fay et al. 1999), now position the Hermannieae along with Byttnerieae, Lasiopetaleae, Theobromeae and at least part of the Helicterae, within the Malvaceae *sensu lato* in the subfamily Byttnerioideae Burnett. Dorr and Barnett (1989) considered the tribe Hermannieae to comprise five genera - *Hermannia*, *Dicarpidium*, *Melochia*, *Waltheria* and *Gilesia*. These they considered to be neatly circumscribed by having five fertile, antipetalous stamens and flat, petaloid (versus cucullate, minute, or squamiform) petals. *Melochia*, *Gilesia* and *Hermannia* all have five carpels (Bayer and Kubitzki 2003). The monotypic Australian *Dicarpidium* is morphologically very close to *Hermannia*, sharing large flat petals, five stamens and lacking staminodes (Bayer and Kubitzki 2003). The name *Dicarpidium* alludes to that genus having the gynoecium reduced to two carpels, whereas *Waltheria* has a single carpel. Table 1.2 (below) summarises the features of the genera within the Hermannieae.

**Table 1.2 Features that unite or distinguish genera within the tribe Hermannieae. Characters for *Hermannia*, *Waltheria* and *Melochia* derived from Leistner (2000) and Dorr and Barnett (1989); *Gilesia* from Whitlock et al. (2001); *Dicarpidium* from <http://www.malvaceae.info/genera/dicarpidium/dicarpidium.html>.**

Genus	# ovules / locule	# locules	Seed Shape	Stamens	Distribution
<i>Hermannia</i>	Many (rarely 1)	5	Curved	Free or joined at base	Africa (>200), Aus (1), N. America (4)
<i>Gilesia</i>	?	5	?	Joined at base.	Aus (1)
<i>Waltheria</i>	1	1	Straight	Tube	Tropics & subtropics, old & new world (67)
<i>Dicarpidium</i>	2	2	?	?	Aus (1+4 undescribed)
<i>Melochia</i>	2	5	Straight	Tube	Trop. Old World (54)

#### 1.2.1.4 Developmental hypotheses for *Hermannia*

As shown in the Table 1.2, why does *Hermannia* only have five free stamens, whereas nearly all other Malvaceae have more than five stamens that are frequently united in a tube? Is this a primitive condition, an atavism, or a derived condition? Edlin (1935) proposed a radical ‘phylogenetic’ arrangement for the Malvaceae based on ‘primitive’ and ‘advanced’ features, illustrated with a diagram (not depicted). He hypothesised that the ‘few, united or regular stamens mark out the Buettneriaceae as more advanced than the Tiliaceae’. He also mentions a number of features that identify the Malvaceae as ‘advanced’ and the Tiliaceae as ‘primitive’. For instance, trees and shrubs are considered primitive, whereas herbs are advanced; numerous stamens are primitive and few stamens are deemed to be advanced. On this basis he regards the Scytopetalaceae as primitive, the Tiliaceae as more advanced and the Hermannieae having the fewest stamens, as the most advanced. Edlin also discusses the problems with Warming’s (1895) earlier arrangement of the Malvaceae which is based largely on the principle of chorisis – a doubling of body parts. In short, Warming believed that *Hermannia* is primitive and through a process of chorisis, the stamens double to become the Tiliaceae and the stamens then become connate leading to the Malvaceae.

### 1.2.1.5 Placement of the Australian taxon *Gilesia biniflora*

*Gilesia biniflora* has a particularly complex and confusing history and warrants special attention regarding its generic status, the correct specific name and its taxonomic position previously proposed as a fifth subgenus between *Marehnia* and *Hermannia*. Additionally, its position within *Hermannia* has been debated and it is the only known Australian representative that may be a species of *Hermannia*. No formal change in status has been found for *Gilesia*, with the *International Plant Names Index* (IPNI) listing *Gilesia biniflora* as currently valid and various Australian “floras” (Jessop, 1986; Harden, 1990) still recognising it as a valid taxon. In the taxonomic revision it is established whether the nomenclature supports *G. biniflora* as being in *Hermannia*, *Gilesia*, or indeed whether Black (1925) was correct in placing it in a separate genus *Hymenocapsa* in the Tribe Lasiopetalae. In the phylogenetics chapter it is determined whether it ought to be regarded as distinct from *Hermannia*.

I have not encountered photographs of *G. biniflora*, but depictions show it as being unique within the Hermannieae in having upright flowers (Jessop and Toelken 1986; Harden 1990). It should however be noted that artists have previously incorrectly depicted pendulous flowers as upright (Henning 1984) and many species do invert their flowers to the upright position subsequent to pollination. The isotype of *Corchorus longipes* (Koch 317), the basionym of *Hymenocapsa longipes* appears to have pendulous flowers (pers. obs.).

### 1.2.2 The Pre-Linnaean history of *Hermannia*

The early history of *Hermannia* is intricately woven with that of the Dutch East India Company: the VOC (Vereenigde Oostindische Compagnie). Thanks to influential members of the VOC, such as the Mayor of Amsterdam, Joan Huydecoper (Schwartz 1983), collectors such as Heurnius were able to visit the Cape and send seeds and specimens of local plants to Europe (Karsten 1967). Employees of the VOC such as Van Rheede and Van der Stel were officially encouraged by Huydecoper to further gardening and botany within the Cape. The *Hortus Medicus* – the Amsterdam Municipal Garden, of which Jan Commelin was director and Huydecoper his colleague, received many of these Cape plants from Van der Stel. Further, Huydecoper commissioned a series of drawings based upon these contributions (Heniger 1986).

These drawings were initiated by Jan Commelin, but finally published by his son Caspar, in the *Horti Medici Amstelodamensis Rariorum Plantarum* (Commelin 1701) in which *H. althaeifolia* and *H. alnifolia* are depicted.

The promotion of Cape plants led to “calling” botanists being made welcome, particularly those from Holland, one of whom was Paul Hermann. Before and after collecting plants in Ceylon, Hermann, a medical doctor with the VOC, stopped at the Cape of Good Hope in April 1672. This makes him the first trained botanist to set foot on Cape soil and collect herbarium specimens from the Cape, including specimens of *Hermannia* (Karsten 1967; Gunn and Codd 1981). His voluminous herbarium and collection of drawings were intended for his flora of the Cape, his *Prodromus Plantarum Africanum*, but due to his early death, no such publication ever appeared (Heniger 1986). Hermann forwarded seeds and specimens to Thomas Bartholinus (1616-1680), a professor of anatomy at Copenhagen, who published the first article devoted entirely to Cape plants entitled “*Plantae Novae Africanae*” (Bartholinus 1675). It is possibly that from this collection the first seeds of *Hermannia* were distributed around Europe, as Jacquin published paintings of eighteen species of Cape *Hermannia* in his *Hortus Schoenbrunnensis* in 1797 and Levrault (1821) wrote about there being large numbers in cultivation in the botanic gardens. Tournefort dedicated the genus to Hermann (Gray 1849), but as formal taxonomy conventionally starts with Linnaeus’s *Species Plantarum* (1753), this genus is ascribed to Linnaeus. Previously, polynomial names of *Hermannia* species were ascribed to *Althaea*, *Ketmia* (eg. Commelin 1701), *Cistus* and *Chamaecistus* (Plukenet 1700).

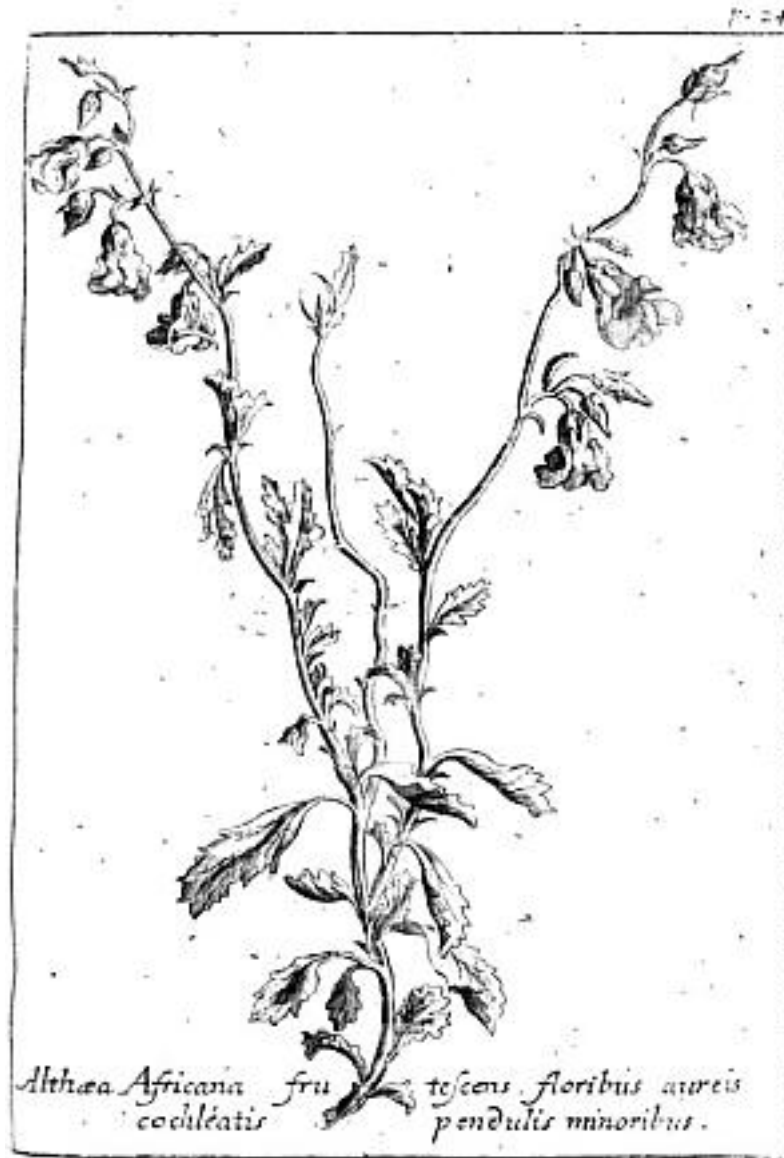
The first illustration of a *Hermannia* is possibly that of *H. micrantha* (Fig. 1.5) published by Volckhamer (1700). This was incorrectly considered a depiction of *H. hyssopifolia* by Gunn & Codd (1981). In the same year Plukenet produced a drawing of *H. verticillata* under the polynomial *Cistus humilis chamaedryos crispatus foliis* in his *Almagesti Botanici Mantissa* (Plukenet 1700). He cited in synonymy an earlier publication in *Hortus Malabaricus*, but this was identified by Dillwyn (1839) as *Sida retusa*.



### 1.2.3 Noteworthy conceptual and taxonomic contributions within *Hermannia*

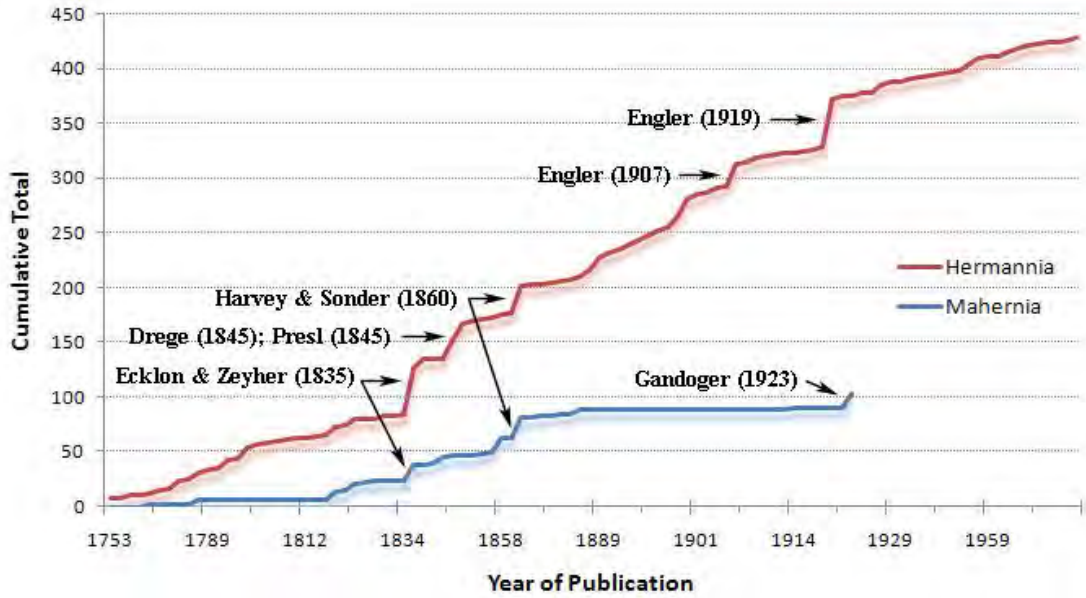
*A detailed taxonomic history follows as part of the introduction to the taxonomic treatment. What follows here is a history focusing on noteworthy conceptual contributions and taxonomic concepts pertaining to higher level familial, generic or infrageneric taxonomies.*

Linnaeus placed the genus *Hermannia* and several genera of Sterculiaceae bearing united anthers into the class Monadelphia in the group Pentandria (monadelphous meaning having filaments united to form a tube around the pistil (Lowson 1946), and Pentandria alluding to having five stamens). In *Species Plantarum* (Linnaeus 1753) he described six *Hermannia* species, followed by *H. trifurcata* in the second edition (Linnaeus 1762) and *H. trifoliata* in his *Mantissa Plantarum Altera* (Linnaeus 1771). Linnaeus described the genus *Mahernia* from *M. verticillata* in his *Mantissa Plantarum* (Linnaeus 1767). In his *Systema Naturae* (Linnaeus 1770) he further consolidated the genus *Mahernia* by including *M. pinnata*, originally described as a *Hermannia* in *Species Plantarum* (1753). Thus, eight species were described by Linnaeus, two of which were placed within the genus *Mahernia*. Fig. 1.6 depicts the increase in species described since Linnaean times. The major contributors are specifically annotated.



*Althaea Africana* fru  
coculéatis *tesens floribus aureis*  
*pendulis minoribus.*

Fig. 1.5 An early illustration of a *Hermannia* by Volckhamer in 1700. This is probably *H. micrantha*.



**Fig. 1.6** Publication dates of new species names plotted cumulatively. Names within Genus *Hermannia* are plotted in red and within the genus *Mahernia* (now subg. *Mahernia*) in blue. The initial publications begin with Linnaeus (1753) and continue till De Winter's publications in 1986. Only three other species have been published since, by Cheek in 2006.

The literature of *Hermannia* has many examples of both black and white and colour plates. Although several pre-linnaean drawings of *Hermannia* exist, Cavanilles (1788) was the first to publish a substantial collection of detailed engravings of 20 species and their floral dissections. Schrader & Wendland (1797) were the first to publish colour plates depicting *Hermannia*, in which three species and their floral dissections were reproduced with almost lifelike accuracy. Reichenbach contributed the largest single body of colour plates of *Hermannia*, with depictions of flowering branches and dissections of 25 *Hermannia* and five *Mahernia* species.

Dardanelle is the only person to have undertaken a dissertation on *Hermannia*. Dardanelle's (1794) doctoral dissertation, supervised by Carl Thunberg, was a 20 page revision of *Hermannia*, encompassing a total of 27 species, including descriptions of seven new species. He placed these into three groups based on whether the leaves were entire, toothed or deeply toothed "*incisopinnatifidis*". After tracing the literature of the species, he provided a description of the characters of the genus and then discussed the virtues of separating *Mahernia* from *Hermannia*. Dardanelle decided that *Mahernia* was still sufficiently distinct from *Hermannia* to warrant the

status of genus, *‘Mahernia tamen minime ab Hermanniiis separari debet; variant enim singulariter genera nonnulla Capensia, ut Irides, Lobeliae, Diosmae, alia.’* Dardanelle then provided a brief Latin description of all 27 species, followed by a more lengthy comparative description of each species. This thesis was formally published six years later as part of a series of theses supervised by Thunberg (Thunberg 1800).

De Candolle (1824) made the first attempt at an infrageneric classification of the genus. He reviewed 42 species of *Hermannia*, separating the species with inflated calyces (sect. *Trionella*), from those without (sect. *Hermannella*). Eighteen species of the genus *Mahernia* were also documented.

Harvey and Sonder published the tome *Flora Capensis* with descriptions and keys to *Hermannia* in 1860. In all, 78 *Hermannia* and 49 *Mahernia* species were encompassed, providing descriptions for a substantial total of 127 *Hermannia* species. More importantly, though, they effectively consolidated the taxonomy of the 70 known *Hermannia* species and 33 *Mahernia* species known at the time. *Hermannia* was split into two sub-genera: subg. *Euhermannia* (henceforth referred to as subg. *Hermannia* as per the *International Code of Nomenclature* (ICN)) with 64 species in eight groups and subg. *Acicarpus* with five species. The 33 species of *Mahernia* were placed into five groups. One year later, Engler placed three species within tribe *Hermannieae* under sect. *Hermannia* Harv., and a further three species, including the new species *H. inamoena* under sect. *Acicarpus*. Harv. (Engler 1895).

Adolf Engler was pioneer of the concept of biogeographical regions and co-creator of the Engler & Prantl system of classification which is still used by many herbaria today (Woodland 1997). He was the last person to describe a large number of *Hermannia* species, describing 48 species over a 26 year period until 1919, mostly in *Bot Jahrb. Syst.* (Engler 1893; Engler 1904; Engler 1919). Engler's greatest contribution to *Hermannia* was in Volume 55 (summarised in Table 1.3 below). He erected Section *Scaphiostemon* with a single species, *H. tenuipes* from Namibia. A further 12 subsections were placed within sect. *Hermannia*. Eight of these sections had previously been recognised by Harvey, with four being new. He also erected three subsections within sect. *Acicarpus*. Engler's *Monographieen Afrikanischer Pflanzen-Familien*

*und-Gattungen* (Engler and Schumann 1900) was important in erecting a new subgenus *Marehnia* (8 species), consolidating the subg. *Hermannia* (13 species) and reducing *Mahernia* to subgeneric level (28 species). Harvey's sect. *Acicarpus* (19 species) was also recognised. Besides providing keys to the species within each section, Engler also placed the species within *Mahernia* into Harvey's five groups as "Reihe" (which translates as 'series'), namely *Verticillatae*, *Pinnatifidae*, *Lacerifoliae*, *Dentatae* and *Tomentosae*. The majority of *Hermannia* species were thus known and described prior to the turn of the 19th century (see Table 1.2, below).

**Table 1.3 Historical account of the publication of new species within the genus *Hermannia* including synonyms. Some authorities that mentioned five or more species in a single publication, whether currently valid or not, are included. Column 2 lists the number of species accepted as valid species in the publication(s), column 3 indicates the number of new species attributed to the author (including homonyms) and column 4 shows the dates of publication(s).**

<b>Authority</b>	<b># of accepted species</b>	<b># of new sp.</b>	<b>Date</b>
Linnaeus	12	11	1753
L.f.	8	8	1781-1782
Cavanilles	6	11	1782-1788
Thunberg	27	5	1794
Jacquin	11	12	1797-1798
Link	5	4	1822
De Candolle	8	7	1824
Ecklon & Zeyher	42	57	1834-1835
Otto & Dietrich	31	3	1840
E. Meyer	17	25	1843
C. Presl	15	15	1845-1846
Turczaninow	19	17	1858
Harvey	28	34	1860
Schinz	5	18	1888-1910
Schumann	31	36	1889-1893
Sessé & Moccamedes	7	2	1894
N.E. Brown	10	10	1895-1909
Schlechter	5	7	1898-1919
Baker	5	2	1901
Hochreutiner	10	0	1907
Engler	48	38	1907-1919
Dinter	14	16	1922
Burt Davy	7	8	1926
Salter	5	6	1946
Holzhamer	6	3	1953
Verdoorn	91	7	1969-1975
<b>Total Number</b>	<b>330</b>	<b>362</b>	

Engler further consolidated his work in a comprehensive description of the sections, with distributions given for the groups and species described in his previous work (1921). In discussing the patterns of biogeography within the genus, he postulated that the centre of evolution –*Entwicklungscentren*” has been in Africa for a long time – as evidenced by Africa housing the major groups of the genus, including *Marehnia* to the North of the equator. He also suggested that the genus is very old as indicated by the occurrence of species in America and Australia. He went further to say that this intercontinental distribution can only be explained by a Gondwanan distribution of *Hermannia*. The only other species to be published in *Mahernia* subsequent to Engler’s (1900) erection of the subgenus was Gandoger’s (1923) 13 new *Mahernia* species and the single species, *M. grossularifolia* described by Druce (1914).

**Table 1.4 The classification of *Hermannia* according to Engler (1921). The subgeneric and sectional divisions of Engler (1921) are shown, with the number of species in each subgenus and section at the time enclosed in brackets.**

subgenus	Sections
<i>Marehnia</i> K. Schum. (12)	No sections given.
<i>Hermannia</i> K. Schum. (62)	<i>Althaeoideae</i> Harv. (8), <i>Patellicalyces</i> Engl. (2), <i>Cuneifoliae</i> Harv. (8), <i>Scaberrimae</i> Harv. (9), <i>Glomeratae</i> Harv. (4), <i>Flammeae</i> Harv. (9), <i>Velutinae</i> Harv. (4), <i>Lateriflorae</i> Harv. (3), <i>Exstipulatae</i> Engl. (1), <i>Pinnatifidae</i> Harv. (7), <i>Cristatae</i> Engl. (1), <i>Parvipetalae</i> Engl. (6).
<i>Scaphiostemon</i> Engl. (2)	No sections given.
<i>Acicarpus</i> Harv. (38)	<i>Modestae</i> Engl. (10), <i>Brachypetalae</i> Engl. (13), <i>Macropetalae</i> Engl. (4), <i>Gariiepianae</i> Engl. (4), <i>Helianthemifoliae</i> Engl. (7), <i>Fruticulosae</i> Engl. (3).
<i>Mahernia</i> (L.) K. Schum. (54)	<i>Waltherioideae</i> Engl. (1), <i>Verticillatae</i> Harv. (11), <i>Pinnatifidae</i> Harv. (8), <i>Lacerifoliae</i> Harv. (6), <i>Dentatae</i> Harv. (14), <i>Tomentosae</i> Harv. (14).

In 1946, Captain Salter, together with his description of five new species, recorded for the first time many salient field observations and principles. These included the habitat, plant height and habit notes that are now recognised as being important taxonomic and ecological characters useful in elucidating the taxonomic identity of *Hermannia* species. Salter provided an appraisal of the state of *Hermannia* at the time, noting that the large number of scattered and inadequate descriptions make taxonomic work difficult. Salter further lamented the lack of plant details recorded by collectors of *Hermannia* specimens. He also noted the importance of flower colour in distinguishing species, a character that is frequently lost upon drying. Perhaps the focus on herbarium specimens by Verdoorn (1980) and De Winter explains why flower colour is seldom mentioned in their work. His contributions to furthering the paradigm of field-based taxonomy are stated plainly by Bullock when providing a rationale for the naming of the genus *Saltera*, in which he declared — “[he] has done so much by example and precept to stress the importance of the study of living plants in the field, in order to arrive at an understanding of their taxonomy” (CITATION: KEW BULLETIN 109, 1958)\*\*\*. It is to the detriment of the state of the taxonomy of *Hermannia*, that his sage suggestions were largely ignored in subsequent collections and treatments.

Merxmüller’s work culminated in an account of 32 species that mainly cover the sect. *Acicarpus* within Namibia (Merxmüller 1968). This publication included a key with brief descriptions, the nomenclature and a list of types and specimens examined. No classification system was followed with species from Engler’s groups *Hermannia*, *Mahernia* and *Acicarpus* mixed together. Nonetheless Merxmüller’s work was thorough and represented the most comprehensive body of work done on *Hermannia* within Namibia.

Pillans (1884–1964) worked on a revision of *Hermannia* from the Bolus Herbarium, but his death intervened before completion. It is difficult to say how close Pillans was to publishing, as I have not been able to find his unpublished work within Cape Town. The words from H. Wild to Pillans in a personal letter dated 12 June 1958 would suggest that he had made substantial progress: *—It is a disgrace that you have had to wait so long [for the types] but perhaps I had better say no more on that score. Suffice to say that the parcel was apparently lost within the precincts of the [Kew] herbarium on two separate occasions... It must have been most*



*depressing for you to wait so long to see a few types when the back of your work was done. With good wishes for your work on what is obviously a more difficult task than mine on the more tropical representatives of Hermannia. I certainly did not find ours very easy.”*

Inez Verdoorn (1980) examined Pillans' notes during her revision, resulting in a single new species being erected. This latest revision focused wholly on the subg. *Hermannia*. She produced an excellent alpha taxonomy of the section *Hermannia* and recorded the details of the hairs present (trichome complement) on all *Hermannia* species. Another boon was the inclusion of an excellent “working key” that groups the plants well and with practice allows for fairly rapid identification of the species. Verdoorn sank subg. *Acicarpus* and subg. *Scaphiostemon* (represented by *H. amabilis*) into subg. *Hermannia*. Most of Verdoorn's work was done at the Pretoria Herbarium and as a result lacked field experience. Thus her revision provided scant insight into ecology and biogeography, resulting in a very conservative concept of the species. Perhaps in an attempt to address the shortcomings of the treatment, for example, the lack of distribution maps or plates, Anne Bean of the Bolus Herbarium produced an unpublished three page overview of Verdoorn's (1980) revision entitled “analysis of *Hermannia*”. The analysis includes rough outlines of the habit, flowers, leaves and stipules and includes brief comments on distribution, flower size, flower colour and diagnostic characters. This work currently resides in the Bolus Herbarium and has remained largely unused.

During the 1970s and 1980s, Dr. Bernard de Winter, an expert in grass identification and a supervisor of Mrs Verdoorn, undertook the task of revising the subg. *Mahernia*. De Winter succeeded in organising the species, compiling diagnostic characters for many of them and producing part-descriptions for many of his new species. An early adopter of technology, de Winter not only was instrumental in bringing computerisation to Pretoria, but also succeeded in creating a character template in the taxonomic software, DELTA (Dallwitz 2000). Retirement prevented Dr. de Winter from completing his revision, although much of the morphological and taxonomic groundwork was done. As this revision was never completed, one of the aims of my current work is to undertake the task of completing de Winter's revision. My work has thus drawn upon his species concepts, his knowledge of the species and the descriptive work has built on his original DELTA template of characters.

The few new species described since Verdoorn's revision in 1980 includes a single species from Ethiopia, the description including SEM images showing the seed sculpturing (Vollesen 1985) and three species of "Marehnia" described by Cheek (2007). Table 1.5 provides an overview of publications which contain dichotomous species keys, the taxonomic groups that they include and the regions that they cover.

**Table 1.5 Publications that have species keys, the number of species, the groups that are distinguished in the key, with the total species recognised in that publication at the time in bold. The coverage indicates the taxonomic group or region covered. Legend: He = *Hermannia* (Genus); Eu = subg. *Hermannia*; Ma = subg. *Mahernia*; Mr = "Marehnia"; Ac = subsect. *Acicarpus*.**

<b>Citation</b>	<b># sp. and groups</b>	<b>Coverage</b>
(Verdoorn 1980)	<b>92</b> Eu	Entire subg. <i>Hermannia</i>
(Engler and Schumann 1900)	8 Mr; 15 Eu; 28 Ma; 19 Ac = <b>73</b>	All African sp.
(Harvey and Sonder 1860)	64 Eu; 5 Ac; 33 Ma = <b>102</b>	South Africa.
(Wild 1961)	<b>18</b> He (subg. not separated)	Zambeziaca area.
(Merxmüller 1968)	<b>33</b> He (subg. not separated)	Namibia
(Oliver 1868)	4 He; 2 Ma = <b>6</b>	Tropical Africa
(Burt Davy 1926)	7 Eu; 8 Ac; 25 Ma = <b>40</b>	Transvaal & Swaziland

Janice Saunders is the only other person I have encountered actively working on the taxonomy of the genus *Hermannia*. She has published revisions for the closely related genus *Waltheria* and although showing a keen interest in the African species of *Hermannia*, her focus has been on the American species. Saunderson's work on these American species thus far has remained largely unpublished, but includes scientific drawings, the collation of specimen label information, microscopy work on the plants including the seeds, comparative measurements of the morphology, species descriptions and the creation of distribution maps.

### 1.3 Biogeography

*Hermannia* is an inter-continental disjunct genus, occurring in Africa including the Cape Verde islands, the Arabian Peninsula, North and Central America and Australia. The only cited collection from Madagascar (*Bojer s.n.*) has proven an erroneous record from Mozambique (Humbert 1959). However other sources that do not cite specimens mention Madagascar (eg.

Arenes 1959; Bayer and Kubitzki 2003). The genus is represented in North America by four species (Standley 1923; Shreve, Wiggins et al. 1964), all occurring in or close to arid zones of the SW United States and adjacent Mexico. In Australia, one species, *H. biniflora* occurs in the southern portion of Australia. The origin of this disjunction remains unknown, although Engler (1919) suggests that the Australian and African species may have been separated for a considerable length of time. The question of whether this represents a dispersal or vicariance event between Africa and Australia is answered in Chapter 3 through the use of molecular dating.

By far the greatest diversity is in Africa where species of *Hermannia* occur in 10 of the 18 African phytochoria and in all 12 of the Southern African phytochoria (Burgoyne, van Wyk et al. 2005). Within the CFR, the centre of diversity of *Hermannia*, *Hermannia* species occur in all 25 centres of endemism *sensu* Low and Rebelo (1996).

#### **1.3.1.1 Diversity of the CFR and Linder's „Cape floral clades“**

The CFR is one of the most species-rich places on earth and is also associated with a very high level of endemism of 68.8% (Cowling 1992; Cowling, Rundel et al. 1996; Goldblatt and Manning 2000; Linder 2003; Burgoyne, van Wyk et al. 2005). Linder (2003) suggests that remarkable conditions must have persisted to have facilitated such high levels of speciation as well as persistence of those species. Linder found that nearly half the species within the Cape could be attributed to 33 ‘Cape floral clades’. He defined ‘Cape floral clades’ as those species which arose in the CFR and in which the majority of species still occur within the CFR. He considered such a high contribution of species by so few clades a special case more typical of island than mainland floras.

#### **1.3.1.2 Known ages of Cape floral clades**

Linder's (2003) initial dating of Cape floral clades from a total of six groups, found that radiations occurred between 18 and 8 Mya, coinciding with the Cenozoic period. Later studies found that the predominance of lineages across 55 succulent karoo and 41 fynbos-endemic lineages in 17 genera or families were less than 20 Myr old (Verboom, Archibald et al. 2009).

More precisely, the analysis found that stem nodes had a mean age of  $8.50 \pm 1.85$  Myr for fynbos lineages and  $5.17 \pm 0.64$  Myr for succulent karoo lineages. However, *Hermannia* does not fit the typical pattern of Cape floral clade taxa that generally inhabit the nutrient-poor mountains of the CFR. The biogeographic patterns within *Hermannia* suggest that the CFR components of the genus may comprise elements with other origins, including the semi-arid Succulent Karoo flora with a centre of diversity in Namibia, elements from tropical Africa and species from the summer rainfall eastern portion of South Africa. *Hermannia* has all three elements well represented and thus provides a rare opportunity to study the contributions of these elements to the diversity of the CFR.

## 1.4 Ecology

Individual *Hermannia* species are typically confined to a single, or a narrow range of particular substrates (pers. obs.). Usually these are nutrient-rich soils derived from granite (eg. *H. meyeriana*), dolerite (eg. *H. glabrata*, *H. supernova*), dolomite (eg. *H. supplicans*), limestone (eg. *H. ternifolia*, *H. trifoliata*, *H. concinnifolia*) and shale (*H. rugosa*, *H. angularis*), though a few species occur on montane, nutrient-poor, sandstone (eg. *H. disticha*, *H. angelica*) or nutrient-poor lowland sand (eg. *H. linifolia*). There is an enormous environmental range across the genus, though individual species tend to have relatively narrow distributions (Verdoorn 1974) and hence narrow environmental ranges. Their breadth of their adaptive range may in part be due to the range of hair types and densities that cover the plants. Most species, except for the most densely hairy, are readily grazed and are thus useful indicators of overgrazing (Le Roux, Kotze et al. 1994). These palatable species sometimes have common names that reflect their utility in feeding stock (eg. *opslag*, see Table 10.3 for common names and translations of Afrikaans names). Some species are unpalatable and have been found to increase in unprotected plots available to goats (Hayashi 1995).

Janzen (1984) proposed that herbaceous plants with small seeds are selectively advantaged by providing palatable leaves to promote the incidental ingestion of fruit, thus effecting dispersal by large grazers. He called this the “foliage is the fruit” (FF) hypothesis. Janzen mentioned ten expected traits of the plants, of which *Hermannia* fits at least eight criteria. There is substantial literature supporting *Hermannia* as a highly palatable species (Le Roux, Kotze et al. 1994;

Botha, du Toit et al. 2001; Milton and Dean 2001), with most species receiving a high grazing index value (Botha, du Toit et al. 2001). Seed of *Hermannia* has successfully germinated from the dung of eland (Shiponeni and Milton 2006), goats and sheep (Milton and Dean 2001). Micromammals appear to relish the leaves (Schradin and Pillay 2006) and tortoises have been found to both consume and disperse the seed of several *Hermannia* species (Loehr 2002). Based on the unusually high palatability and tough seed characteristics, *Hermannia* should be further examined to ascertain whether it is a candidate for FF dispersal.

Many of the species of subg. *Hermannia* (never subg. *Mahernia*) have flowers that invert once pollination has taken place. The reason for this has never been posited, though it seems that there are two likely advantages to this action. Firstly, pollinators tend to find it easier to enter from below and are never seen entering upwards facing flowers. Colour changes appear to rapidly take place within many of the species, typically fading or changing towards a red or brown colour, suggesting that the plant is making fertilized flowers less attractive to the pollinator. However, inverting flowers additionally tie in nicely with Janzen's FF hypothesis, in that the inverted flowers are closer to the tips of the branches where the leaves are concentrated. Many *Hermannia* species have caducous leaves, with leaves confined to the young branches and they are good at resprouting from below the level of grazing. An animal foraging for leaves would presumably carefully eat the leaves off the branches avoiding the leafless branches, but because the capsules are erect, not drooping, they would inadvertently consume the fruit as well.

There is a single ecological examination of *Hermannia* that details the close relationship between a butterfly, *Aloeides dentatis dentatis* and its host plant *H. depressa* (Henning 1984). Otherwise ecological information on features such as pollination and dispersal is confined to scattered observations, collector notes, or references to general ecology within the descriptions of species.

To date, this is the only recorded pollination account for *Hermannia*. However, if visitation is a rough proxy for pollination, then it appears that pollination is accomplished by a variety of insects (pers. obs.; (Gess and Gess 1991; Gess 2005), with some *Hermannia* species being generalists (pers. obs.) and others being visited by only a single insect species. These specialists

include foraging by the pollen wasps *Masarina hermanniae* and *M. strucki* (Gess and Gess 2004) and three species of *Jugurtia* (Gess and Gess 2004). Nectar for *H. incana* is reported to comprise roughly equal amounts of fructose and glucose with trace amounts of sucrose (Scogin 1979). This composition is generally associated with bird pollination (Heinrich 1975). Furthermore, two verbal accounts of floral visitation by birds (J. Vlok pers. comm.), a photograph by Dennis Hanson of a malachite sunbird, *Nectarinia famosa* visiting *Hermannia amoena* and my own observations of sunbird visitation suggest that birds may play a role in the pollination and possible evolution of this genus.

The range of capsule types suggests that there may be at least three means of dispersal. A few species within sect. *Hermannia* have round inflated calyces that appear to be adapted for wind dispersal. Independently evolved, presumably also for wind-dispersal, are the capsules of *H. grossularifolia* and other allied species in which it is the ovary that is massively inflated, not the calyx. The horns on the capsules of the sect. *Acicarpus* may be an adaptation for epizoochorous dispersal. *H. palmeri* has modified stellate hairs resembling grappling hooks that are unambiguously suited for the role of attaching to passing beasts. The remaining sections have generally been considered passively dispersed, as seeds of subg. *Mahernia* are without apparent dispersal mechanisms or appendages. A white hilum has been noted on a number of *Hermannia* seeds (Verdoorn 1980), though it is doubtful whether this could be considered a food source, i.e. an elaiosome to attract ants (Slingsby and Bond 1985). However, harvester ants (*Messor cf. capensis*) have been observed severing capsules from *Hermannia erodioides* plants and carrying them back to the nest where it formed the predominant biomass visible at the entrance to the nest at that time of year (pers. obs.). This may be where the seeds subsequently germinate, or they may undergo secondary dispersal by bat-eared foxes or anteaters that ingest the seed while feeding from ant mounds (Milton and Dean 2001). The intercontinental distribution and a distribution across the length of Africa indicate the efficacy of the dispersal of some species in the long-term. This is contrasted by the number of narrow endemic, apparently nascent species that are confined to specific substrates or niches, suggesting that seed dispersal and gene-flow is spatially highly limited.

## 1.5 Need for the study, aims and thesis prospectus.

*Hermannia* featured in the first herbarium collection of Cape plants by Paul Hermann in 1672 (Gunn and Codd 1981). There are now over 17 000 specimens in South African herbaria and more than 536 names documented by the *International Plant Name Index* (IPNI). Many new species within subg. *Mahernia* have been proposed and utilized by De Winter, but not formally described. The National Herbarium Database for South Africa, PRECIS, does not support the incorporation of manuscript names and, as a result, a significant one-third of the records for *Hermannia* have not been assigned to species. Thousands of records have also been assigned to nomenclaturally valid, but taxonomically incorrect species names. Thus any output from PRECIS will likely produce many spurious distributions. There is thus a dire need for a taxonomic and nomenclatural reassessment and integration of this information into herbaria.

Many of the species concepts resulting from De Winter's incomplete taxonomic treatment of the subg. *Mahernia* are questionable as a result of being almost entirely herbarium-based, with many taxonomically relevant characters such as floral shape and colour having been largely ignored. Ecological notes for *Hermannia* are few, with substrate not having had due consideration when delimiting species. As a result, many distinct species have been lumped into broad species concepts and narrow endemics have been taxonomically ignored. Distribution maps are useful for flagging outlying and thus possibly new endemic species and for creating distribution layers from which climatic envelopes may be derived. Existing, automatically generated, floristic datasets are often considerably flawed, based on poor geo-referencing and plagued with taxonomic problems. It is thus a priority to produce maps that accurately represent the distribution of the plant and that are taxonomically correct. The combination of poor locality and ecological information has led to a reduced recognition of diversity, with resultant impacts on any subsequent work requiring these records, eg. species lists or analyses of biodiversity.

Most descriptions, including those in the recent revision of subg. *Hermannia* (Verdoorn, 1980), are not accompanied by drawings or photographs. The majority of published descriptions are inadequate for diagnosing species (Salter 1946), leaving identification up to herbarium staff who have to contend with uncertain manuscript names, incomplete species concepts and most

importantly an inadequate reference to the genus. Herbarium staff are often reluctant to undertake identifications, particularly of the subg. *Mahernia*, leading to a snowball effect of unidentified or incorrectly identified specimens. An organised photographic compilation of species would greatly assist in providing an overview of the variation within the genus and in depicting the variation within species.

In order to improve our understanding of the origins and processes underlying species diversity, especially in the CFR, Hawkins (2006) stresses the importance of including lineages with different life-forms and life-history strategies that may show different patterns of radiation. Barraclough (2006) concurs with Hawkins in suggesting complementing Cape clades with sister groups or lineages that are species poor in the Cape. Many studies to date examine diversification mainly within the CFR. eg. *Muraltia* (Forest, Nanni et al. 2007); *Bruniaceae* (Quint and Classen-Bockhoff 2006); *Geissorhiza* (Goldblatt 1985), but few have had substantial representation outside the CFR. This has been addressed in a recent meta-review of 12 families/genera (Verboom, Archibald et al. 2009), although it focuses on the dating of radiations and does not examine actual species patterns within the groups.

One of the chief aims of this work is to provide researchers with a practical basis for future research into the morphologically and geographically diverse genus *Hermannia*. The unpublished character analyses and nomenclatural work of De Winter is utilized and expanded upon. Hypotheses developed through thirteen years of study and observation of the genus, both in the field in the herbarium and through discussion with De Winter, are assessed where practical and pertinent. A phylogenetic and evolutionary framework for classification and analysis of diversification within the genus, including an estimate of diversification and divergence times for key groups within the genus, is provided. Finally, a range of tools is provided on DVD to further both research on and discovery of *Hermannia*.

*Mahernia* is the focal subgenus for several reasons: The subg. *Mahernia* has not yet been revised and is in a state of taxonomic and nomenclatural turmoil, whereas subg. *Hermannia* was revised by Verdoorn in 1980. The size of the genus (+200spp.) is too widespread (East Africa



and America) to sample fully during this period. Investigating the subg. *Mahernia* is logistically more realistic, as it occurs mostly within South Africa. A brief prospectus of the thesis follows.

**Chapter 2** provides an **overview of the morphology of *Hermannia***. This aims to clarify the terms used in the thesis, as well as to provide a summary of the range of variation that has been encountered within the genus that has never been illustrated or described in detail before. Images are provided illustrating many of the terms.

**Chapter 3** examines **the phylogenetics of the genus**, encompassing all major groups. The monophyly of *Hermannia*, with respect to related genera and species previously placed in other genera, is tested. This chapter includes molecular dating that aims to provide an initial hypothesis on the age of radiation of key groups within *Hermannia*, particularly with a view to ascertaining whether the sect. *Hermannia* can be considered a ‘Cape clade’ sensu Linder.

**Chapter 4** uses the phylogeny from Ch. 3 to provide **a novel and natural classification** for the genus. The distribution of the species are then shown within their groups. The distributions have also been overlaid onto a climate map to ascertain overall climatic patterns for each group and to detect climatically anomalous species.

**Chapter 5** details **character evolution and ancestral character state reconstruction** based upon the phylogeny to better understand the current patterns of diversity.

**Chapter 6** provides an **analysis of various diversity measures** of *Hermannia* to examine contemporary distribution patterns and to better understand past evolutionary processes.

**Chapter 7** provides an **analysis of the phytochoria** within Africa and particularly South Africa. Climate change is briefly assessed to investigate the general distributional changes predicted.

**Chapter 8** is a **general discussion** highlighting the key findings of the study and looking at future prospects for research within the genus. The chapter ends with a guide to using the online atlas, CASABIO.

**Chapter 9** provides the references for the thesis.

**Chapter 10** provides the appendix including further methods, an electronic key to the species in subg. *Mahernia*, a character list, a regional guide to identifying Summer Rainfall species, common names and ethnobotanical uses.

**The Taxonomic Revision** includes a list of manuscript names and their latest equivalent, accepted species, a dichotomous key, species descriptions and scans of the floral dissections.

## 2. An overview of morphology in *Hermannia*

### 2.1 Introduction

Given the wide range of habitats in which *Hermannia* occurs, it is not surprising that considerable morphological diversity accompanies its taxonomic diversity. Morphological diversity in other taxa has been correlated with environmental speciation, with floral variation having been associated with pollinator-driven speciation (van der Niet, Johnson et al. 2006). Reproductive isolation may result from adaptation to different pollinators (Grant 1993) or different edaphic conditions (Macnair and Christie 1983). Thus a firm understanding of morphology is essential for further understanding the forces leading to modern diversity of the genus.

As no former publication has discussed the morphology of *Hermannia*, the main objective of this chapter is to outline the diversity of characters encountered during both macroscopic and microscopic explorations of the genus. A secondary objective, in conjunction with the DELTA character list (Table 11.0.10), is to create a platform for mutual understanding and agreement of terms used to describe the genus. The various characters and character states are discussed, both to introduce these features to a researcher unfamiliar with the morphology of the genus and to evaluate the characters for taxonomic purposes.

### 2.2 Methods

Macroscopic features were examined on herbarium specimens or photographic images. Microscopic features were assessed with the aid of a Wild M10 microscope. Features that vary between species are discussed under the headings of habit, rootstock, stem, indumentum, stipule, leaves, peduncle, bract, pedicel, calyx, petal, anther, stigma, capsule and seed. The order in which the characters arise follows that of their sequence within the DELTA database compiled for this study (See Table 11.0.11) and consequently the sequence within species descriptions as well. This chapter highlights the variation observed within *Hermannia*, as well as discussing the definition and delimitation of characters utilized in the electronic key, Intkey. **Character states**

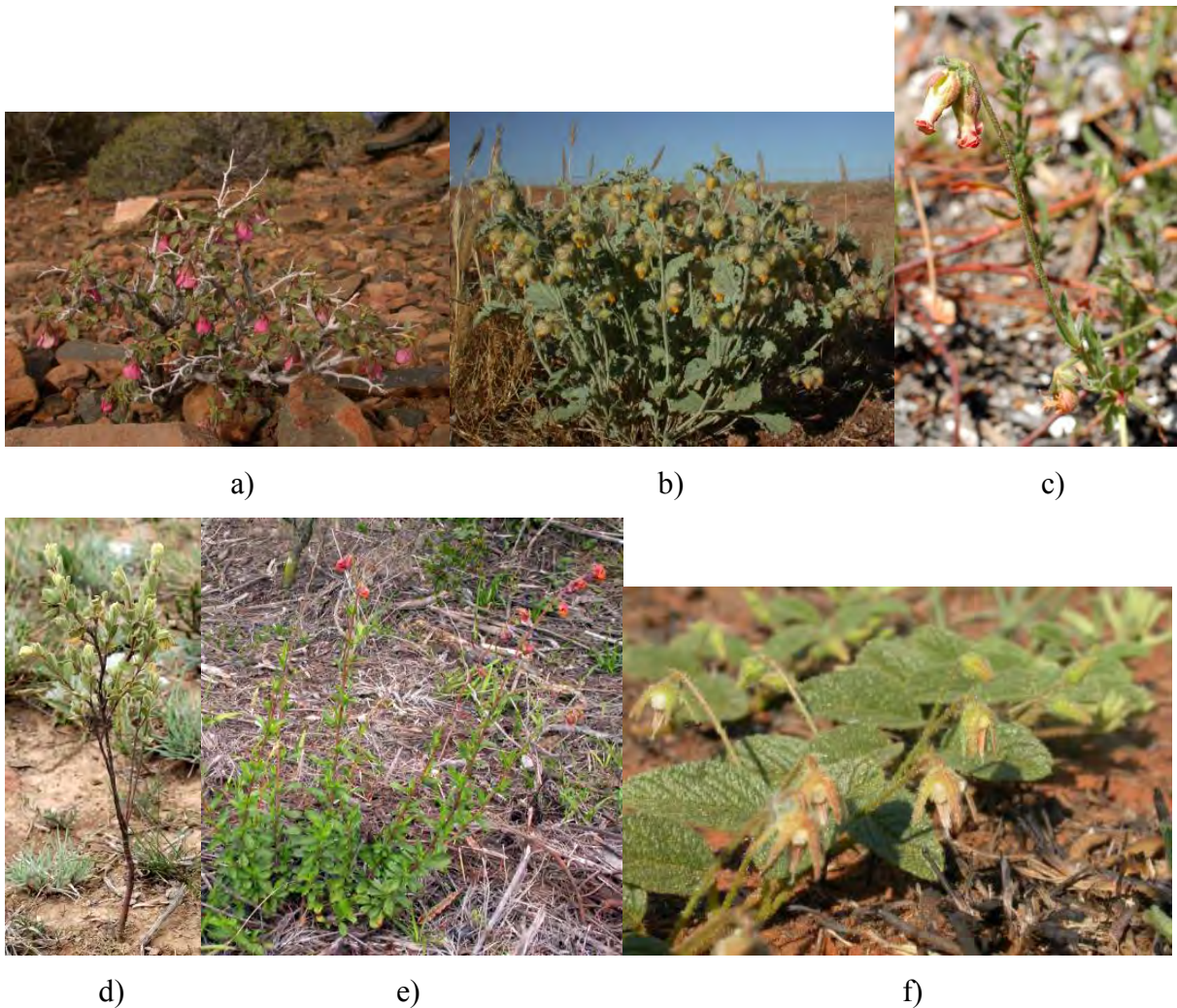
**used in DELTA are underlined for easy reference.** As a consequence of morphological work being focussed on the subg. *Mahernia*, much of the variation described is from my more intimate knowledge of this subgenus.

## 2.3 The characters

### 2.3.1 Habit

Woody stems provide rigidity and support, allowing upright, tree-like, or bushy forms. Herbaceous stems on the other hand allow plants to hug the ground, or sprawl across grass or through vegetation. Species typically either have woody or herbaceous stems, although woody stemmed species may additionally possess younger stems with more flexible herbaceous growth. The possession of both traits within the subgenera of *Hermannia* has allowed for a wide variety of gross forms between species (Fig. 2.1). Low-growing, ground-hugging to decumbent species are spread throughout the genus, with several clades confined to a low-growing habit [Ch. 3]. The sprawling form occurs in both summer- and winter-rainfall areas (see Fig. 11.0.5 in the appendix for a map of the summer- and winter-rainfall areas within Southern Africa) in multifarious habitats. It appears to be primarily an adaptation to grazing, either by hugging pebbles (eg. *H. linnaeoides*) or rocks (eg.. *H. octopussyae*), or by spreading below grass level (eg. *H. depressa*). *Hermannia* utilizes ascending peduncles with a strongly recurved pedicel to enable pollination, despite the architectural constraints associated with combining a low-growth form with a pendulous flower. Several species of sect. *Hermannia* with trailing branches have the terminal portion of the stems raised off the ground, with the apex of the branch drooping. Lawrence (1955) provides clarification regarding terminology associated with the sprawling form. In sprawling species where there is not rooting at the nodes, it is termed a procumbent growth form. The decumbent growth form has similarly sprawling branches without rooting at the nodes, but in this case the plants have the terminal portions raised from the ground. When a sprawling species roots at the nodes, it is considered repent. This is a very rare condition within the genus *Hermannia*. Ascending growth forms are probably the most common form throughout the genus, possibly due to their multiple morphological origins and the generality of the term encompassing many growth forms between sprawling and suberect. Both subherbaceous and

woody plants produce this growth form. Ascending plants may result from multi-stemmed shoots that are sub-vertical, intricately branched stems, or weakly-erect plants. Erect single-stemmed species with few branches are infrequent and generally have a reseeding life strategy eg. *H. salviifolia*. Their leaves are typically caducous (short-lived, dropping early), forming slender few-branched stems with terminal inflorescences. It is suspected that these forms occur in fire-prone areas and are relatively short-lived. Fruticose or bushy plants are typical of the more woody species eg. *H. spinosa*.



**Fig. 2.1 Growth forms. a) fruticose (*H. spinosa*), b) ascending (*H. comosa*), c) decumbent (*H. litoralis*), d) erect single-stemmed reseeders (*H. salviifolia*), e) erect multistemmed resprouter (*H. flammea*), f) procumbent (*H. tomentosa*).**

### 2.3.2 Rootstock

De Winter recognised three forms of rootstock: a woody taproot (Fig. 2.2), an erect, woody root-stock and a branched system of roots. De Winter's system has not been followed due to the difficulty in assigning species to these categories as few herbarium specimens have roots. Furthermore, the difference between an "erect woody rootstock" and a "woody taproot" is unclear. Most species demonstrate a primary root, with radiating, secondary adventitious roots. The woody taproot is evident on some specimens of *Hermannia* and corresponds to the multi-stemmed resprouter that produces stems rapidly after a fire, producing flowers in the same year. Summer-deciduous resprouters have been confirmed for *H. cernua*, a species that appears dead in summer, losing its leaves and then produces small leaves throughout the branches in early autumn (pers. obs.). *H. stricta* on the other hand is more similar to a resurrection plant, in that the leaves appear dead in summer. When rains appear, the entire plant rehydrates and becomes green after a day or two (pers. obs.). This is one of the species that is resinous throughout the plant.

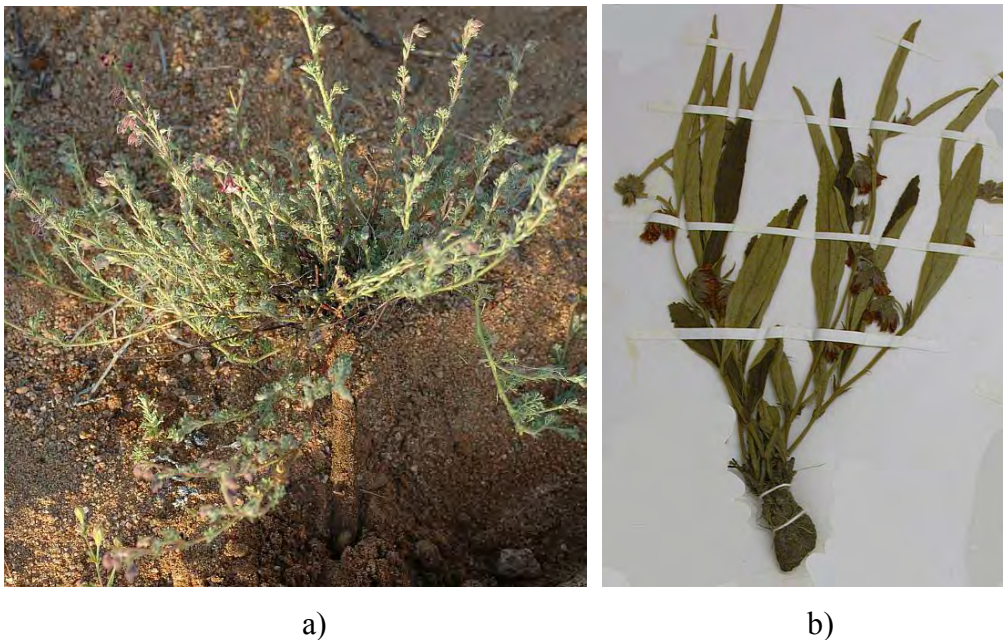


Fig. 2.2 Woody rootstocks. a) *H. meyeriana*, b) *H. lanceolata* (Buitendag 737 (PRE))

### 2.3.3 Stems

Stems vary from thin and branch-like to robust and trunk-like (Fig. 2.3). The branch-like stems occur predominantly in the subg. *Mahernia*, including the herbaceous-stemmed *H. gerrardii*. The best examples of thick tree-like trunks are in the Section *Hermannia*, with *H. reeferi* on the West Coast and *H. onychotenax* (Fig. 2.3c) in the Richtersveld. These bushes can attain heights in excess of 1m with stems exceeding 10cm in diameter. Lichens favour the trunks of these long-lived perennials, especially in the misty coastal zone (Fig. 2.3a,b). This is perhaps an indication of their longevity. Stems frequently lose their indumentum as they age, with many old stems becoming bare of indumentum (Fig. 2.3d). Some species are endowed with a silvery-waxy coating (Fig. 2.3f). This is frequently longitudinally fissured (Fig. 2.3f). A few species have glossy stems due to deliquescent glands (Fig. 2.3e). This imparts a resinous look to the stem and surely acts as a potent anti-herbivory mechanism. eg. *H. fruticulosa*.

Stems of herbaceous species are typically green (Fig. 2.3g), whereas more woody stems tend to be brown or grey. Sub-woody stems are usually brown, but not stiff. In a number of species with herbaceous stems, these are red and this is frequently reflected in the leaf colour. This is likely attributable to anthocyanins that are generally regarded as a defence against sun-damage eg. *H. supplicans*. Red leaves and branches were successfully induced in *H. orgasmiodorata* by moving it from the shade to full sunlight with a white surface beneath.

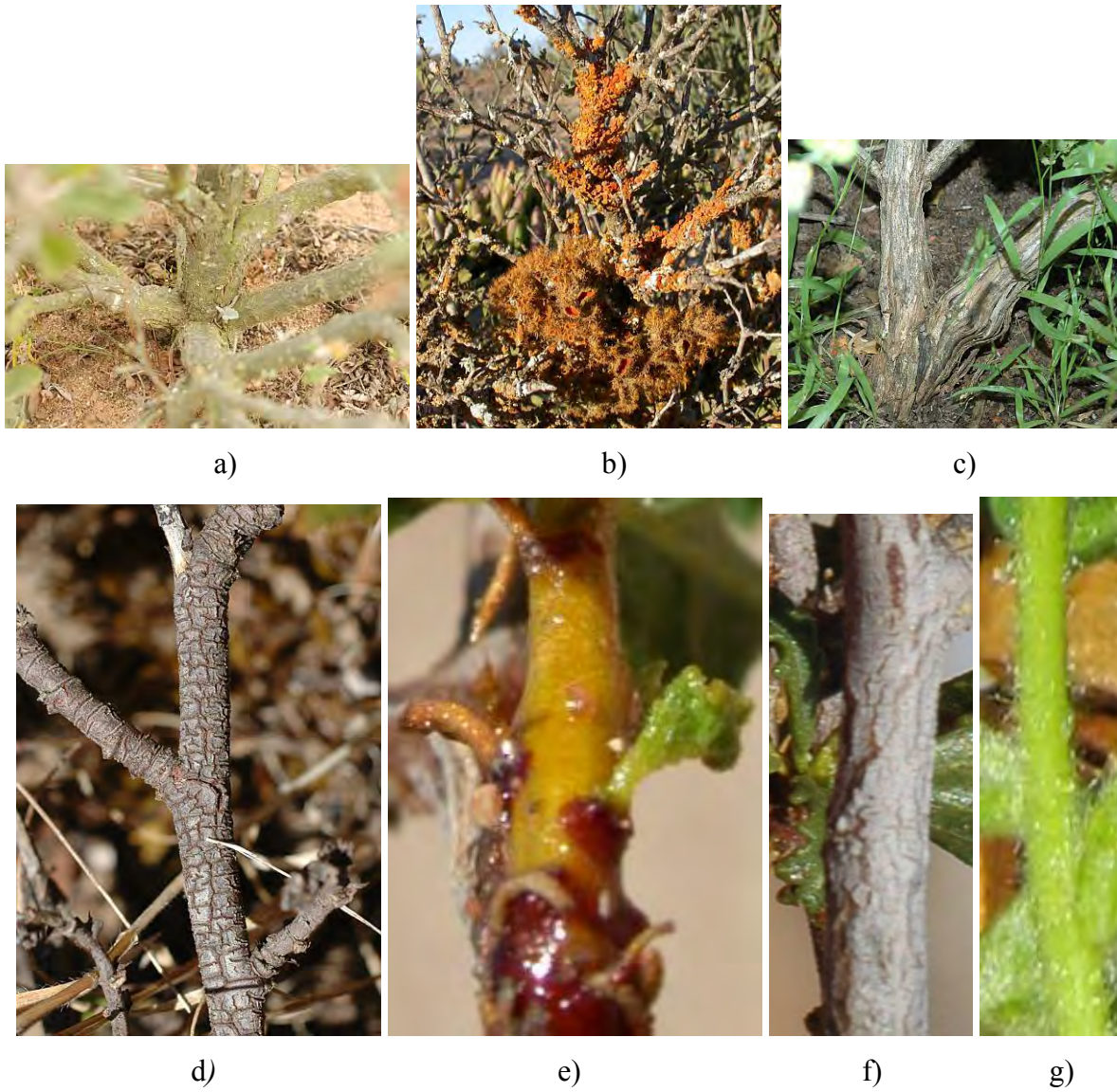
Branching is usually alternate, although dichotomous branching has been recorded for a single species, *H. supernova*, resulting in a rounded bush. In the case of basal sprouting, the stems arise either directly from the rootstock, from a number of underground shoots, or on short thick stems that then produce a cluster of young branches terminally. Most bushy species branch in the mid-regions to upper regions of the stem, sometimes with more than one stem, or a stem and peduncle at a node eg. *H. dinkyflora*. In the case of virgate species like *H. salviifolia*, this mainly takes place near the top of the plant.

Branches, normally arising at the nodes, are typically thinner than the main axis, though in some species they are of approximately equal thickness. The angle that branches make varies from 90 degrees, to nearly parallel with the other branches. *H. trifoliata* has branches at nearly



right angles to the stem lower down, but higher up they are closer to 45 degrees. Branching sometimes appears to be 90 degrees, but on closer inspection is revealed to be 45 degree branching with stems rapidly bending to attain a much more open angle. eg. *H. decumbens*.

Differentiation between young and old stems can be cryptic, with newer green stems grading into the older stems. Young stems are typically green in herbaceous plants, but in woody plants they are frequently shades of red, brown or grey. In more obvious cases colour differentiation can be stark, with new growth being green and older stems being brown, reddish-brown, grey, silver, white or nearly black. In many species there is obvious differentiation in thickness between young and old stems. Differentiation may also be marked by a cluster of thin stems arising from a point on an older stem – indicative of resprouting. Young stems are typically smooth, but old stems may be marked or patterned by old lenticels, striations, cracks, peeling bark, lichens or stipular scars. Indumentum is also typically sparser on older stems, either due to an artefact of thickness leading to a lower hair density, or through the gradual erosion of trichomes. Additionally, young stems have stipules and leaves, whereas in old stems these tend to be absent, or brown and crispy.



**Fig. 2.3 Branch diversity.** a-c) thick tree-like trunk, with lichen visible (a and b), smooth bark (a) and with longitudinally fissured bark (c); (d and f) with cracked bark; e) with deliquescent glands forming a resinous coat; a-f) woody stems; g) a herbaceous stem. a) *H. skyfii*, b) *H. pfeilii*, c) *H. onychotenax*, d) *H. rugosa*, e) *H. fruticulosa*, f) *H. stricta*, g) *H. nessii*.



### 2.3.4 Indumentum

De Winter considered indumentum to be important both in distinguishing species of *Hermannia* and grouping them. Trichomes are useful for the diagnosis of genera and species in a number of families. For example, in the Brassicaceae they are useful for diagnosing genera (Al-Shebaz, Beilstein et al. 2006), whereas in the Plantaginaceae they have been used in diagnosing subdivisions (Rahn 1992). Whilst the family Malvaceae, in which *Hermannia* is situated, usually have stellate hairs (Mabberley 2002; Bayer and Kubitzki 2003), *Hermannia* exhibits a great many varieties and these have been used in the revision of subg. *Hermannia* to distinguish numerous species (Verdoorn 1972).

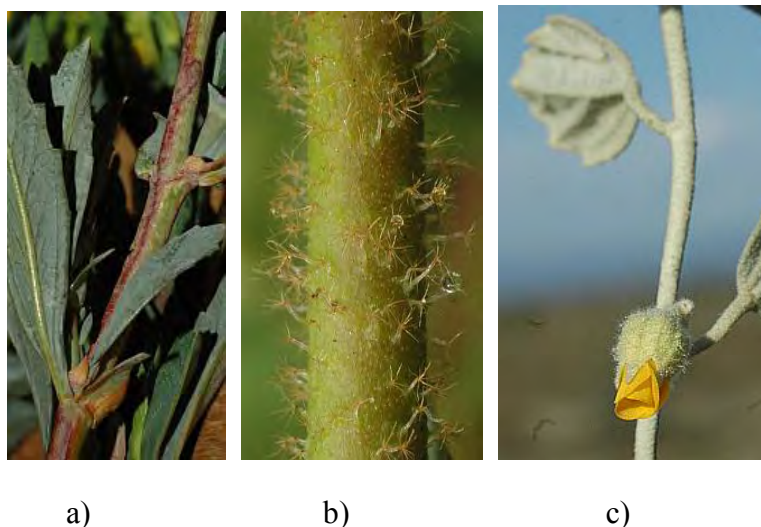
The variety of hair types on the various organs are known as the trichome complement. There are a variety of kinds of glandular, simple, multicellular and stellate hairs. The functions of trichomes in plants were reviewed by Wagner et al. (2004), although *Hermannia* has never specifically been examined. Hairs provide adaptations for brighter, drier and hotter conditions as well as a defense against macro- and micro-herbivory. Despite these defences, nearly all *Hermannia* species are palatable and have been observed being fatally defoliated by caterpillars, slugs and snails (pers. obs.).

Indumentum may be absent (glabrous) (Fig. 2.4a), or varying from very sparse (subglabrous) through to very dense (Fig. 2.4c). In the creation of concise descriptions and for coding indumentum density in the morphological matrix, this set has been reduced to glabrous, sparse, moderately dense or dense. What has not been explicitly coded, but may be added as comments, is that where different types of indumentum occur, the overall density is given. However, glandular hairs may be very sparse and stellate hairs very dense. This difference can be at least interesting and possibly even diagnostic, but descriptions are already extremely lengthy, so the neglect is considered necessary to maintain relative simplicity.

#### 2.3.4.1 Texture

Overall indumentum texture has been coded by De Winter as puberulous (sparsely hairy), pubescent (softly shortly hairy), tomentose (dense, fine erect hairs), villous (long weak, crisped

hairs), hispid (stiff bristly hairs), scabrid (stiff and rough typically stellate hairs), felted (felt-like, dense intertwined hairs) and lepidote (with flat appressed, scale-like hairs). In practice there tends to be a gradation between the textures and no easy way to define them. Frequently though, the texture is not noticeably interesting, with this character therefore remaining uncoded.



**Fig. 2.4** Various textures from a) glabrous to b) scabrid to c) tomentose. a) *H. denudata*, b) *H. gerrardii*, c) *H. vestita*.

#### 2.3.4.2 Trichome colour

Although trichome colour may be introduced, altered or lost in the preservation process, it is typically preserved. In *H. disermifolia* hair colour has been attributed to “tanniferous substances” that are found in stellate trichomes and phenolic globules that are present in the glandular hairs (Jordaan and Theunissen 1992). De Winter paid careful attention to hair colour, with some 10 “colours” coded: white, silvery white, silvery green, silvery yellow, grey, yellowish, brownish, pale brown, golden brown and yellowish green. In practice the state-set is probably best reduced, with many colours obvious in the extreme, but too frequently not differentiable. Trichomes are typically transparent/clear, with tints of various colours. Thus transparent hairs may appear silvery in the light, or white hairs may appear grey (Fig. 2.4c). Yellow hairs grade into brown, which towards the darker extreme may appear golden-brown (Fig. 2.4b) or amber when infused with red. The apical glands of glandular hairs also may assume a pale to dark amber, red or purple colour.

### 2.3.4.3 Glandular hairs

Glandular hairs vary from minute, simple, sessile, globose hairs, to large, multicellular-stalked hairs with a multicellular apical cell with a rounded or angular shape. The difference between multi-cellular and simple hairs can be cryptic and ambiguous as shown in (Fig. 2.5a vs. b, below). The term ‘septate’ as used by Appidi et al. (2008), referring to the partition between cells in a hair stalk has not been adopted, with multicellular implying septate. This term may be preferable and should be considered for future classification of trichomes. Some species possess only one or more kinds of glandular hairs, whereas most species possess either a mixture of glandular and stellate hairs, or are without glandular hairs. In several species, exemplified by *H. fruticulosa*, the sessile hairs are submerged into the tissue and deliquescing, releasing a resin-like covering. Many species possess sessile glands that resemble tiny dots (Fig. 2.6c) and may easily be mistaken for adhering dirt. Indeed, sand and dirt adhering to glandular hairs is likely to contribute to resisting herbivores (Lev-Yadun 2006) eg. *H. bredaensis*. Oftentimes hairs are sessile to subsessile, with both forms appearing on the same part of the plant. Stalked hairs are usually terete (or pin-shaped when the stalk is thin) (Fig. 2.5b, below), but conical and flattened stalks occur as well. This latter condition consists of, in the case of *H. umbratica* and a few other species, flattened cells that join at right angles to each other – creating a chain-like appearance.

The apical cell of a glandular hair may be transparent or opaque and may be clear to dark purple, amber or red. The cell varies in size from minute (Fig. 2.6c) to large. Although typically globose, when elongated this cell becomes club-shaped (usually if present, sparsely so on the inside of the calyx), often with multiple cells visible. When flattened the head becomes discoid (Fig. 2.5c, below).

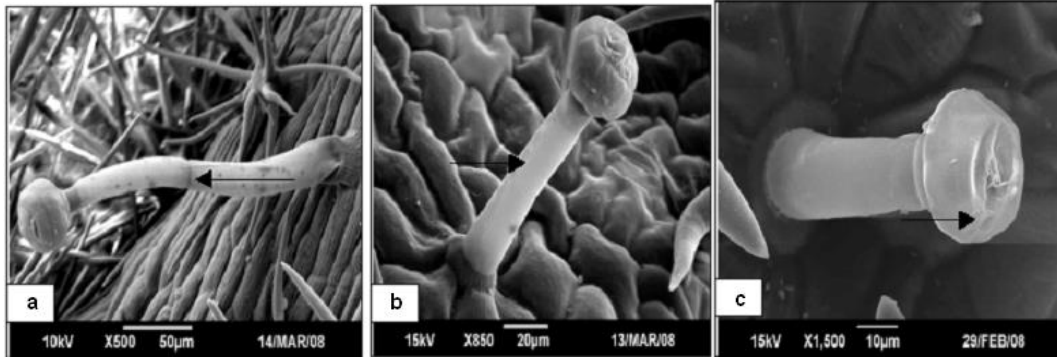
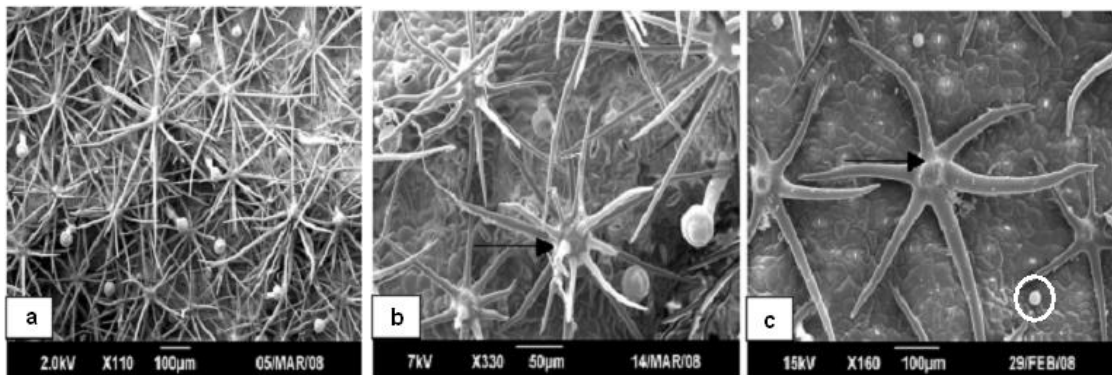


Fig. 2.5 An SEM image of glandular capitate trichomes of *Hermannia* cf. *althaeoides*. Two kinds of glandular hairs are visible, in a) bicellular (septate) long-stalked hair; b) unicellular stalked (non-septate) pin-shaped hair. In c) the discoid head can be seen. All images courtesy of Appidi et al. (2008).

#### 2.3.4.4 Stellate hairs

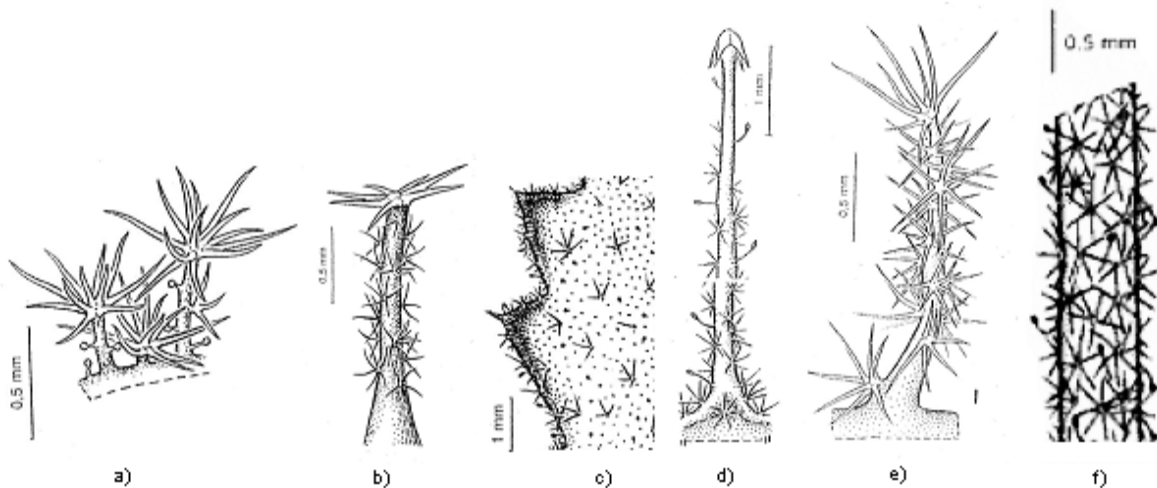
Stellate hairs are very diverse within *Hermannia*, accounting for the vast majority of indumentum detected on plants (Fig. 2.6). The core Malvaceae are characterised in part by the presence of stellate hairs (Bayer, Fay et al. 1999). These trichomes consist of a base with radiating arms/branches. They vary in size from minute (barely visible, even with a microscope) to large (clearly visible with the naked eye). More than one size may occur on a portion of a plant, leading to increased overall density and multiple layers of hairs, the upper frequently obscuring underlying hair types. The hairs are often distinguishable qualitatively by the smaller hairs being sessile and the larger hairs having a bulbous base. The base may be absent in the case of sessile hairs, or bulbous based, or stalked. Bulbous bases comprise a single, bloated, globose cell that may be transparent or opaque, colourless (clear), or red, brown or amber. Stalked bases are elongate, multi-cellular and may have the same colouration as the bulbous bases, although they are more typically opaque. The length of the stalk may vary from sub-sessile to many times the length of the branches (Fig. 2.6a). The stalks are usually without hair except for a cap of radiating branches. The four American species of subsect. *Cristatae* [Ch. 4] are an exception, in the stalk being endowed with either sessile stellate hairs (*H. texana* and *H. pauciflora*) (Fig. 2.6b), or stellate hairs mixed with pin-shaped glandular hairs (*H. palmeri*, *H. inflata*) (Fig. 2.6d). Only one South African species of *Hermannia* possesses this unusual characteristic, *H. comosa*, which is in a different clade from the American taxa, being in the sect. *Hermannia* [Ch. 3].

Stellate hair branches vary from horizontally flattened (adpressed), (Fig. 2.6c) to mostly upright (tufted), to hairs in 3 dimensions from flat to upright (radiating) (Fig. 2.6a; Fig. 2.6b). The branches also vary in thickness from slender to robust (Fig. 2.6c) and in length from short and bristly to long and woolly. Most branches are approximately straight, but long slender branches may be curved or twisted (shaggy). Two of the American species exhibit unusual tomentum states: *H. pauciflora* has terminal hairs that are robust and flat, whilst *H. palmeri* has robust terminal branches on the fruit that are modified into strongly reflexed barbs for epizoochorous dispersal (Fig. 2.7b). Air spaces are frequently visible near the base of robust arms. In the case of *H. cuneifolia*, the arms are conspicuously connate, forming a disc, with only the tips of the arms protruding. These are referred to as silvery scales in the case of *H. pulverata* and *H. bolusii*, on account of the thin, silver nature of the discs. In some species the arms are aligned in a particular direction, either antrorsely towards the apex or retrorsely towards the petiole.



**Fig. 2.6** Stellate hairs on *H. cf. althaeoides*. a&b) long- and slender-branched radiating hairs on the abaxial leaf surface. c) A short- and robust-branched adpressed few-armed hair. This image may also depict a sessile gland (encircled). SEM images modified from Appidi et al. (2008).

Many species possess reduced hairs, either throughout the plant, or only on particular portions such as the margin of the calyx, the tips or margins of the leaves, on petals, or the underside of the stipule. These stellate hairs are usually reduced to either paired hairs, or single hairs. They are nonetheless distinguishable from simple hairs by being connate at the base in the case of paired hairs, or having a bulbous base in the case of single hairs.



**Fig. 2.7 Stellate hair diversity.** a-e) American species (modified from Rojas, unpublished), f) Central African species (modified from Cheek 2007). a), b), d) and e) are unusual stellate hairs found on capsules. c) and f) depict leaf and stem hair respectively. a), c), d) and f) depict combined stellate and glandular hairs, whereas b) and e) are exclusively stellate hairs. a), b), d) and e) have larger terminal hairs, with b) modified into a flattened star and d) modified into a barb. f) Depicts stellate hairs appressed, c) tufted and e) radiating. a) *H. inflata*, b) *H. pauciflora*, c) *H. pauciflora*, d) *H. palmeri*, e) *H. texana*, f) *H. pseudofischeri*.

#### 2.3.4.5 Simple hairs

Simple hairs are defined in this study as solitary single celled hairs that do not have a raised base. They range from short and bristly, to long and woolly. They are seldom present on typical plant parts, or occur in lower density than the surrounding hairs, being most prevalent on the margins of leaves, stipules or calyces. It is sometimes difficult to discern between long woolly hairs and stellate hairs when they become dense and messy. Bristles are the short form of simple hairs. Bristles are interspersed with other trichomes on many organs, but are usually the only kind of trichome on anthers, petals and the style. In the case of anthers, they occur along the length of the anther, but also may clump at the base to form a beard. The number of hairs on the anther, or density of hairs on the beard varies from absent to over a hundred bristles and is thus a potentially useful character for distinguishing cryptic species.

#### 2.3.4.6 Multicellular hairs

Multicellular hairs are seldom encountered and frequently fall under other hair types such as glandular hairs. Multicellular hairs have only been encoded when the multiple cells that make up the hair are obvious.

#### 2.3.5 Stipules

Stipules are usually small and dissimilar from the leaves, usually occurring on both sides of the petiole, or occasionally only one side. They may also be indistinguishable from leaves, forming leafy whorls, or similar to the leaves with minor differences distinguishing them. Although usually having an entire margin, they may be deeply dissected, or divided into separate elements from the base. On woody species the stipules tend to be caducous, falling off readily as the stem ages. They are almost always green, but vary substantially in shape and size, varying from inconspicuous tags, to long, linear stipules. The most common shape is triangular, or ovate-triangular. *H. althaeifolia* has the largest stipules in the genus, reaching nearly 2cm in length and a centimetre in width.

A curious feature is that in some species the stipules increase in size towards the end of the stems. The younger stipules expand rapidly until a maximum size and then start to decrease in size as they wither. The significance of this occurrence is unknown.

The adaxial stipule surface normally has a far sparser, typically subglabrous indumentum. The adaxial surface is frequently markedly different from the abaxial surface, both in density and kinds of trichome present. The glandular hairs or simple hairs often only occur on the adaxial surface.

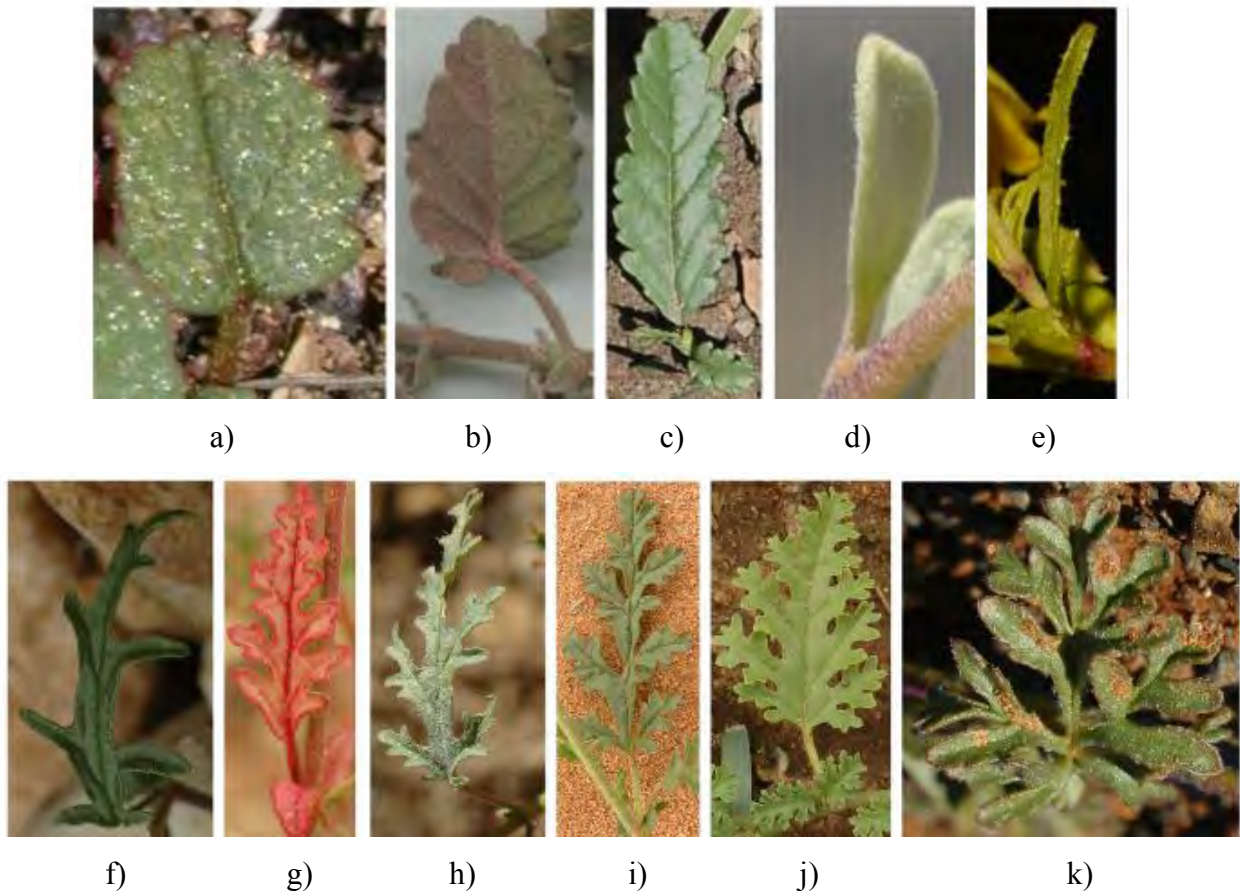
#### 2.3.6 Leaves

##### 2.3.6.1 Petioles

Leaves vary from sessile (Fig. 2.8e) to long-petioled (Fig. 2.8h). The petiole is usually terete, but may be shallowly to strongly grooved, attaining a u-shaped form. The petiole is occasionally flattened, though never becoming winged.

### 2.3.6.2

### Leaf shape



**Fig. 2.8** Leaf shape varies in outline from cordate (a), to orbicular, to elliptical (c), to oblong. Those leaves with a narrower apex vary from broadly ovate (b), to lanceolate (d) to linear (e). All these shapes occur to a greater or lesser degree in outline in dissected leaves as well (g-k). Leaf dissection varies from deeply lobed (f), to bipinnatifid (j), to tripinnatifid. The palmate/pedate leaf shape (k) is known from only one species. a) *H. linnaeoides*, b) *H. nana*, c) *H. sneeubergensis*, d) *H. trifurca*, e) *H. glabripedicellata*, f) *H. dinkyflora*, g) *H. supplicans*, h) *H. haemata*, i) *H. serpens*, j) *H. lacera*, k) *H. pedata*.



Leaves in *Hermannia* vary greatly between species on account of varying combinations of leaf shape, size, margin and indumentum (Fig. 2.8). These tend to vary considerably less within a species, allowing one to readily identify most species by the leaves alone. *H. cylindrifolia* is the only species with a terete leaf, all others having flattened leaves. Most species of subsect. *Mahernia* and sect. *Hermannia* from the winter-rainfall and arid regions have narrow leaves. The leaves of *Hermannia* are rarely filiform (eg. *H. modesta*), being more typically linear, lanceolate or oblanceolate. Broader leaves are fairly common both in the summer- and winter-rainfall areas, across the sections of *Hermannia*, including elliptic, ovate, oblong, cuneate and orbicular forms, with gradations between them. Orbicular and cordate leaves are relatively rare and only found in the summer rainfall regions (eg. *H. malvifolia* and *H. umbratica*).

### 2.3.6.3 Leaf margin

Entire leaf margins are common in sect. *Hermannia* but less so in subg. *Mahernia*. Sculptured margins vary from obscure to tri-pinnatisect. The leaves of *Hermannia* are never pinnate, but rather variously lobed, becoming pinnatisect, bi- to tri-pinnatisect, or pedate (palmate, with divided lateral lobes). The lateral lobes of lobed leaves are thought to initiate in a subsequent phase to the leaf primordium growth, in which the lateral lobes are initiated at parts of the leaf margin termed ‘lateral blastozones’ (Piazza, Jasinski et al. 2005). These lateral blastozones are capable of establishing new axes of growth in the lamina, thus explaining the development of compoundly-lobed leaves in *Hermannia*.

Lowson (1946) distinguishes within a unicostate leaf between *pinnatifid* leaves where the incisions do not extend half-way to the midrib; *pinnatipartite* leaves where the incisions reach considerably more than half-way; and *pinnatisect* where the incisions are almost to the midrib. The term pinnatipartite has not been utilized in descriptions thus far, but should be considered for further descriptions. Leaf sculpturing may be evenly or unevenly spaced and frequently does not occur across the entire margin, but is confined to the apex, the upper third, or to the entire leaf except for the base. The leaf margin is often crenate (with rounded points), serrate (with apically-facing teeth) or dentate (with outward facing teeth). In the case of the *Glabrata* group, the indentations are deep, but not to the midrib, forming lobed leaves. As the leaf indentations increase further, they become pinnatifid and once reaching the midrib are termed pinnatisect. Pinnatisect, bi- and tri-pinnatisect leaves are only found in the subg. *Mahernia*, with the

exception of *H. abrotanoides*, *H. paucifolia*, *H. myrrhifolia* and *H. confusa* that are in sect. *Hermannia*. A palmate shape is neatly produced by the recently discovered *H. pedata* and obscurely by *H. paucifolia*. Pinnate leaf outlines can either be sharply lacerate (eg. *H. myrrhifolia*), or bluntly rounded (eg. *H. orgasmiodorata*). Many species have wavy margins, both in a vertical plane and along the length of the leaf. Margins are sometimes dorsally rolled or folded along the length of the leaf (conduplicate).

#### 2.3.6.4 Leaf indumentum

Leaves show the greatest variation in indumentum (Fig. 2.4) and generally represent the general trichome complement well. All three hair types sometimes occur on leaves, with any combination and variation of these hairs. The abaxial surface tends to have denser indumentum than the adaxial surface. Discolorous leaves are due to an extreme case of differences in indumentum density, the leaves being grey-tomentose abaxially and thus contrasting with the green leaves above (eg. *H. alnifolia*). The margin and the apex may have a different complement of hairs, typically with reduced, single, or paired stellate hairs, eg. *H. confusa* that is one of several species with a long trichome at the apex of each leaf. Leaf indumentum may be even throughout the leaf, or strongly concentrated on the nerves, or between the nerves (the areoles). This can be characteristic for a species, with the concentration of indumentum being independent for the adaxial and abaxial surface.

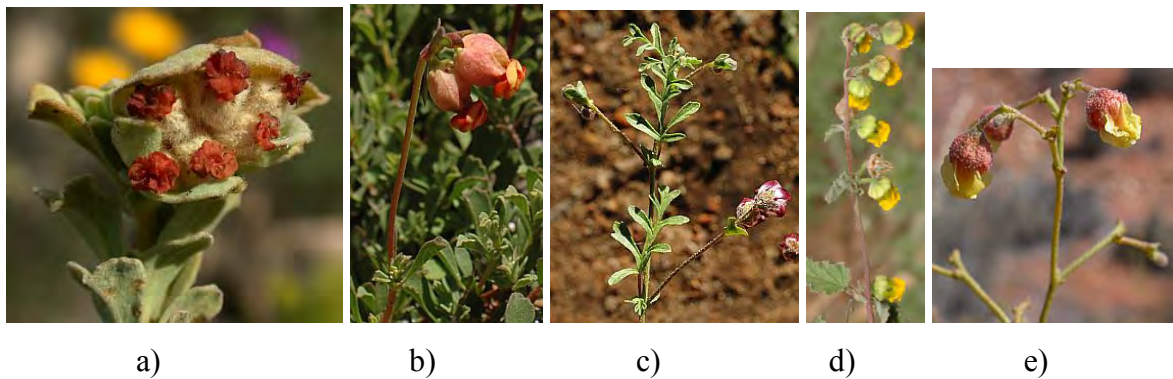
#### 2.3.6.5 Leaf Venation

Leaf venation is *unicostate* (a single main vein), but nonetheless complex due to the variety of leaf forms. The veins can be strongly or weakly raised or depressed which is usually but not always mirrored on the abaxial surface. Linear leaves tend to have the midrib only. Broader leaves generally have secondary and even tertiary veins visible. The number of secondary veins tends to be related to the length of the leaf, from zero to around seven veins. In lobed and pinnatifid leaves, leaf tissue frequently follows veins. In some species, little more than 1 mm of leaf tissue contours the veins, presumably as an adaptation to aridity. Especially abaxially, indumentum may be confined to the veins, or between the veins, with certain trichomes only occurring on the veins on some species. Many Malvales have leaves with palmi-nerved veins, the

basal secondary veins often the thickest, with either two or four secondary veins. In palmate species the leaf tissue tends to follow these veins.

### 2.3.7 Inflorescence

Inflorescences consist of a peduncle and pedicel(s) that are distinguished from each other by the presence of bracts, an abrupt narrowing of the stalk, or a change in indumentum or colour. The pedicel terminates in the calyx of a single flower. A synapomorphy for subsect. *Acicarpus* [Ch. 5] is having a single flower per inflorescence. “*Marehnia*” tends to have complex inflorescences comprising multiple flowers per inflorescence. The subg. *Mahernia* comprises species with single or paired flowers in an inflorescence, with one species, *H. woodii* occasionally having a third flower. Peduncles are substantially longer and flowers sometimes bigger in the case of single flowered compared with paired inflorescences. Section *Hermannia* usually has two flowers per axil, these sometimes forming complex inflorescences eg. *H. hyssopifolia*, *H. macra* (Fig. 2.9).



**Fig. 2.9 Inflorescences:** a) a congested cluster of cymes, b) terminal pair of cymes, c) paired cymes of subg. *Mahernia*, d) a “raceme” of single or paired cymes, e) a compound inflorescence. a) *H. trifoliata*, b) *H. ternifolia*, c) *H. akkersdamensis*, d) *H. alnifolia*, e) *H. paucifolia*.

#### 2.3.7.1 Bracts and bracteoles

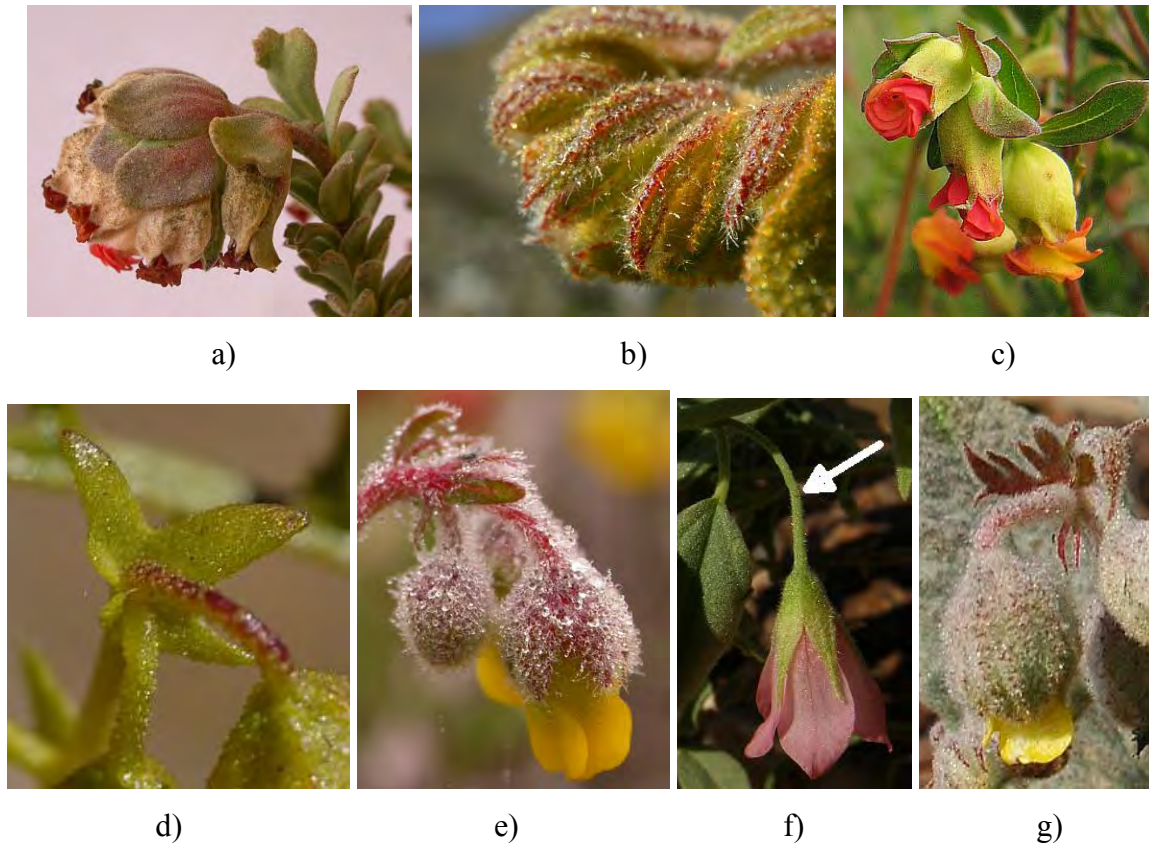
Bracts have been inadequately described due to the complexity of variation, both within species and between species. Lowson (1946) defines *bracts* as ‘specialised leaves borne on the reproductive shoots of plants’. Lowson also refers to bracts as leaf structures in the axil of which

a flower arises. If present on a flower-stalk in the form of reduced leaves, these are called *bracteoles*. Lowson states that ~~there are usually two bracteoles placed laterally in~~ *Dicotyledones* (now eudicots (APG 2009))”. In *Hermannia*, compound inflorescences usually have a number of bracts that are indistinguishable from bracteoles. In single and two flowered inflorescences, bracteoles are positioned just above the junction of the pedicel and the petiole.

Bayer (1999) notes that in the tribe Hermannieae, flower pairs surrounded by four bracts usually prevail. In *Hermannia* this is an oversimplification, as only in subg. *Mahernia* are flowers typically paired and four bracts is by no means typical. Varying usually from one to several, bracts/bracteoles are frequently difficult to count due to being variously connate or lobed. This makes the distinction between a single lobed bract and several connate bracts challenging. Occasionally absent, bracts vary in size from vestigial (Fig. 2.10f), to larger than the leaves (eg. *H. trifoliata*, Fig. 2.10a). Most species, especially of the subg. *Mahernia*, comprise two triangular bracts pointing upwards (Fig. 2.10d). Bracts are variously connate, to lacerate (Fig. 2.10g) and point in various directions, though usually positioned dorsally on the peduncle. Hooded bracts that are concave may protect the floral buds (Fig. 2.10b). In a number of potentially serotinous species, these bracts may serve to protect the seed from fire, eg. *H. salviifolia*, *H. trifoliata*.

### 2.3.7.2 Calyx

The typically green calyx comprises a cap with protruding lobes. The indentation between these lobes is referred to as a sinus (Verdoorn 1980). Calyces vary from much shorter than the petals, to longer than the petals. The calyx can be lobed to near the base, to almost entirely connate with vestigial lobes. All calyces are lobed, with lobes generally triangular, either sharply so at the base, or gradually grading into a point. The lobes can be short with a broad base, to long with an acuminate apex, sometimes verging on lanceolate. In shape the calyx may be open reflexed, to open, to bell-shaped, to globose with a narrow tube. The veins on the calyx usually feed the lobes and may be obscure or obviously raised. The most prominent vein feeds the calyx lobe point, though secondary veins may also occur alongside it. These veins are most obvious abaxially.

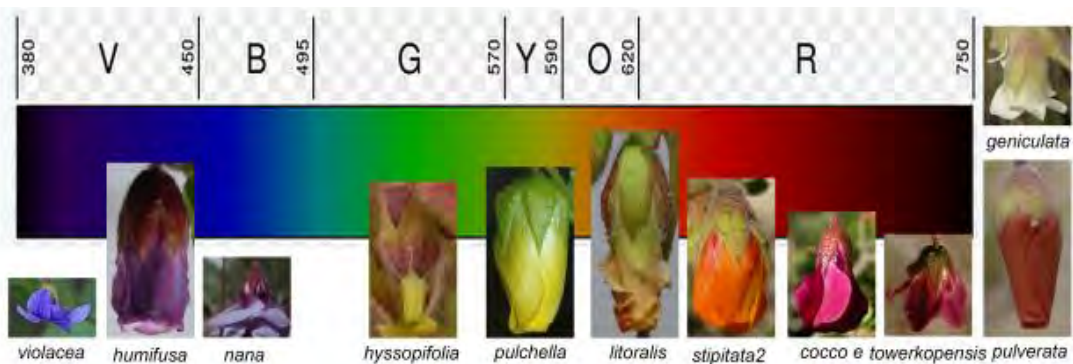


**Fig. 2.10 Bracts:** a) and b) protective leaf-like bracts, c) hooded, d) asymmetrical bracts connate at the base, e) free bracts, f) vestigial bract, g) lacerate bract. a) *H. trifoliata*, b) *H. salviifolia*, c) *H. diversistipula*, d) *H. pulchella*, e) *H. acocksii*, f) *H. affinis*, g) *H. cordata*.

In texture the calyx can be papyraceous to fleshy and glabrous to extremely hairy. The indumentum varies from glabrous to densely tomentose. The margin of the calyx is frequently endowed with a fringe of hairs, typically either of simple hairs, or reduced stellate hairs. The adaxial side of the calyx has a very different indumentum to the abaxial side. It is typically glabrous or subglabrous, either with inconspicuous sessile or subsessile glands, club-shaped glands, or reduced stellate hairs that are frequently apically pointed. In *H. boranensis* the calyx has been found to tear in two unequal pieces at anthesis (Cheek and Dorr 2007).

### 2.3.7.3 Petals

Grotewold (2006) provides a general review of flower colour and pigmentation in angiosperms through which much of the colour variation in *Hermannia* can be explained. Three chemically distinct pigments are responsible for the range of flower colours in plants: Betalains, carotenoids and anthocyanins (Grotewold 2006). As betalains are confined to the Caryophyllales, only the latter two pigments produce the colour variation in *Hermannia*. Carotenoids are universal in plants, providing a protective function and are likely responsible for the yellow to orange flowers of the subg. *Hermannia*. Further evidence for this is found in the flowers of *H. pulverata*, the only brown flowered species, which is in the same subgenus. Brown flowers are said to arise from the combination of carotenoids coexisting with red or purple anthocyanins (Grotewold 2006). Anthocyanins are responsible for the majority of orange, red, purple and blue flower colours (Grotewold 2006). These pigments can explain the colour range displayed by the section *Mahernia* (Fig. 2.11). Several species have white flowers and in the case of *H. octopusssyae* may have “depth” added to the cream flowers through the inclusion of non-coloured flavonoids.



**Fig. 2.11 The range of colours from violet to red. The compound colours, white and brown are displayed on the right.**

Flower colour changes are widespread within the angiosperms and usually occur after pollinator visitation (Weiss 1991). Modification of the anthocyanins may result in increased anthocyanin pigmentation and hue changes (Grotewold 2006). Adding a sugar decoration to the anthocyanidin induces a hypsochromic shift to the blue, a phenomenon that has been noticed in

the *H. coccocarpa* group. Alternatively an increase or decrease in pigments has been found responsible for colour changes (Grotewold 2006).

#### 2.3.7.4 Stamens

The filaments arise from the base of the ovary and are usually free and unattached to adjacent filaments (free filaments are termed polyandrous (Lowson 1946); *pentandrous* being the term for five separate filaments). Some species have joined filaments, the *adelphous* condition, contrasting with very few species in which the filaments are free but loosely joined by interlocking hairs on the anthers, a *syngenesious* condition. In the closely related genus *Waltheria*, the American species and a few African species the filaments are strongly connate at the base to form a tube around the pistil – the *monadelphous* condition. In many species, the filaments are somewhat connate.

The filaments are *dorsifixed* being attach to the anther just above the base to near the middle of the anther. The filaments are frequently *adnate* to the anther, being joined along part of the length of the anther. This is especially true of the sect. *Hermannia*. The anthers are typically *dorsifixed* (immovable), though rarely the anthers may be hinged and moveable on the filament (*versatile*).

Below the anther, the filaments typically possess expanded portions peculiar to *Hermannia* known as arms or wings. Although used interchangeably, I tend to refer to the appendages as *arms* when they are narrow and thick and *wings* when thin and broad. The filaments are usually approximately linear till above the arms, when they may stay approximately the same size till the anther, or narrow gradually, or narrow abruptly and then remain narrow till the anther. The filaments are typically glabrous or subglabrous though occasionally significantly hairy. The hairs are usually tiny stray stellate or simple hairs that have spilled over from the arms.

The arms are infrequently absent (eg. *H. pauciflora*), more typically being gradually winged, to bearing conspicuous arms. These arms are usually distinguishable from the filaments by having a different opacity, thickness or indumentum density. The position of the arms distinguishes between the subg. *Mahernia* and subg. *Hermannia*. In subg. *Hermannia* the arms

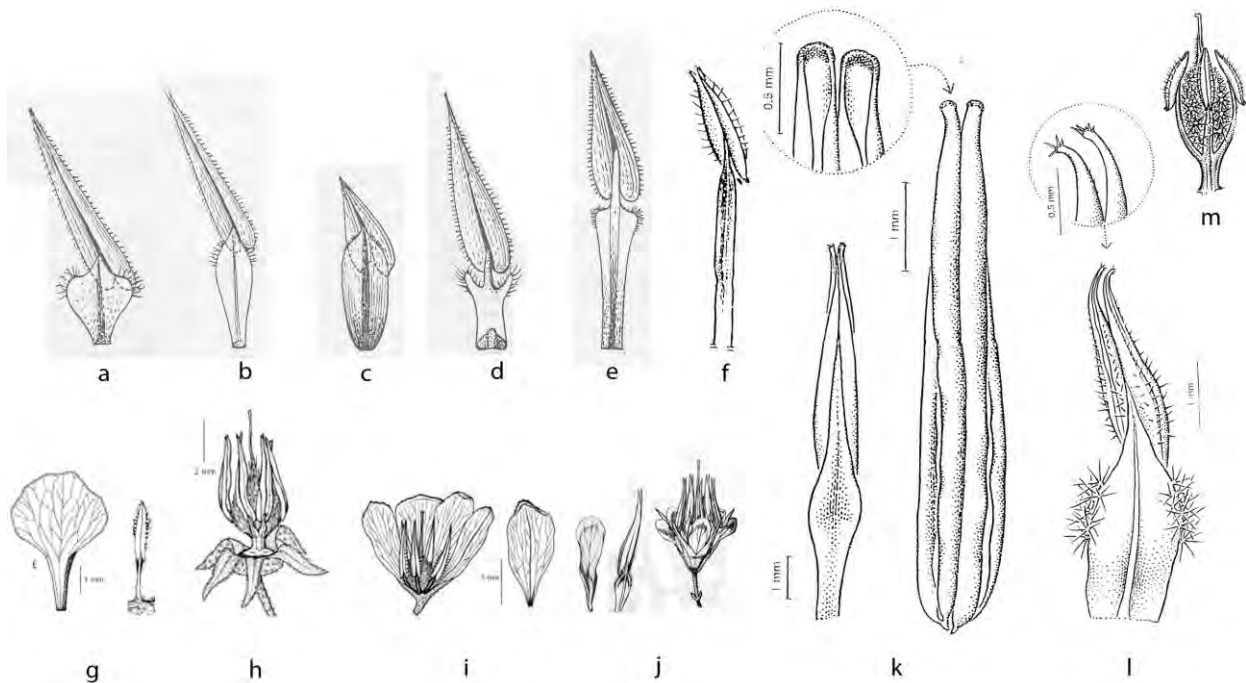
overlap the base of the anther and when obscure consist merely of a gradually expanded and gradually narrowed wing of the same tissue as the filaments. This applies to most species of subg. *Hermannia*, although they can nonetheless have substantially expanded wings. In contrast, the wings in subg. *Mahernia* are more typically abruptly expanded below the arm and almost invariably abruptly narrowed above the arm. If likened to a leaf margin, they are sometimes bluntly dentate (pointing outwards), though more frequently bluntly serrate (pointing upwards) or crenate (rounded). The arms are sometimes bluntly horn shaped (curved upwards like bulls horns), with the apex overlapping the base of the anther. Substantial rounded thickening may occur on the arms, either on the apex, the upper ridge, or the entire arm. This thickening sometimes continues between the arms forming a thick ridge, or thickened along the bottom ridge forming a bib, or substantially thickened below forming a basin.

Trichomes are generally much smaller on internal floral parts than on the vegetative parts of the plant and usually comprise stellate hairs or glandular hairs and rarely reduced stellate hairs or simple hairs. The density varies from glabrous to very densely hairy. The position of the indumentum also varies between species, with the densest indumentum usually encountered on the apex of the arms, or the upper ridge of the arms. In some species this indumentum interlocks with the neighbouring arms to hold the anthers and filaments in position.

#### **2.3.7.5 Anthers**

Although some species of *Hermannia* have poricidal dehiscence (see circular inset in Fig. 2.12k), the majority of species display longitudinal latrorse anther dehiscence, with longitudinal apertures down the length of the anther through which dehiscence occurs (Fig. 2.12). Following the example of Verdoorn (1980), the opening at the stomium (the region of an anther where dehiscence takes place) has been termed pores, though a 'pseudopore', 'slit', or 'aperture' may be a more appropriate term. The flowers are inverted, so that a shower of pollen is released when the flower is disturbed. Anthers are usually lanceolate in shape, although some species have shorter anthers that are rounded and elliptical in shape. The anthers may elongate apically forming long, membranous or submembranous horns (Fig. 2.12l). Basally the anthers may form conspicuous sacs or pouches. These pouches occasionally curl upwards.





**Fig. 2.12** Filaments and anthers of *Hermannia* a - m). a), b), c) and j) show the characteristic filaments of the subg. *Hermannia* that are broadened above the base of the anther. d) and e) are characteristic of the subg. *Mahernia*, with filaments dilated and narrowed beneath the base of the anther. g), h) and i) are representatives of “Marehnia” with approximately linear filaments. j) is from the subsect. *Acicarpus*. f), k), l) and m) are all American species from the subsect. *Cristatae*, with k) and m) depicting anther apices. m) also shows the filaments united into a filament tube/column. a-e) are reproduced from (Wild and Goncalves). g-i) are reproduced from the descriptions of those species (Cheek 2007). f), k) and l) are reproduced with permission from Rojas (unpublished) from descriptions of those species by J. Saunders. a) *H. angolensis*, b) *H. torrei*, c) *H. floribunda*, d) *H. depressa*, e) *H. staurostemon*, f) *H. pauciflora*, g) *H. vollesenii*, h) *H. pseudofischeri*, i) *H. pseudathiensis*, j) *H. boraginiflora*, k) *H. palmeri*, l) *H. inflata*, m) *H. pauciflora*.

In non-glabrescent anthers, the indumentum of the anther typically comprises short to long bristles, although tiny stellate hairs or paired stellate hairs may co-exist. The bristles are generally ranked in one or two longitudinal rows along the adaxial and less often the abaxial length of the anther, alongside the pores. In species descriptions, these rows of hairs have been associated with the upper lip (abaxial side) and lower lip (adaxial side). There is rarely indumentum on the connective tissue between the anthers and occasionally indumentum on the abaxial side of the anthers. Bristles are frequently concentrated on the base of the anther forming a beard. This beard may comprise as few as one or two bristles, but often has a dense cluster of over 30 bristles. These beards may point upwards (antrorsely) or downwards (retrorsely) depending on the direction of the basal sac and rarely form a flattened horizontal “mohawk-like”

beard. A few species (eg. *H. althaeifolia*, *H. amoena*, *H. incana*, *H. talpida*) have been encountered with bristles on the apical tip.

#### 2.3.7.6 Ovary

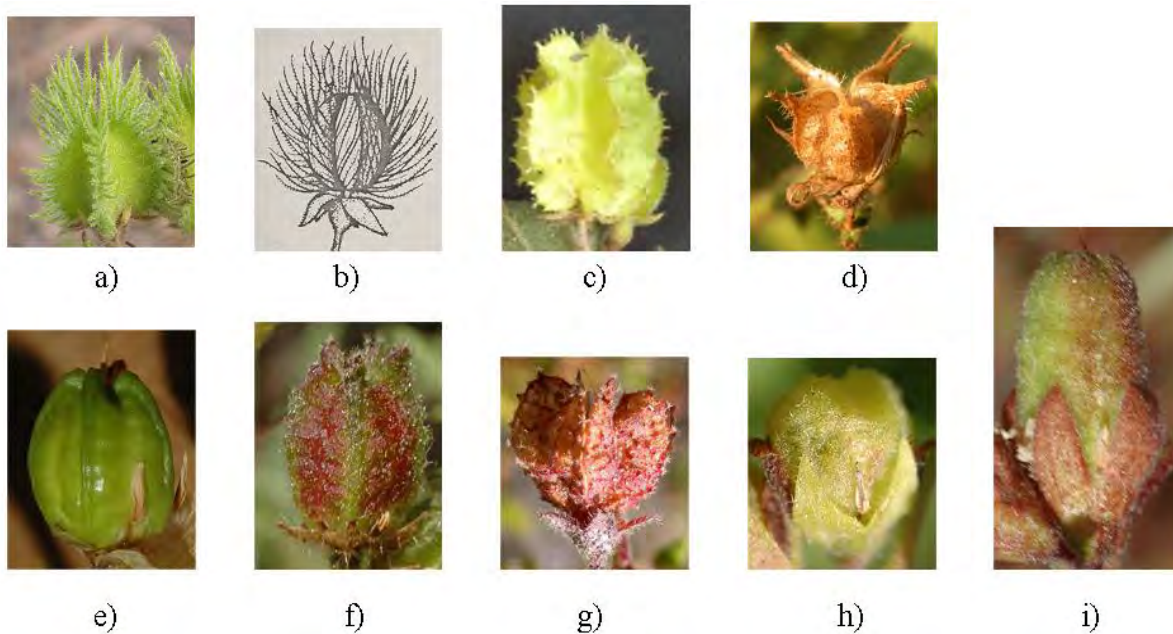
The ovary is globose to elliptical, comprising five locules and with the exception of one or two species with the smallest ovaries (eg. *H. argillicola*), have at least two ovules per locule. A number of features discriminate between species of *Hermannia*. Longitudinal pockets may occur around the base of the ovary where a filament is nestled. This is presumably a further innovation to ensure the filaments are held in position. Glabrescent ovaries are rare, although the pockets are usually more glabrescent than the surrounding ovary. The ovary may be rounded, or have longitudinal concavities running from the base to the apex. Species of subg. *Hermannia* in which the ovary is expanded around the septae forming sharp angles, produce angled capsules. Ovary indumentum may comprise tiny or larger stellate hairs, reduced stellate hairs, simple hairs or glands. The indumentum is typically concentrated on the angles or at the apex. In extreme cases such as in the subsect. *Cristatae*, these hairs form long filamentous processes along the length of the angles.

#### 2.3.7.7 Style

The style usually comprises five united style branches. Occasionally these fray with time and rarely are separated either at the apex, or separate briefly then re-unite towards the apex. No obvious knob or other such feature at the apex of the style is known from *Hermannia*, although this portion may be somewhat more sticky or glossy than the rest of the style. The style often has tiny bristles or stellate hairs that vary from stray hairs close to the ovary, to the entire style being covered till the apex. The degree to which the style is covered by hairs may be used to distinguish between species.

### 2.3.7.8 Capsule

I consider the capsule to be a useful character for differentiating groups within *Hermannia*. Subg. *Mahernia* has rounded capsules (Fig. 2.13g-i), whereas subg. *Hermannia* has somewhat angled or horned capsules (Fig. 2.13e-f). The horns can be single or paired (Fig. 2.13d) at each locule apex. In the American species, as well as *H. merxmulleri* and *H. cristata*, large tubercled hairs form filamentous processes down the length of the capsules angles (Fig. 2.13a-b). Capsule walls can be submembranous to chartaceous to firm to hard. Capsules tend to split from the apex down, generally passively releasing the seed. Some capsules, especially those with submembranous capsules tend to retain the seed till they break down. These fragile capsules are exemplified by the lightweight, windblown, capsules of some species, in which it is the calyx that is massively inflated eg. *H. abrotanoides* and *H. comosa* in sect. *Hermannia*; *H. inflata* in subsect. *Cristatae* and *H. vollesenii* (Cheek 2007) in the “*Mahernia*” group. In the entirely unrelated species, *H. grossularifolia*, it is the ovary itself that inflates. Personal observations show one species, *H. erodioides* to have the entire capsule moved for more than 10m to an ant nest (pers. obs.). However, it could not be ascertained certain whether this facilitates dispersal of the plant, or merely serves as food for the ants. Transport of capsules or seed by ants have not been recorded from any other species. The indumentum of capsules is typically similar to that of the ovaries, though the hairs may be larger and more degraded due to age and less dense due to the expansion of the ovary.

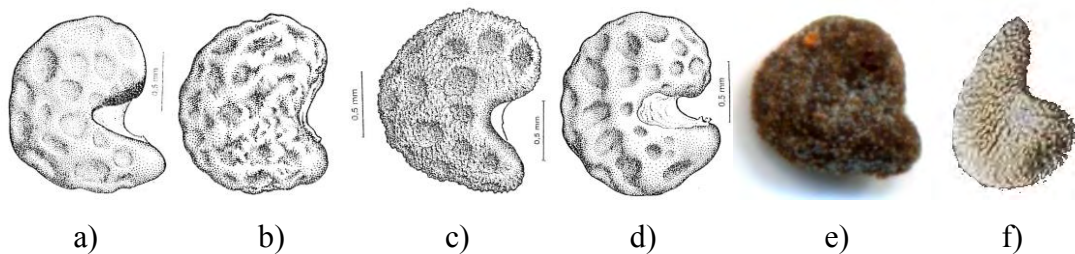


**Fig. 2.13 Capsule characters.** a) to g) angled capsules, h) and i) rounded capsules. Capsules a) to f) from subg. *Hermannia* and g) to i) from subg. *Mahernia*. a) to c) from the subsect. *Cristatae*, d) from subsect. *Acicarpus*, e) to f) from the sect. *Hermannia*, g) from the sect. *Pinnatifidae*, h) from the sect. *Tomentosae* and i) from the subsect. *Mahernia*. Angles of a) and b) with filamentous processes, c) with winged capsules and tubercles, d) with short horns, e) and f) with longitudinal ridges, g) sub-inflated, h) rounded. a) *H. cristata*, b) *H. merxmuelleri*, c) *H. pauciflora*, d) *H. glanduligera*, e) *H. denudata*, f) *H. echinocapsulare*, g) *H. sisymbriifolia*, h) *H. crassifolia*, i) *H. litoralis*.

### 2.3.7.9 Seed

A feature distinguishing *Hermannia* from other genera within the Byttnerioideae is the presence of many seeds per locule. *H. argillicola* is one species that defies this rule, with a single seed per locule and there may be other species if small-capsuled species are examined. Seeds are described as reniform, sub-reniform, comma-shaped (Fig. 2.14f), kidney-shaped (Fig. 2.14b) or C-shaped (Fig. 2.14d). There is sometimes a small white point of attachment which has not been known to attract ants (i.e. an elaiosome). The wall of the seed may be smooth, rough, granulate eg. *H. micropetala* (Wild 1961); minutely tuberculate eg. *H. modesta* (Wild 1961) or be sculptured with fine wrinkles (Fig. 2.14f), “radiating wrinkles” eg. *H. tomentosa* (Wild 1961), rugose eg. *H. glanduligera* (Cheek and Dorr 2007), transversely banded eg. *H. modesta* (Cheek and Dorr 2007) or “transversely furrowed” (Oliver 1868). As the seed desiccates these wrinkles

may become more obvious. Only the American species and species from “Marehnia” have conspicuous pits or dents across the wall (Fig. 2.14a-d). In the case of “Marehnia”, these pits have been described as foveolate (*H. pseudofischeri*, *H. athiensis*, *H. macrobotrys*, *H. paniculata*, *H. uhligii*) or deeply foveolate (*H. vollesenii*) (Cheek 2007) and represents a potential link between the American and tropical African species. Many species of “Marehnia” additionally have papillae that vary from scattered (*H. boranensis*) to dense (*H. glanduligera*) and vary from white (*H. glanduligera*) to glossy and black (*H. modesta*) (Cheek and Dorr 2007). Seeds vary in colour and include dull red in *H. pseudofischeri* (Cheek 2007), light brown to dark brown (Fig. 2.14e) to black in *H. grandiflora* (Verdoorn 1984). Darkness of seed has been found to relate to the tannin content. The tannins often remain white until the last stage of development (Dickie and Stuppy 2003), a phenomenon witnessed in many *Hermannia* species (pers. obs.). Phenolics like tannin cause the cross-linking of polysaccharides, which leads to increased wall-strength and resistance to micro-organisms (Dickie and Stuppy 2003). The tannin content also affects the ability of the seed to withstand the digestive system, a requirement for dispersal by endozoochory (Milton and Dean 2001). Sue Milton has demonstrated the ability of *Hermannia* seed to disperse by animals in Renosterveld (Milton and Dean 2001). Seeds are thought to be viable for periods in excess of 20 years, judging by the ability of *Hermannia* to grow from seed subsequent to fire (pers. comm. Jan Vlok).



**Fig. 2.14** Seeds of *Hermannia*. a-d) modified from drawings by F. Rojas (unpublished), showing pitting characteristic of American species. e) and f) showing the granular surface and wrinkles respectively that occur on African species. a), c) and d) are roughly C-shaped. b) & e) are sub-reniform. f) is comma-shaped. a) *H. texana*, b) *H. inflata*, c) *H. palmeri*, d) *H. pauciflora*, e) *H. angelica*, f) *H. erodioides*

### 2.3.7.10 Pollen

A thorough pollen study was accomplished by Coetzee (1979), incorporating light microscopy and scanning electron microscopy (SEM). A number of measurements were obtained for the pollen. Pollen of the Hermannieae is usually spheroidal to prolate. Spinulose grains are absent from *Hermannia*, being restricted within the Hermannieae to heterostylous species of *Waltheria* and *Melochia* (Bayer, Fay et al. 1999). The only qualitative measurement of interest is that the number of apertures can be three (Fig. 2.15, below) or four. This difference lies within the Section *Hermannia*, in which 33 of the 114 *Hermannia* species examined had four apertures instead of the more common three apertures. These species correspond loosely to a Karoo clade (Chapter 3). *Hermannia* pollen (closest to *H. stricta*) was found off the coast of Angola, with decreasing abundance from 30ka to the present (Dupont, Behling et al. 2008).

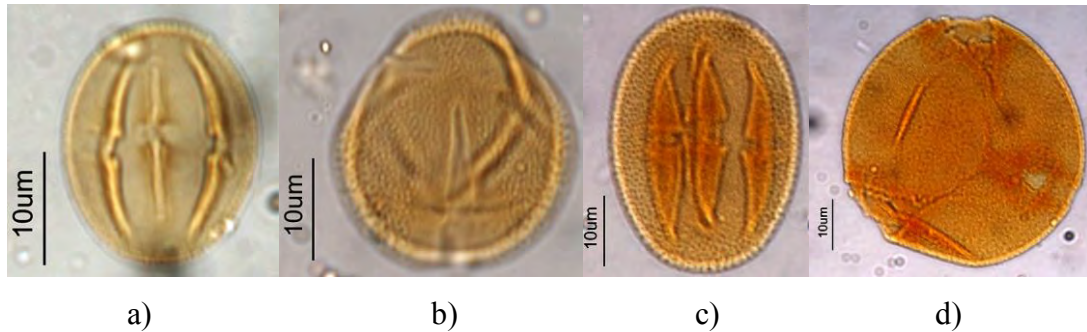


Fig. 2.15 Pollen grains from the Alan Graham Collection visualized using a light microscope. a) *H. betonicifolia* (now *H. gerrardii*) equatorial view and b) polar view; c) *H. inflata* equatorial view and d) polar view. Images with permission Jan Saunders *vide* F. Carvajal (unpublished).

### 2.3.8 Positioning of anatomical elements

I have observed that a number of anatomical elements hold each other in place, or serve to hold other organs in position. The calyx in many species, particularly those with a campanulate calyx, serves to both protect the petals and to hold them in position. In *H. gracilis*, the blade of the petals has a pocket in which the adjacent petal neatly fits. This maintains both rigidity and the tightly imbricate formation. Many species possess tightly folded flaps at the base of the petals, known as the claw. These flaps typically hold the filaments in place, or in some cases the anthers themselves. They may also serve as channels in which the nectar is presented to a foraging proboscis, likely being drawn apically by capillary action. The addition of hairs on the flaps or the sinus serves to provide additional interlocking connectivity with anthers or filaments that are

endowed with hairs. The indumentum on the shoulders of the filaments, particularly of the subg. *Mahernia* also interlock with adjacent filaments.

## 2.4 Concluding comments

This chapter provides a first attempt at summarising the substantial morphological variation within *Hermannia*. Future morphological studies of the genus would greatly benefit from a more comprehensive and improved visual documentation of the genus. With the exception of the pollen study by Coetzee (1979), images of pollen by Jan Saunders and SEM work on a single species by Appidi et al. (2008), all other knowledge of the morphology of the genus is based on dissecting microscopy and macroscopic features. There is potentially much to be gained by using other imaging techniques such as compound and electron microscopy across a broader range of plant organs within the genus. Particular character states are frequently confined to specific groups at varying taxonomic levels. Much of this potentially phylogenetically important information is currently unavailable due to inadequate understanding or poor definitions of features and poor sampling. The majority of the knowledge of the microscopic variation also comes from my dissection of subg. *Mahernia*. As Verdoorn (1980) did not produce a character matrix or a synthesis of character variation, subg. *Hermannia* may still be considered largely neglected from a morphological perspective.

Therefore I propose that future work focus on:

- a) An SEM study encompassing the variation of indumentum types encountered in *Hermannia*.
- b) A graphical chart or handbook that depicts and standardises the various morphological terms. This should include SEM images of indumentum.
- c) An electronic key, that incorporates these standardised terms.

### 3. Phylogeny reconstruction

#### 3.1 Introduction

As with any group, a phylogenetic framework is crucial to the study of *Hermannia*, as it forms the basis for our understanding of the evolution of the genus. A phylogeny can allow contemporary morphological, ecological and distributional patterns to be placed in an evolutionary context. Although *Hermannia* displays a broad range of morphological variation, filament morphology has generally been considered sufficient to separate *Hermannia* into two roughly equal groups i.e. subg. *Hermannia* and subg. *Mahernia*. These groups were initially recognised as separate genera (Bentham and Hooker 1862), then as sections (Schumann 1895) and finally taxonomically stabilized at subgeneric level (Engler and Schumann 1900; Verdoorn 1980). Inflorescence type and capsule morphology distinguish sections within subg. *Hermannia*, but beyond these characters there are no robust morphological characters which can be used to further divide the subgenera. In this study two kinds of datasets have been obtained from which relationships may be inferred: a DNA dataset based on the only region that could be sequenced successfully for a large proportion of the species – the nuclear ITS region and a morphological dataset obtained through the observation and measurement of specimens. This morphological dataset is supplemented by a dataset derived from a pollen analysis of the Malvaceae by Coetzee and van der Schijff (1979). A number of analyses are used to obtain a hypothesis of relationships.

##### 3.1.1 The broader picture: subfamilial relationships

The most complete analysis of the Malvaceae (sensu lato) has led to the proposition of 9 subfamilies (Bayer and Kubitzki 2003). Tate *et al.* (2005) examined one subfamily, Malveae and found subgeneric alliances to be untenable. Instead molecular analysis supported only two clades, of which three of the outgroups utilized in this study, *Tarasa*, *Fuertisimalva* and *Anisodonteia* were embedded within “clade A” of core Malvaceae, Malveae. The position of *Hermannia* within the Malvaceae has also been questioned and it seems likely that a similar appraisal of generic alliances will not be particularly meaningful without a concerted effort to incorporate a number of small genera confined to regions such as Australia.



### 3.1.2 Previous groups within *Hermannia*

No previous attempts have been made to produce an explicit phylogenetic hypothesis for *Hermannia*, using either molecular or morphological data. Relationships have nonetheless been postulated based on a combination of morphology and distribution. For instance, both Engler (1919) and Verdoorn (1980) proposed that the species from America are closely related to *H. cristata* from South Africa based on their crested capsules (Engler 1921). The revision of subg. *Hermannia* by Verdoorn (1980) was purely morphologically based, with little relationship information provided due to an emphasis on identification. Although not explicitly stated, it is clear from her taxonomic key that she deemed the cristate-horned species separate from the simple-horned species (Engler's subgenus *Acicarpus*) and that a third group existed corresponding to Engler's subgenus *Hermannia*. What follows is the previous attempts to place species into groups based on morphological similarity, first at sub-generic level and later at unranked levels below this.

Schumann in Engler (1900) divided the 73 species then known into four subgenera: *Marehnia*, *Acicarpus*, *Hermannia* and *Mahernia*. A fifth subgenus, *Scaphiostemon* was erected by Engler (Engler 1919), but the only representative species, *H. tenuipes* has been sunk by Verdoorn (1980) into *H. amabilis* as part of subg. *Acicarpus*. This was followed by subsequent workers such as Salter (1946).

The subgenera *Hermannia*, *Mahernia* and *Acicarpus* were all subdivided into a number of groups by Harvey (1860) and later by Engler (1919) who added several new groups. Harvey (1860) placed species into 13 "groups" below subgeneric level and Engler (1919) placed species into 12 "Reihe" at the same rank that Harvey placed them. That Engler's Reihe (designated in his treatment with the section symbol §) cannot be considered to be sections, is that they were embedded within five sections, eg. sect. *Hermannia* contained §*Althoideae* Harv. They are thus approximately equivalent to 'sub-section' or 'series' (Fig. 3.1). Despite describing the groups and using them formally by designating authors, neither of these groups have rank specified, nor are they nomenclaturally valid. The subg. *Mahernia* is without a recent treatment that groups

species, although De Winter placed species into a number of tentative groups which he neither named nor published. He placed great importance upon indumentum, which his groups largely reflect. A DNA-based assessment of the homology of indumentum and its utility in grouping species is highly desirable and possibly within reach in the near future, this is beyond the scope of this thesis.

### 3.1.2.1 The subsect. *Cristatae*

The subsect. *Cristatae* is enigmatic in that it comprises three groups that differ considerably in characteristics, but that nonetheless have potentially homologous characters in common with both sect. *Hermannia* and subsect. *Acicarpus*. For instance Engler's group *Cristatae* contains *H. cristata*, a short resprouter from the summer rainfall region of South Africa, bearing red flowers that mature into a capsule endowed along the septa with filamentous processes. These filamentous processes make it a strong candidate as the closest extant relative to *H. merxmuelleri* - the tallest perennial species known, with unique flowers that are ash-coloured "–*einerea*" on the outside and purple on the inside. Verdoorn (1980) proposed that the cristate hairs found on the capsules of two Southern African and three of the four American species may unite them across the continents. These species may thus form a clade within the subsect. *Cristatae*, as, with the exception of *H. inflata*, all American species have strongly angled capsules bearing filamentous projections along the septa. *Hermannia texana* bears a floral resemblance to *H. cristata* in having red flowers and leaves that are more similar in shape and indumentum to *H. merxmuelleri* than the remaining members of the American clade. *H. palmeri* and *H. pauciflora* appear morphologically to be closest related, although the yellow petals of *H. palmeri* are frequently reflexed: a condition that is shared in common with *H. quartiniana* and *H. violacea* of the subg. *Mahernia* and *H. paniculata* and *H. stuhlmannii* of "–*Marehnia*". *H. inflata* is unusual in a number of ways: it is the only member of the American species with terminal flowers, these flowers are enclosed in a large chartaceous calyx, the septa is not fringed with filamentous processes and the petals have an apical row of conspicuous enlarged cells that J. Saunders has termed *pustules*. This latter feature is unique to *H. inflata*. Purple flowers are absent from subg. *Hermannia*, with the exception of *H. merxmuelleri*, *H. inflata* and *H. stuhlmannii*. Unless this is a modern adaptation to pollination, this may suggest *H. inflata* shares a closer link to *H. merxmuelleri* and

*H. stuhlmannii* than to other American species of subsect. *Cristatae*, as no other species of subg. *Hermannia* has purple flowers.

### 3.1.2.2 “Marehnia”

The final element of the subsect. *Cristatae* is the potentially coherent group “Marehnia” from tropical Africa, recognised by Schumann (1900) as a subgenus and by {Engler, 1900 #1530} as a section. The majority of the 14 species that make up the group appear to have yellow flowers in terminal inflorescences that bear a number of flowers. The leaves resemble the generalized form of species within sect. *Hermannia* being substantial in both length and width. The capsules are atypical for the subsect. *Cristatae*, being without fringed processes and at most having short apical points. They are typically round to ovoid, either with or without angled walls or conspicuous septal ridges (eg. *H. exappendiculata*), thereby bearing a similarity more to the sect. *Hermannia* or the sect. *Mahernia* than subsect. *Acicarpus*. Around six species of “Marehnia” have seeds with a conspicuously *foveolate* or pitted condition of the seed testa. *Hermannia inflata* is the only American species which does not have obvious pits in the seed coat. Thus the one American species that like species of “Marehnia” does not have fringed capsules and thus poses the most likely link between the continents, is the same species that also does not have an obviously foveolate testa.

### 3.1.3 Linking the American, tropical and southern African species.

The American species may either have their origins from a prior pan-Gondwanan distribution, or the result of long-distance dispersal from Africa. Their distributions have been considered “very old and long established in its present range” and thus evidence of Gondwanan vicariance (Livingston 1921). Considering the option of long-distance dispersal, the disjunct African group “Marehnia” may be an important link in their dispersal from Africa. The affinities of this East African group are unclear, though numerous other Cape genera that have relatives in East Africa have been shown to have been linked between north and south via a Miocene arid track (Balinsky 1962; Coleman, Liston et al. 2003).

In summation, there are a number of morphological links that may explain the origins of the American species, but further characters are required to understand the links between Africa and America. Molecular data present independent characters that could resolve the relationships between these species and are able to provide a hypothesis of when the separation of these species took place, relative to the break-up of Gondwanaland. A number of key issues remain unresolved in *Hermannia*. These include the validity of the two subgenera, as well as additional subgroupings that have been proposed, based upon morphology, by De Candolle, Engler and Schumann. The other particularly enigmatic species are two species from the Drakensberg that have no obvious relatives. The grouping and relationships within *Hermannia*, as well as the timing of diversification within the genus is thus considered a priority and is explored in this chapter.

#### **3.1.4 Molecular approaches**

Due to a number of inherent problems with inferring relationships from morphology, phylogenies derived solely from morphological data should be treated with caution (Blackwelder 1967; Tomlinson 1984). Molecular characters regularly provide character-rich information that is unaffected by local environmental conditions and may be used to test species groups based on morphological characters. For example, Shaw and Allen (2000) sequenced 18 species of the bryophyte family Fontinalaceae and found that groups of species based on leaf characters were polyphyletic and that the leaf characters were labile within the genus *Fontinalis*. Scotland et al. (2003) argue that a small selection of critically chosen morphological characters can effectively be integrated with molecular data. In recent years sequencing has become the primary source of molecular phylogenetic hypotheses (Alvarez and Wendel 2003), as it provides a large number of characters with states that are largely unambiguous and regions independent of morphology allowing a test of morphological relationships (Hillis 1987). Sequencing may be used to contrast with, or confirm, existing morphologically based hypotheses of relationships. In the past, molecular phylogenies have been aimed at resolving higher level phylogenies such as relationships between families (eg. Quinn, Price et al. 2002; Zhang and Renner 2003; Palmer, Soltis et al. 2004; Goldblatt and Manning 2006). In recent years due to sequencing becoming quicker, cheaper and with more rapidly evolving gene regions having been found (reviewed for chloroplast DNA in Shaw, Lickey et al. 2005; Shaw, Lickey et al. 2007), focus has shifted to

resolving terminal taxa, i.e. species. Many genera and families from South Africa have already had a significant proportion of their species assessed (eg. Bakker, Culham et al. 2000; Meerow and Snijman 2001; Manning 2004; Goldblatt and Manning 2006; Hopper, Smith et al. 2009; Sauquet, Weston et al. 2009; Verboom, Archibald et al. 2009; Moore, Verboom et al. 2010).

#### **3.1.4.1 Gene trees, species trees and systematics: a cladistic perspective**

The most reliable indicator of phylogenetic accuracy is considered to be congruence between datasets (eg. Willows-Munro, Robinson et al. 2005), particularly between plastid and nuclear datasets, multiple loci and molecular and morphological data. Conflicts between trees can arise through a number of causes (Brower, DeSalle et al. 1996), an interesting case being that of reticulate evolution, examined in Vriesendorp & Bakker (2005). Martis et al. (2013) analysed 72% of the genes in rye (*Secale cereale*) and concluded that reticulate evolution or introgressive hybridisation played a role in both the evolution and speciation of rye. The use of both plastid and nuclear genes in constructing a phylogeny is highly desirable due to the dissimilar means of inheritance (Rieseberg and Soltis 1991; Nylander, Ronquist et al. 2004). The uniparental inheritance of chloroplast genes means that they usually reflect the maternal lineage of an individual through seed dispersal, whereas the biparentally inherited nuclear genes reflect a combination of parents through the dispersal of pollen and ovules. Using two independent sources of data that result in consilient trees boosts confidence in the tree, whereas conflicts may suggest hybridization (Whitehouse 2002), incomplete lineage sorting (Jakob and Blattner 2006), allelic-level variation among individuals, or other population-level processes.

#### **3.1.5 The advantages and disadvantages of the ITS gene region.**

Characteristics of plastid DNA and their potential limitations include its maternal inheritance and a far slower rate of evolution than nuclear DNA (Soltis and Soltis 2001). This slower rate has been cited as the rationale for studies that have utilized solely nuclear regions (eg. Barker, Vanderpoorten et al. 2004). Thus a combination of multiple gene regions is usually required in order to obtain sufficient resolution at species level (Cronn, Small et al. 2002). However

chloroplasts are higher in concentration than their nuclear counterparts and the DNA contained within the organelle tends to be better protected than nuclear DNA (Whitehouse 2002). These characteristics facilitate amplification, important when obtaining DNA from herbarium specimens. A favoured nuclear region is ITS that by 2003 had been incorporated into 66% of published papers which included plant sequence data, of which 34% of papers were exclusively ITS (Alvarez and Wendel 2003). Its popularity has been attributed to a number of favourable characteristics such as biparental inheritance; universality in amplifying across a broad spectrum of plant and fungal taxa; easier amplification than low-copy nuclear regions due to the potential for thousands of repeats; intragenomic uniformity due to concerted evolution; a rate of evolution of the gene region that frequently makes it appropriate at a specific, generic and frequently familial level; and apparent low functional constraint of the region implying that sequences evolve frequently and neutrally (Alvarez and Wendel 2003). Phylogenies can be misleading for well-understood reasons, with ITS, a region used in this study being particularly problematic. Misleading phylogenies may arise due to incomplete lineage sorting, gene duplication, the presence of pseudogenes and hybridization (Alvarez and Wendel 2003; Bailey, Carr et al. 2003). Divergent ITS sequences complicate phylogenetic inference due to uncertainty with orthology/paralogy. For instance, independently evolving paralogous genes that are treated as homologous, lead to an incorrect inference of relationship (Mayol and Rossello 2001). These multiple sequence types may arise from genomic incorporation of pseudogenes, array duplication events, or intra- or inter-array homogenisation (Alvarez and Wendel 2003). The widespread use of ITS is testament to the remarkable homogeneity of copies of paralogous genes, which has been attributed to concerted evolution of the entire repeat (Hillis and Dixon 1991). In summary, a combination of cpDNA and nrDNA is generally required in order to confirm phylogenetic relationships within plants, to provide robust support and to provide resolution at the level of species.

### **3.1.6 Why use molecular dating?**

*Hermannia* is a genus of many species, particularly in the Cape and it is pertinent to ask how this species diversity arose. A well-sampled phylogeny may be used to understand the timing of speciation events, particularly when combined with knowledge of the geographic distribution of clades and the events that took place during periods of rapid speciation. In recent years dating

techniques have been applied to: uncover the driving forces and events that have led to radiations; date the age of dispersal between continents; search for common patterns of radiations between genera and families (Sauquet, Weston et al. 2009); and to date the radiation of orders within the angiosperms (Wikström, Savolainen et al. 2001). Within South Africa, a special issue of *Molecular Phylogenetics and Evolution* in 2009 focused on using dating to understand the impressive diversity of the CFR and surrounding regions. Dating is also used to reconstruct ancestral distributions and directionality of migrations, with Valente et al. (2010) having produced log-lineage-through-time plots that were used to visualize the temporal dynamics of diversification of proteas.

### **3.1.7 Dating – tying up key divergence events with associated factors**

The timing of species divergences and the linking of these dates to causal factors such as climatic events is important to understanding the historical development of a group. For instance: what environmental characteristics were conducive to the speciation of *Hermannia*? When was speciation most prolific? What key events may have led to the explosion of around 200 species within Southern Africa? How and when did *Hermannia* reach East Africa, America and Australia? These latter intercontinental distributions may be explained by vicariance due to the splitting up of Gondwanaland, through long-distance dispersal, or through an iterative dispersal across one of a number of land-bridges. Timing of separation of species across the continents is key to establishing which of these events is most likely.

### **3.1.8 Timing of radiations and dispersal events**

Molecular methods have been used to estimate the age and rate of diversification of organisms (Richardson, Weitz et al. 2001; Ricklefs 2007; Verboom, Archibald et al. 2009; Moore, Verboom et al. 2010). Both the techniques and the calibration dates utilized in molecular dating been heavily debated and criticized (Graur and Martin 2004; Heads 2005), with the effect of undersampling having been examined by Linder et al. (2005). The relatively recent use of relaxed molecular clocks has allowed for dating across multiple gene-regions and can incorporate multiple simultaneous fossil calibrations (Renner 2005). Frequently paleoclimatic or

fossil data is used to provide a “youngest” date for a group. However, there is no pollen or fossil evidence to provide an internal node for *Hermannia*. This necessitates looking for secondary dates.

### **3.1.9 Calibrating the phylogenetic tree**

To calibrate the phylogeny for dating, it is useful to constrain the tree with maximum and/or minimum divergence age estimates based on independent evidence. Multiple fossils have been found to place minimum dates on major clades within the angiosperms (Wikström, Savolainen et al. 2001). Numerous issues have been identified with estimates derived from molecular dating. These include errors associated with small datasets and stochastic errors (Hillis 1996 in Wikström, Savolainen et al. 2001) and difficulties with correctly inferring rate change across the tree (Sanderson 1997). Previous assumptions of roughly constant rate change across the tree were addressed by nonparametric rate smoothing (NPRS) that assumes autocorrelation of rate changes, i.e. the rate of change is inherited from ancestral lineages by their immediate descendants (Wikström, Savolainen et al. 2001). NPRS has largely been surpassed by the introduction of relaxed clock techniques that additionally take into account rate heterogeneity across the tree. Sauquet (2009) compared three relaxed clock methods, including the uncorrelated lognormal method UCLN method as implemented in BEAST and found similar age estimates for most nodes.

#### **3.1.9.1 Calibration Dates – the suitability of using the split up of Gondwanaland**

Having species in America and Africa allows for the possibility of using the break-up of Gondwanaland to provide a maximum date of around 120-80 Mya (Upchurch 2008), but only if a divergence predating this event can be found. Four models of Gondwanan breakup are reviewed by Upchurch (2008), with many recent papers suggesting that trans-oceanic dispersal plays an important role in the history of many organisms (Baum, Smith et al. 2004; Renner 2004). Utilizing Gondwanaland as a date becomes increasingly complex, as there is still a real, but decreasing chance of dispersal across the ocean, as the continents move further apart. This rules out the possibility of utilizing Gondwanan separation as a date for distinguishing the American *Hermannia* species from the African species, especially as molecular dating shows the



order Malvales to be post-Gondwanan, having originated 80-95 Mya (Sanderson and Magallon 2001) with a later refinement to 80-84 Mya (Wikström, Savolainen et al. 2001; Forest, Grenyer et al. 2007).

### **3.1.9.2 Dates nodes at higher taxonomic levels – orders and families**

The literature includes several estimates that provide divergence dates at higher taxonomic levels that provide possible root ages for calibration purposes. The rosid clade, including the Malvales, Sapindales and Brassicales amongst others has its earliest fossils dating to at least the Santonian to Turonian ( $\pm 84$  Mya –  $\pm 89.5$  Mya) (Dilcher and Crepet 1984; Magallon, Crane et al. 1999). The sister order to the Malvales has vacillated between the Sapindales and Brassicales. Earlier estimates of the angiosperm tree placed the Sapindales sister to the Malvales, with the Brassicales sister to this group (Wikström, Savolainen et al. 2001; Davies, Barraclough et al. 2004; Soltis and Soltis 2004). Under a supertree approach to reconstructing the angiosperm tree (Davies, Barraclough et al. 2004), Sapindales was also found to be sister to Malvales, with Brassicales as the next closest order. Estimates under nonparametric rate smoothing of *rbcL* sequence data place the split between Sapindales and Malvaceae, at  $\pm 88.4$  Mya, with the date for the Malvaceae/Brassicaceae split at  $\pm 92.6$  Mya (Davies, Barraclough et al. 2004).

### **3.1.9.3 A fossil date for the Bombacaceae**

A fossil date utilized in the calibration of the angiosperms is a minimum age of 69 Mya for the Bombacaceae (Wikström, Savolainen et al. 2001). Two species of *Adansonia* were thus included in the phylogeny, one from Madagascar and *Adansonia digitata*, one of two African species. These species are dated to 37.06 Mya, which is within the age specified by the fossils and provides a minimum age for the breakup of Madagascar from Africa, or a dispersal event between Madagascar and Africa.

Secondary dates for the age of the split of Malvales from Brassicales/Sapindales have been found in several papers. The Malvales appear to originate 80-84 Mya (Wikström, Savolainen et al. 2001; Forest, Grenyer et al. 2007). However, the terminal dates given in Wikström (2001) have

been found to be typically more recent than fossils indicate (Wikström, Savolainen et al. 2001; Linder and Hardy 2004). Davies et al. (2004) utilized a supertree approach, combining maximum likelihood reconstruction with NPRS to attain a date of around 90 Mya for the Malvales/Sapindales split, with the Malvales/Brassicales divergence around 3 million years earlier. Magallon and Castillo (2009) found a stem age of 91.85 for the Malvales-Brassicales. Given the varying dates, it was decided to utilize a stem-age of 82 Mya, as several older papers and a well-sampled analysis focusing on Cape taxa (Forest et al., 2007a) retrieve a date of around 82 Mya.

#### **3.1.9.4 Dating using the Cape coastal limestones**

The Cape coastal limestones have been utilized to constrain a maximum age for species (Quint and Classen-Bockhoff 2008). Calcretes laid down during the Miocene and Pleistocene are considered to have last been completely inundated  $\pm 3$  Mya during the last major sea-level transgression of over 300m (Siesser and Dingle 1981). Due to the physiological constraints imposed upon alkaline-adapted species, species endemic to these calcretes ought not be older than this age. A conservative maximum age of 5 Mya has been utilized to calibrate the limestone-endemics, as utilized for the Bruniaceae (Quint and Classen-Bockhoff 2008). The recent dated overview of the Cape flora (Forest, Grenyer et al. 2007) support this hypothesis, showing limestone genera to have radiated within this timeframe. However, successful cultivation under glasshouse conditions in acid-soil of *Hermannia* species confined to limestone in nature demonstrates that their occurrence purely on limestone may be a result of constraints imposed by the current climatic conditions. It is suggested that lower temperatures or increased rainfall could allow these endemics to persist on non-alkaline substrata. This would confound dating that is based on the premise that a suitable habitat has only been available since  $\pm 3$  Mya. Sandy plains may also have provided suitable habitat for these endemics under different climatic regimes. A further concern is that the 300m sea-level rise may not have entirely covered all limestone outcrops. Pleistocene limestones in the Bathurst region reach over 330m (Siesser and Dingle 1981) despite several million years of erosion since sea transgression. These islands of limestone may thus have acted as edaphic refugia, allowing limestone endemics to persist through transgressive periods.

### 3.1.9.5 Dating using inland limestones

A limestone calibration point for *H. linnaeoides* in the Kimberley region was explored, providing dates based on Thorium, Palladium and Uranium isotopes ranging between 108-174kyr (Szabo and Butzer 1979) for the lacustrine limestone and lacustrine marl. However, these dates were found to be incompatible with resulting molecular estimates of around 2.38 Mya between *H. linnaeoides* and *H. brendaensis*. The non-compliance of *H. linnaeoides* to the limestone dates may be due to multiple horizons of limestone that surface at varying times over the Pleistocene, providing moving suitable habitats through time. The limestone date is also from a single site, Rooidam, other sites potentially being much older. The aforementioned relaxation of edaphic constraints may also have occurred during more mesic climatic conditions. This constraint was therefore abandoned in this analysis.

### 3.1.10 Objectives

**This chapter has the following objectives:**

- a) to produce a phylogenetic hypothesis for *Hermannia* to test its monophyly and to identify well-supported clades.
- b) to determine the phylogenetic utility of morphology to increase species-level resolution in *Hermannia*.
- c) to taxonomically place key taxa of uncertain affinities.
- d) to date key events in the history of *Hermannia* including the radiation of major lineages and key dispersal events between geographic areas and biomes.
- e) to determine whether *Hermannia* can be considered a Cape clade and in particular a Cape Super Group.

## **3.2 Materials and methods**

### **3.2.1 Collection of material**

Plants were collected in the field together with GPS co-ordinates, pressed voucher specimens, photos and young leaves for DNA extraction. Of the attempted material, approximately (Table 10.8) 160 taxa were successfully sequenced for the nuclear (ITS) region and at least 16 for the chloroplast region. In general, morphological data were taken from the best voucher representing the species including, where possible, flowers, fruit and duplicate specimens. Where possible, the voucher is a representative specimen of that species.

### **3.2.2 Extraction of DNA**

In total, the sequencing of DNA of more than 207 species was attempted, mainly from fresh material representing all resolved clades. In the case of the “*Marehnia*” group from tropical Africa where fresh material was not obtainable, extraction was attempted from some 20 samples from the Pretoria herbarium, with only *H. uhligii* resulting in a successful sequence. Initial extraction led to the gumming up of the DNA solution due to the presence of mucilage that is frequently found in Malvaceae (Khaut and Kulachek 1971; Matthews and Endress 2006; Pakravan, Abedinzadeh et al. 2007). Utilizing smaller amounts of young leaf material of ca. 9 mm<sup>2</sup> mostly resolved this issue. These fragments were finely ground in liquid nitrogen with a pestle and mortar. The leaf powder was incorporated into a 700 µl hot CTAB mixture containing 18µl of mercaptoethanol and 1% PVP-40. This solution was then incubated for at least 90 minutes with mixing by inversion every half hour. 24:1 isoamyl:alcohol was then added to the suspension and the samples hand-mixed by inversion for 5 minutes. The samples were subsequently centrifuged at 18 000 rpm for 5 minutes and the supernatant placed in a new micro-centrifuge tube. Freezer-chilled isopropanol was added and the mixture hand-mixed by inversion for five minutes, before placing in a freezer at -5°C overnight to allow for precipitation of the DNA.

To recover the DNA pellet, the mixture was centrifuged at 18 000 rpm, the liquid then drained and the tube allowed to drip-dry inverted on tissue for 10 minutes. 95% ethanol was twice applied to the pellet as a wash and the pellet dried for about three hours in a silica-gel desiccator. 50µl of 0.1X TE (1mmol Tris-HCl pH 8.0; 0.1 mmol/L EDTA) was added to the dried pellet to create the stock DNA solution. The DNA was run on 1% agar gels to check DNA levels.

### 3.2.3 PCR amplification

Amplification used reagents as outlined in Table 3.1, below.

**Table 3.1 Table of ingredients and volumes used in PCR reaction.**

<b>Quantity</b>	<b>Reagent</b>
5µl	DNA TEMPLATE
29.7µl	H <sub>2</sub> O
5µl	NH <sub>4</sub> BUFFER (10X)
5µl	MgCl <sub>2</sub> (25 mmol/L)
2µl	DNTP'S (12.5 mmol/L)
1.5µl	PRIMER X (0.25µM)
1.5µl	PRIMER Y (0.25µM)
0.3µl	TAQ (0.5 U)
50.0µl	REACTION

PCR was accomplished on a *Hybaid Sprint*, with the following thermal profile cycled 30 times: 94°C for 2 min to start, 94°C for 1 min, 52°C for 1 min, 72°C for 75 sec, 72°C for 7 min and hold at 4°C. Raw DNA and PCR products were visualized in agar on a *mini-XL* gel rig, using 0.5X TBE buffer and 1% EtBr. PCR products were sent to Macrogen™ for cleanup and sequencing.

### 3.2.4 Assessment of gene regions

Table 3.2 (below) provides an overview of the regions attempted, indicating the success obtained. The last four regions amplified multiple bands. The following regions were attempted with the standard protocol at raw strength, 10<sup>-1</sup> and 10<sup>-2</sup> strength, but met with little or no

success: trnL-trnF‡, trnM-trnS‡, 3'trnV-ndhC\*, rpl32-trnL\*, psbD-trnT\*, ndhF-rpl32\*, PsbJ-petA\*, TrnF-ndhJ (Perez, Arroyo et al. 2006), matK 1F -1R‡, rpoB-matK†.

**Table 3.2 The primers attempted for sequencing *Hermannia* and the success rate. \* referenced in (Shaw, Lickey et al. 2007) ‡, in (Shaw, Lickey et al. 2005), † in (Lahaye, van der Bank et al. 2007), ITS 4-5 and the modified 5m referenced in (Saar, Polans et al. 2001), the 18S KRC and ITS2 in (Torrecilla and Catalan 2002), psbA-TrnH in (Chase, Cowan et al. 2007), 390F & 1326R in (Cuénoud, Savolainen et al. 2002).**

Primers	Outcome
ITS 4-5m	The most successful of the regions attempted. Amplification success generally led to sequences of high quality, except where long mononucleotide runs (homopolymers) caused subsequent slippage, thus preventing successful reading of downstream bases.
ITS 4-5	Reasonable amplification, though many sequences showed 'mixed peaks', possibly due to the presence of fungal endophytes or the primer binding to two or more sites on the template.
ITS2&KRC	Best success amplifying with undiluted DNA
psbA-trnH	6 out of 24 reactions amplified.
390F & 1326R	2 out of 5 sequences amplified.
trnQ-5'rps16*	Partial amplification, partial success in sequencing, mononucleotide problems.
trnG-trnS‡	2 out of 30 amplified successfully, 2 amplified dimly, three had double banding.
petL-psbE*	Reasonable amplification but double banding.
atpI-atpH*	Partial amplification, double banding present.
rps16-trnK*	18% success rate. Good amplification but double and triple banding.

### 3.2.5 Root and outgroup choice

The choice of outgroup as members of the Grewioideae was based on the findings of Whitlock et al. (Whitlock, Bayer et al. 2001), reproduced in Fig. 1.4. Here the Malvoideae was found to be more distant from the Byttnerioideae in which *Hermannia* is nested. Where only *Hermannia* species are present within a phylogeny, rooting is done on the branch between subg. *Hermannia* and subg. *Mahernia* – based on the strong support for their reciprocal monophyly (see below).

### 3.2.6 Sequence analysis

ITS sequences were generated for 201 accessions of *Hermannia*, comprising 72 species of subg. *Hermannia* and 59 species of subg. *Mahernia*. This sampling represents close to 50% of the species recognised for both subgenera in this thesis. All major groups previously recognised within the genus have been sampled, as has much of the range of morphological variation. The workflow was PC based, utilising Codoncode Aligner v 3.01. Proprietary alignment algorithms in Codoncode Aligner were found to deal with substantial gaps better than Muscle or ClustalW. However, the software could not integrate single sequences into the existing modified alignment, thus necessitating the export into Bioedit in the FASTA format. Polymorphisms, occasionally present in the ITS dataset, were encoded as ambiguous characters as discussed by Grant and Kluge (2003). Once alignment was complete, the gaps were encoded using Seqstate software (Müller 2005) using the *simple method* as suggested by Simmons and Ochotorena (2000). This utilizes PAUP\* and encodes the resulting gap characters into a NEXUS file. Sequences were subsequently analysed using MrModeltest 2.3 (Nylander 2004) to determine the simplest model that would fit to the data. For the chloroplast sequences, the molecular dataset was introduced into Mesquite. The sequences were aligned using ClustalW and the resulting alignment adjusted with the ends trimmed.

Alignments were exported as TNT files and imported into TNT (Goloboff, Farris et al. 2008). A “new technology” parsimony search (Goloboff, Farris et al. 2003) was performed with the default values. The ‘\_best trees’ were identified 100 times by the algorithm, resulting in three trees. These were viewed as a consensus. A second run was done running jackknife, with P=36 and collapsing branches where support values were below 60.

A second file was exported as a MrBayes Nexus format (Huelsenbeck and Ronquist 2001). Bayesian analysis was performed using the software MrBayes (Ronquist and Huelsenbeck 2003). Four chains were run for 10 million generations using the inverse Gamma and NST=6 model. An initial burnin of 25% of the total trees was used and a 50% majority rule consensus tree constructed, providing the posterior probabilities for each node.

### 3.2.7 Analysis of vegetative and floral characters

In order to obtain characters for use in morphological analysis, representative vouchers or herbarium specimens were investigated under a Zeiss Z-10 stereo microscope. Live or fresh specimens were used where possible; otherwise a flower was removed from a herbarium specimen and soaked in a solution of surfactant in order to soften the tissue for dissection. All characters were encoded using the taxonomic package DELTA (Descriptive Language of Taxonomy) (Dallwitz, 1980). Larger organs such as leaves were measured using a ruler, whereas smaller organs such as flowers and pedicels were measured using an eyepiece reticule. Where appropriate the range of the organ was recorded using the DELTA convention: (extreme minimum) typical minimum – typical maximum (extreme maximum) i.e. (XX)xx–xx(XX). The typical minimum and maximum encompassed the variation of the voucher itself. The extreme ranges were reserved for the variation of the species, such that DELTA could be used for identification purposes and to describe the range of variation of the species. Qualitative characters such as leaf and filament shapes are difficult to describe, so have been encoded as a set of options, with an attempt given to both describe the variation and to encompass the likely descriptions that users of the electronic key (attached) may use.

The initial DELTA dataset encoded by De Winter was both incomplete for each species and utilized an unspecified selection of specimens for each species. This resulted in overly broad species concepts that were not suitable for taxonomic analysis. In the analysis of morphological characters, species that were encoded by De Winter were seldom placed as sister taxa with my own encoding of the species. This shows that our manner of coding differed substantially, which necessitated that all species data recorded by de Winter be redone.

Twenty-two continuous measurement characters for 114 taxa were utilized for the morphological analysis of phylogeny. These are provided in the appendix, in Table 10.4, Table 10.5 and Table 10.6. The state delimitations in Table 10.5 were chosen through dividing the range of each character into quartiles. The optimum means of dividing characters is to plot the state range and look for natural breaks in the total range. However there were few obvious breaks in the dataset and thus it was decided to utilize quartiles. The final states are provided in Table 10.6. These 22 characters (Table 10.4) were exported from DELTA and converted in Mesquite to



a TNT compatible dataset. This dataset was reduced to 107 taxa for morphological analysis in TNT. The TNT analysis was run using the “new technology” options on the default settings for 70 trillion generations. The best score of 541 was hit twice with six trees being retained.

A parsimony analysis of the dataset was undertaken using both PAUP\* and TNT, with the characters of the tree examined using Mesquite. Pollen characters were included, as explained in 3.2.8 below.

Sixteen discrete characters from the DELTA dataset created for descriptive purposes, were exported into Microsoft Excel and from Excel made into a TNT file. These characters were analysed in TNT with the 30 best hits criterion stipulated.

### **3.2.8 Pollen analysis**

Pollen characters were extracted from Coetzee & van der Schijff (1979) for morphological analysis. Their study examined much of the Malvales and thus characters and states that were not applicable to *Hermannia* were removed (such as characters to do with pollen spikes which are absent in *Hermannia*). All remaining characters were utilized in the analyses. The numbers in the following set correspond to entry numbers in the publication. The character states are enumerated in Table 10.6, with characters being: 1 - Polar diameter of colpate pollen or diameter of porate pollen; 2 - Equatorial diameter of colpate pollen or diameter of porate pollen; 9 - Colpi length; 10 - Thickness of exine; 11 - Apertural exine thickness; 12 - Polar thickness of exine; 13 - Length of lacunae; 14 - Width of lacunae; 15 - Muri width; 16 - Sexine texture; 17 - LO-pattern; 18 - Sexine thickness / nexine thickness; 19 - Colour of pollen (excluded from analysis); and 20 - Number of apertures.

Multi-state characters and discretized measurements obtained from Coetzee and van der Schijff (1979) were subsequently analysed using new technology searches in TNT. Where a character measurement comprises two values, these values represent the minimum and maximum measurements. Five outgroup taxa were included with 139 *Hermannia* species encoded. This resulted in a dataset of 144 taxa with 14 discrete characters. As TNT is specifically designed to

handle continuous measurements (Goloboff, Mattoni et al. 2006), these characters were initially encoded as continuous characters (i.e. state A-C). Later these states were treated as single states (i.e. state A&C) which led to results more allied to that of the molecular tree and knowledge of the relationships of the species informed by the molecular phylogeny. Initial analysis also showed that pollen colour was not phylogenetically informative displaying weak patterning across the tree. This character (#19) was thus excluded from subsequent analyses resulting in 13 useful characters. A driven search (Goloboff and Pol 2007) was selected with default values of 5 additional addsequences, a score bound of 323, a random seed of 23408 and options for `-replace existing trees` and `-auto-constrain` selected. The minimum length was increased to 20 trees, which was not reached in the analysis. A sectorial search was implemented with XSS using the default values. Ratchet, drift and tree fusing options were utilized with the default settings.

As TNT can utilize continuous characters (nonetheless discretizing them), a second analysis was conducted with the minima and maxima of the discretized characters considered as continuous bounds. This analysis utilized the same settings as before. The 30 species in common between the DELTA, pollen and molecular datasets were analysed with the same settings for the combined analysis. Output from TNT was done by exporting trees using `data|save data|trees` option, with the resulting files manipulated in Mesquite.

### **3.2.9 Combined analyses**

#### **3.2.9.1 Molecular and indel analysis**

Molecular and indel datasets were combined into a NEXUS file that was used to generate the combined analysis. Thirty species were selected which were represented in all three datasets: morphological, pollen and molecular. The data were manually inserted into a combined text (.txt) file. The appropriate statements were included to allow TNT to read the file. This was then run using the new technology criterion which terminated having found 30 best hits.

### 3.2.9.1.1 Viewing the results

Trees from TNT were saved as a graphics file and printed directly, or displayed using Mesquite. Outputs from Mr Bayes were first combined with a burn-in of 10% of the total trees and the resulting files viewed in either Dendroscope (Huson, Richter et al. 2007), or Mesquite. For Mesquite, the basic NEXUS files were imported, with the resulting combined (.con) tree files linked to the NEXUS file.

### 3.2.10 Molecular dating

Existing sequences were combined with new outgroup sequences from Genbank in the software Genious. A proprietary Genious alignment was run, followed by a Muscle alignment on standard settings. Indels specific to outgroups were removed and the cleaned alignment exported to Datamonkey ([www.datamonkey.org](http://www.datamonkey.org)). This online software identified identical sequences that were removed from the alignment. Rate heterogeneity across the tree was also identified. Datamonkey selected a GTR model as the most appropriate for the dataset, confirming the prior finding of MrMTgui (Nuin 2005) that implements MrModelTest (Nylander 2004).

BEAST (Drummond and Rambaut 2007) was used to jointly estimate topology and infer divergence time, with parameters set using BEAUTi v1.5. To account for uncertainty in the calibration age, the priors were set with a root-height between the Brassicales and Malvales set at  $82\pm 3$  Mya. A normal probability distribution was specified for all priors at root nodes. The Malvaceae excluding *Hermannia* were specified at  $40\pm 3$  Mya (calibration date from Forest, Grenyer et al. 2007). Two limestone dates were specified with a uniform distribution of 0-5MY, corresponding to the time that the South Coast limestones are considered to have been exposed (Quint and Classen-Bockhoff 2008). These dates were based upon the nodes between two limestone and non-limestone species pairs, being *H. ternifolia* and *H. flammea* from sect. *Hermannia* and *H. sperata* and *H. meyeriana* from the Lacerae of subsect. *Mahernia*.

A GTR model was specified with estimated base frequencies and a Gamma heterogeneity model with four categories selected. A Yule model with a relaxed lognormal clock was implemented, with rates being estimated. The tree prior was also set to a Yule process with a

randomly generated starting tree. All other operators were left as standard, with an MCMC run of 15 million generations completed, with sampling every 1000 generations. 600 trees were discarded for the burnin, with the remaining 14400 trees combined into a single maximum clade credibility tree, with median age heights specified in Treeannotater v1.5.3 (<http://tree.bio.ed.ac.uk/software/treeannotator/>). The tree was viewed in Figtree v1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree>), the nodes ordered, error bars made visible and the scale axis reversed to provide a receding age scale with 0 as the present.

## 3.3 Results

### 3.3.1 Molecular

#### 3.3.1.1 Nuclear ITS analysis

ITS sequences were generated for 201 accessions of *Hermannia*, comprising 72 species of subg. *Hermannia* and 59 species of subg. *Mahernia*. As mentioned under Methods, this sampling represents close to 50% of the species recognised for both subgenera in this thesis. All major groups previously recognised within the genus have been sampled, as has much of the range of morphological variation.

The Bayesian results are summarised in Fig. 3.1, while the strict consensus of 30 trees retained from the parsimony analysis is presented in Fig. 3.3. There are no conflicts between the two but, as is usually the case, the Bayesian tree is better resolved and shows better support for many clades. This forms the basis for the current discussion.

The chosen outgroups contain species that are sampled from most of the Malvoideae subfamilies, but particularly those closely allied to *Hermannia*. (According to Leistner (2000), *Hermannia* belongs in the tribe Byttnerioideae along with *Waltheria* and *Melochia*. However, this is embedded within the family Malvaceae which contains a number of subfamilies.) All the major outgroups are resolved with high levels of both Bayesian and parsimony support. Using *Hibiscus* as a representative of the stem outgroup, Malvoideae, resolves the remaining Malvaceae (sensu lato) as sister to the Sterculioideae (*Brachychiton*) and Dombeyoideae (*Dombeya* and *Melhania*) (Fig. 3.1). The Grewioideae fide Bayer et al. (1999) are represented by *Corchorus* and *Triumfetta*. These were previously in the former Tiliaceae.

In all analyses the genus *Hermannia* is resolved as monophyletic. A clade comprising *Waltheria* (subfam. Byttnerioideae), *Triumfetta* (subfam. Grewioideae) and *Corchorus* (subfam.

Grewioideae) is strongly supported as sister to *Hermannia* in the Bayesian analysis, although support for this relationship is lacking under the parsimony criterion.

Under both the Bayesian and parsimony analyses, *Hermannia* constitutes two strongly supported monophyletic groups – one corresponds to *Mahernia* and the other to *Hermannia*, interpreted as subgenera, as will be formalised in Ch. 4. Clades within the sect. *Mahernia* have relatively low support under the parsimony criterion, but Bayesian analysis strongly supports distinguishing the “summer rainfall” species from those of Cape affinity.

### 3.3.2 Testing the monophyly of previously recognised taxonomic groups

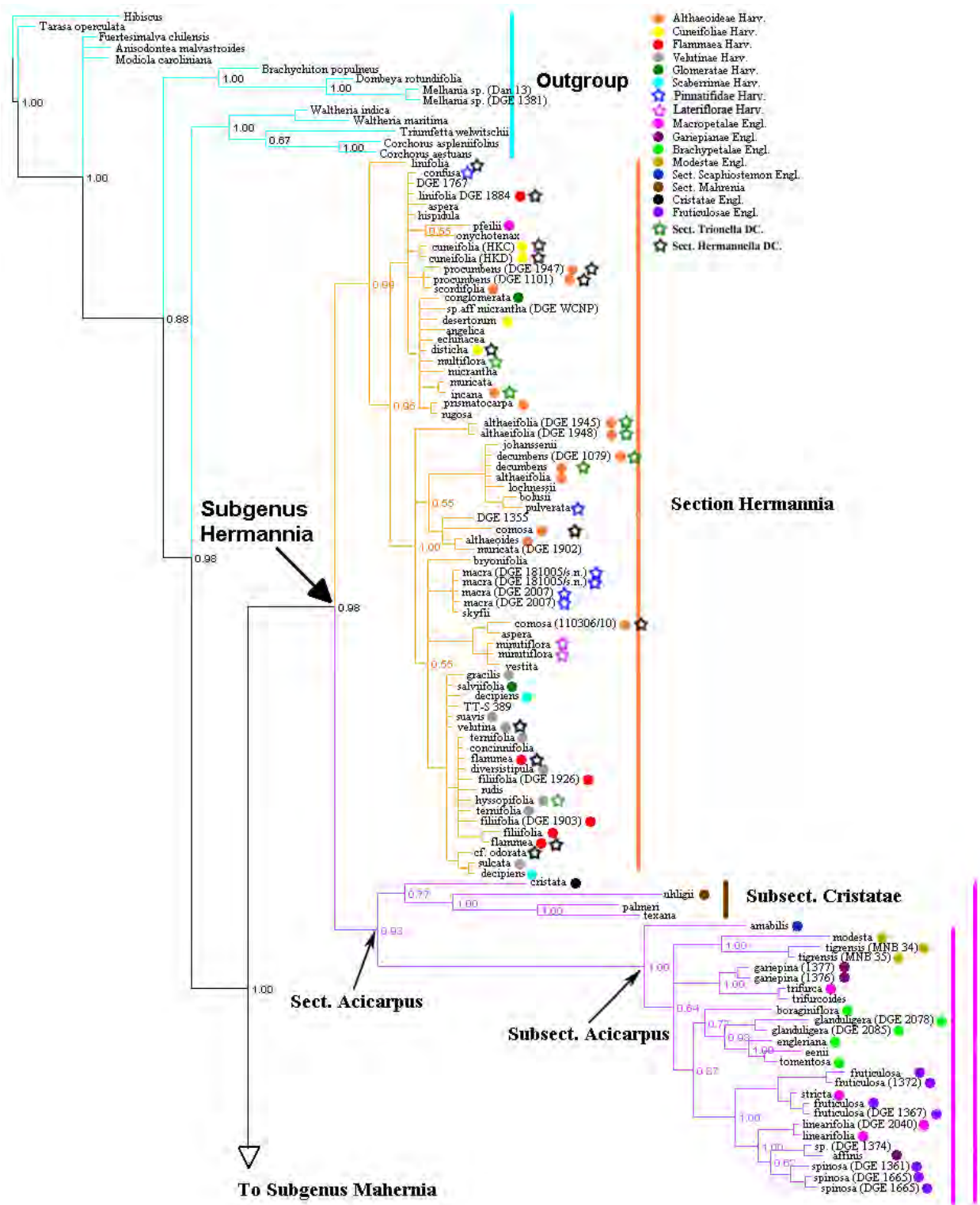
The main clade within subg. *Hermannia*, corresponding to the new sect. *Hermannia*, contains a number of groups previously recognised by Harvey. The *Althaeoideae*, *Cuneifoliae*, *Flammeae*, *Velutinae*, *Glomeratae*, *Scaberrimae* all erected by Harvey, fall into a well-resolved clade recognised here as sect. *Hermannia* (formalised in Ch. 4). Species from the former groups *Althaeoideae*, *Flammeae*, *Cuneifolia* and *Glomeratae* are polyphyletic, being scattered within separate minor clades within sect. *Hermannia*, whereas the monophyly of the *Velutinae* and *Scaberrimae* cannot be disputed or supported given the current phylogeny.

There is a well-supported clade (erected in Ch. 4 as subsect. *Cristatae*) that includes the South African species *H. cristata*, a single East African representative, *H. uhligii* and two American species, *H. palmeri* and *H. texana*. The American species have never been assigned to a group. *Hermannia cristata* is the only species that Engler placed within his sect. *Cristatae*. This species is sister to *H. uhligii* and the sampled American species.

Sister to the subsect. *Cristatae* is a large clade of species having mostly pink flowers and neatly circumscribed by having a single flower per axil and horned capsules. This clade is erected in Ch. 4 as the subsect. *Acicarpus* that combines a number of former groups erected by Engler. *Hermannia amabilis* was placed in its own sect. *Scaphiostemon* Engl. that is sister to the remainder of subsect. *Acicarpus*. Two of the four annual species are included in a well-supported clade of the *Modestae* Engl. The *Garipinae* Engl. is found to be polyphyletic, with *H. affinis*

being nested within the *Fruticulosae* Engl. The South African representatives fall within the *Macropetalae* Engl. and are found to be polyphyletic. The *Brachypetalae* Engl. form a moderately supported clade sister to the majority of the *Fruticulosae* and *Macropetalae*.

The subg. *Mahernia* has a well-supported basal node that comprises six species, with *H. cedarbergensis* (= *H. incisa*) being the only member of the *Pinnatifidae* Harv. The other eight species placed by Harvey in the *Pinnatifidae* were later sunk by Engler (1900) into the subg. *Hermannia*. Two well-supported clades are distinguished within sect. *Mahernia*. These clades are erected at subsectional level in Ch. 4, with the summer rainfall species forming the subsect. *Tomentosae* and the predominantly winter-rainfall species forming the subsect. *Mahernia*. The phylogeny shows that the groups *Dentatae* Harv. and *Verticillatae* Harv. are polyphyletic, occurring in both the subsect. *Tomentosae* and subsect. *Mahernia*. All members of the group *Tomentosae* Harv. fall within the subsect. *Tomentosae*. The subsect. *Mahernia* comprises species from four groups recognised by Harvey. Three species fall within a well-supported clade wholly comprising representatives of the *Lacerifoliae* Harv. The coordinate clade comprises many species of the *Dentatae*, the *Verticillatae* and the *Pinnatifidae*. The *Dentatae* comprise morphologically very dissimilar species from disparate localities and habitats.





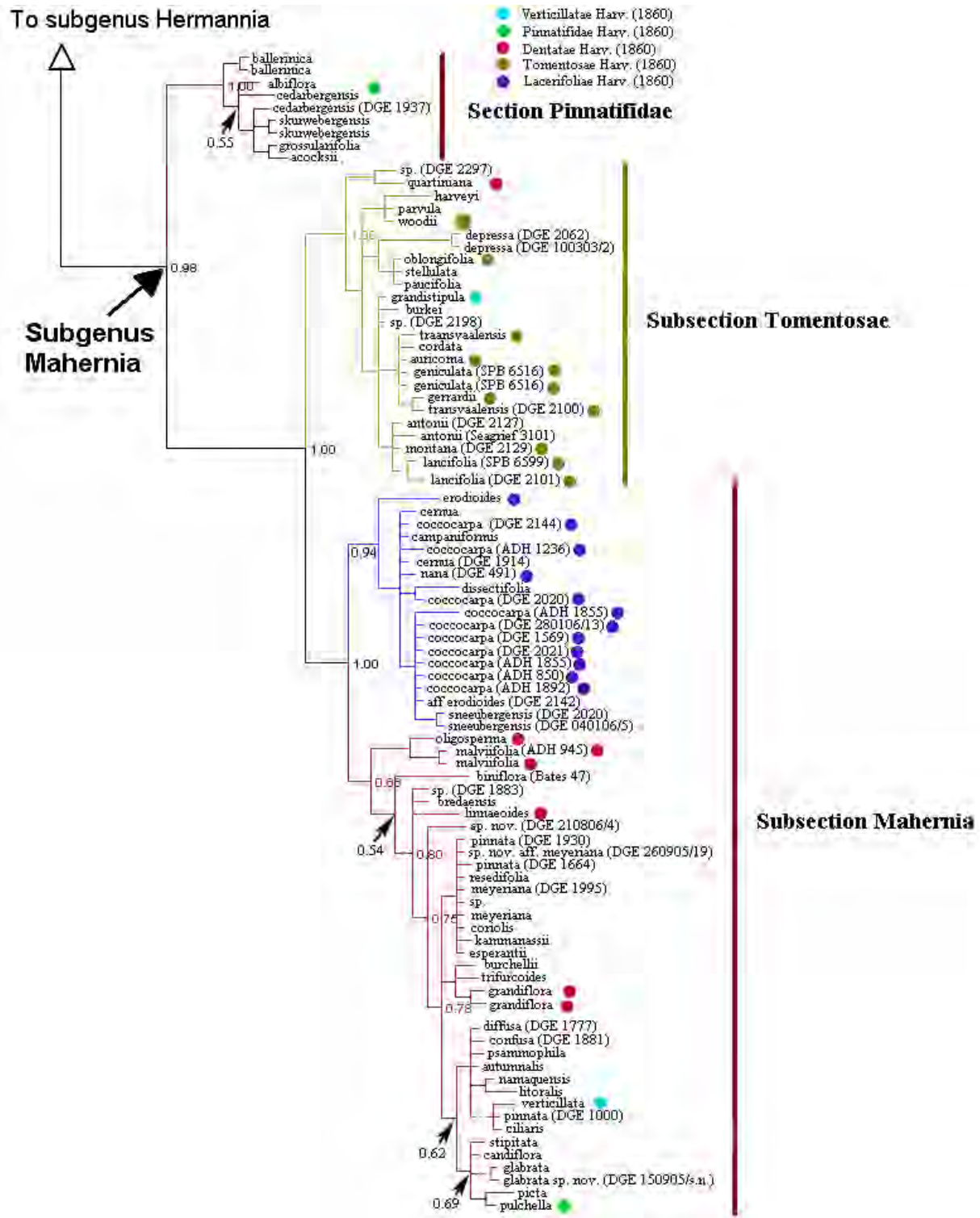


Fig. 3.1 Phylogram of Bayesian analysis of molecular and indel characters using two data partitions and the GTR +  $\Gamma$  model of evolution. Top image shows subg. *Hermannia* and lower image subg. *Mahernia*. A strict consensus of the trees from a run of 10 million generations is shown. The posterior probability (PP) is shown to the right of each node. The coloured dots refer to groups recognised by Harvey or Engler, the stars for groups erected by DC. and the major groups on the right formally proposed in Ch. 4.

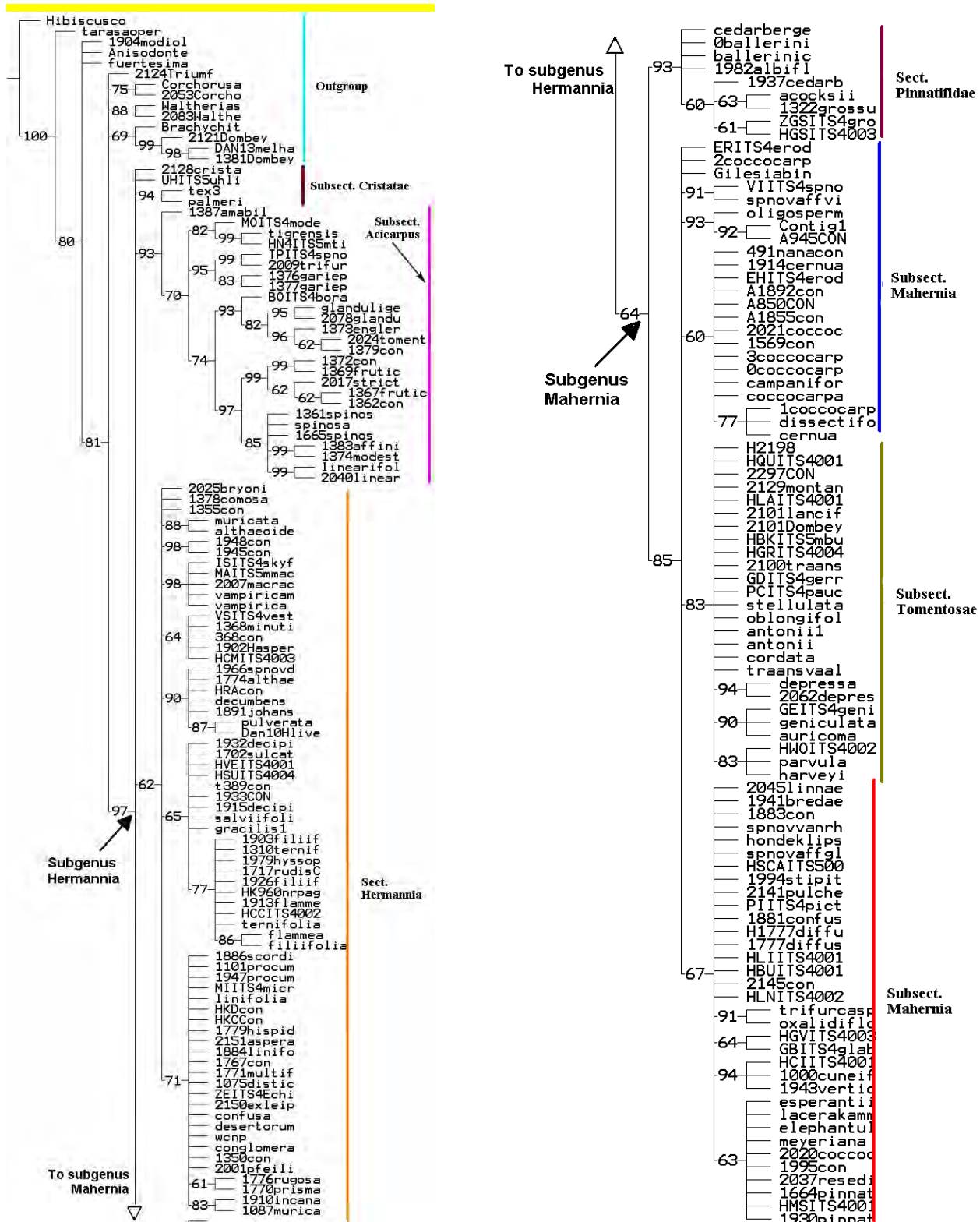
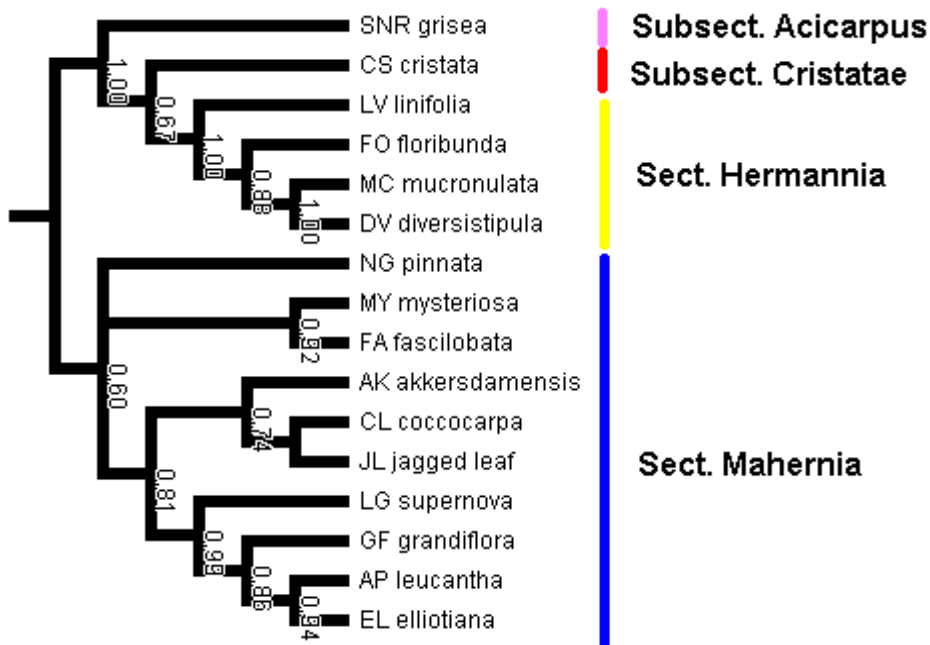


Fig. 3.2 Jackknife tree for molecular (including indel) characters. 1000 replicates using TNT. Cut-off = 60. The groups formalized by this study in Ch. 4 are shown to the right of the accessions. The sample names may be cross-referenced with species in Table 10.8 (395).

### 3.3.3 Chloroplast analysis



**Fig. 3.3** Phylogenetic tree of the chloroplast region trnQ-rps16. Bayesian posterior probability values are depicted on a majority rule consensus tree. Without having an outgroup, the tree has been rooted between sect. *Hermannia* and sect. *Mahernia*. These groups do not contradict the ITS tree.

Only 16 species were successfully sequenced for the chloroplast marker trnQ-rps16. Results of the Bayesian analysis are consistent with the ITS analysis in that the tree can be rooted such that subg. *Hermannia* and subg. *Mahernia* are reciprocally monophyletic. Within subg. *Hermannia*, *H. grisea* from the subsect. *Acicarpus* is sister to the remainder of the sect. *Hermannia*, rather than to *H. cristata* alone, but the clade is only weakly supported and thus does not contradict the well-supported relationship found in the ITS analysis. *Hermannia linifolia* is also retrieved as sister to the remaining Section *Hermannia*. Thus, as far as they are available, chloroplast data generally support the findings of the ITS analysis.

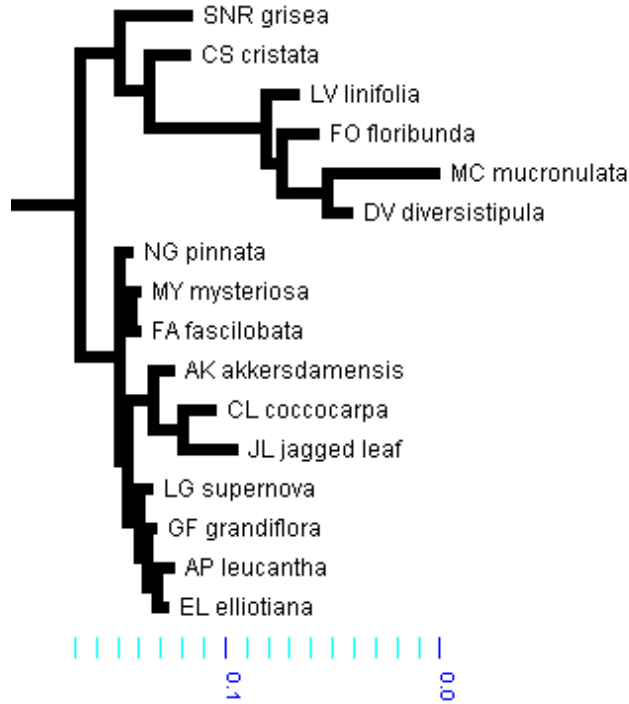


Fig. 3.4 Phylogram of the phylogeny shown in Fig. 3.3, branch lengths are proportional to the genetic change. The scale bar represents the change relative to the entire sequence length.

### 3.3.4 Morphology

The morphological analysis resulted in a strict consensus of six MPTs and is not presented as there is little resolution. Only a single clade is resolved, comprising *H. middelburgensis*, *H. staurostemon*, *H. geniculata* and *H. lancifolia* - a group of sprawling species with yellow flowers, occurring in the Lydenburg area. This forms a polytomy with all the remaining species. These species all fall within the sect. *Tomentosae*.

#### 3.3.4.1 Pollen Analysis

The analysis of pollen characters shows a lack of terminal resolution in the consensus of the four most parsimonious trees (Fig. 3.5). Nevertheless, several patterns emerge. Broadly, the pollen can be grouped into the sect. *Hermannia* type (group 1) and the mixed type (group 2) comprising the sect. *Acicarpus* (subg. *Hermannia*), the sect. *Tomentosae* and sect. *Mahernia* (both from subg. *Mahernia*) (these group numbers are not indicated in Fig. 3.5). There are four species whose pollen does not fit in with this classification. Group 1 contains two species from the Drakensberg in subsect. *Mahernia*, as well as *H. parviflora* from subsect. *Tomentosae*. The

only exception within group 2 is *H. velutina* which belongs to sect. *Hermannia*. A species of particular interest in the pollen analysis is *H. hyssopifolia* which arises together with red-flowered species of the informal group “Flammeae”. This species was previously placed by de Candolle in the group *Trionella* (characterised by having an inflated calyx), while Harvey placed it within the group *Velutinae*. Both of these groups are in sect. *Hermannia* and are distinct from species of “Flammeae” in being characterised by yellow flowers. Both molecular and pollen evidence would suggest that it is better placed within the “Flammeae”.

### 3.3.5 Combined molecular and morphological analysis

Fig. 3.6 shows the result of a parsimony analysis run using TNT’s “New Technology” search. The analysis was run till the best tree with a score of 1043.500 was found 100 times, producing a single tree. Rooting restrictions in TNT meant the tree has been rooted on the outgroup *H. cristata* which has been found to be sister to the rest of the subsect. *Acicarpus*. Nonetheless, it can be seen that this phylogeny is found to be consistent with the ITS tree (Fig. 3.2). The subg. *Hermannia* and the subg. *Mahernia* are both found to be monophyletic, as is subg. *Mahernia*. The sect. *Pinnatifidae*, represented by *H. cedarbergensis*, is sister to the remaining species of subg. *Mahernia*. *Hermannia malvifolia* from the Drakensberg is sister to subsect. *Mahernia* (the Cape group), which is sister to the subsect. *Tomentosae* (the summer rainfall group). Within subsect. *Mahernia*, the candy-striped red and white flowered species (*H. resedifolia* and *H. glabrata*), are polyphyletic. Within the subsect. *Tomentosae*, *Hermannia depressa*, the widespread non-yellow flowered species is sister to the rest of the clade. Three sprawling species form a group, but are sister to a morphologically dissimilar pair comprising *H. parviflora* and *H. oligosperma*. The species in the clade that contains *H. grandistipula* and *H. geniculata* have little in common with each other, besides having yellow or yellow-derived flowers (*H. geniculata* being white-flowered but derived from a yellow-flowered ancestor) and occurring in the summer rainfall region. The large-leafed species (*H. transvaalensis*, *H. gerrardii* and *H. geniculata*) form a derived cluster.

The total evidence tree is derived from a greatly reduced dataset of only 30 shared taxa, with little pattern shown within the genus. However, similarity to the Bayesian tree may be an artefact of the strong signal within the more plentiful molecular characters overwhelming the contributions from the other datasets.

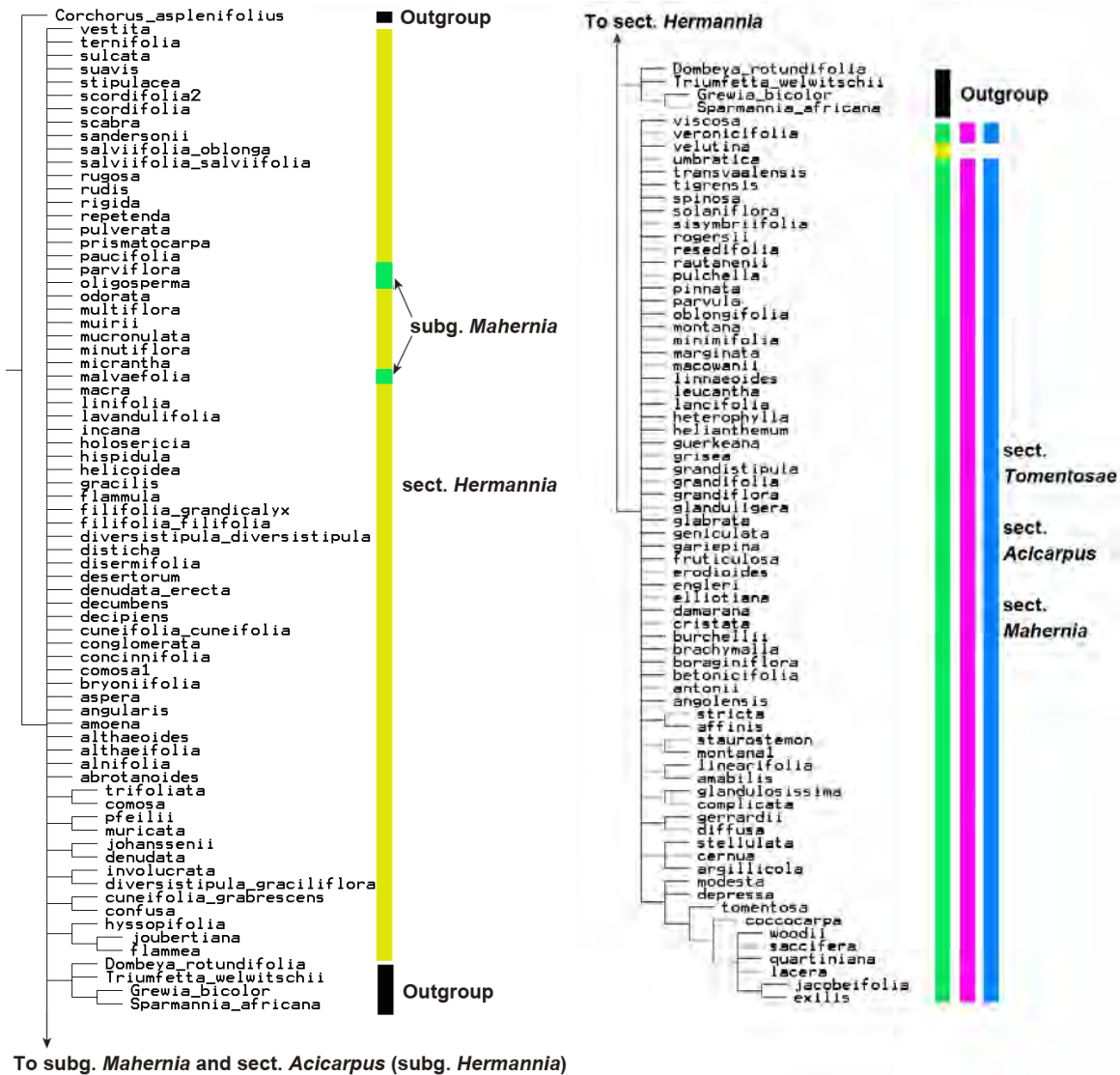


Fig. 3.5 Strict consensus of 4 MPTs based on an analysis of pollen characters. The portion of the Phylogram showing sect. *Hermannia* (subg. *Hermannia*) is shown on the left, with sect. *Tomentosae* and sect. *Mahernia* (both from subg. *Mahernia*) and sect. *Acicarpus* (subg. *Hermannia*) shown on the right. There are outliers of subg. *Mahernia* embedded within the clade of sect. *Hermannia* (left hand side) and a single member of sect. *Hermannia* embedded within the clade on the right side.

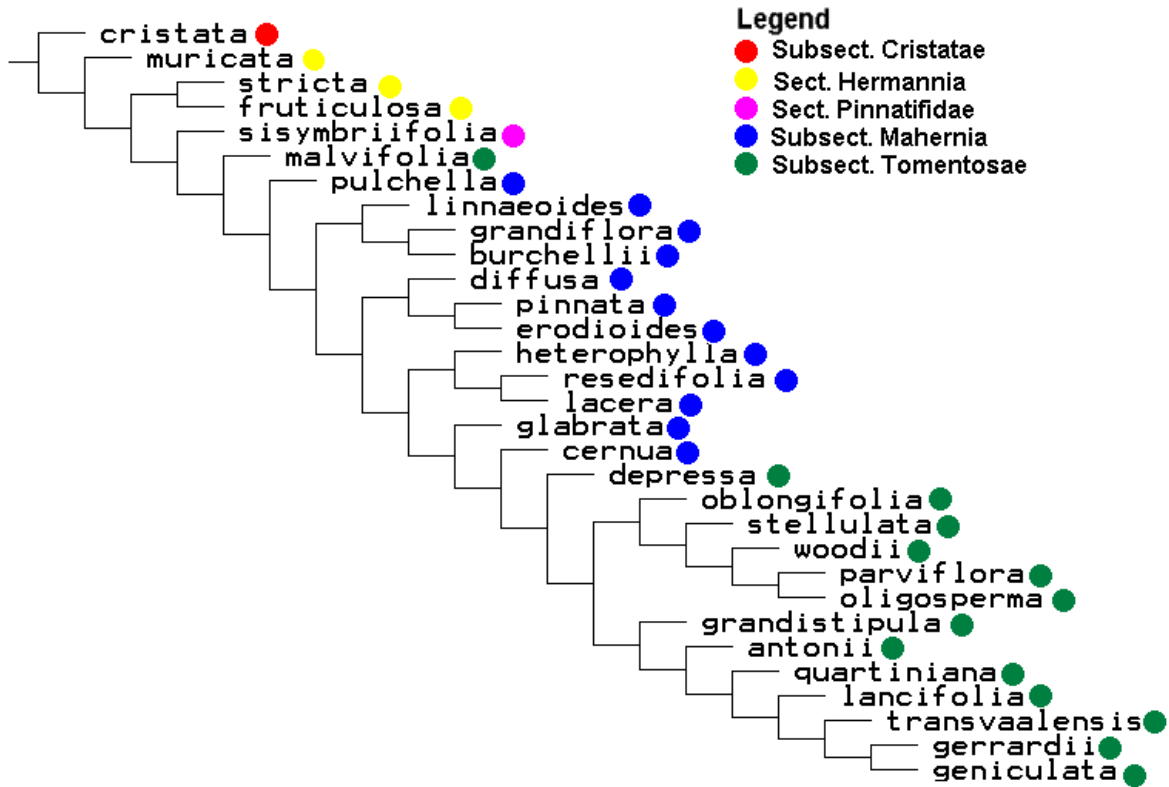


Fig. 3.6 The single most parsimonious tree for 30 species combining DNA, pollen and morphology.

### 3.3.6 Molecular dating

#### 3.3.6.1 Divergences of the major clades

Divergence dates given below are estimates obtained from analysis of the molecular dataset using the software Beast. Error estimates are around 10% of the node age as shown by the error bars. The root node separating the Malvaceae and Brassicales resolves within the 82 Mya specified, at  $\pm 81.65$  Mya (Fig. 3.7). The Grewioideae, comprising the genera *Triumfetta* and *Corchorus* arose  $\pm 65.97$  Mya. The divergence of a representative of *Waltheria* that occurs in Africa, *W. indica*, from a Brazilian species is around 20 Mya. The remaining genera of Malvoideae arose intermittently until recently, with the African baobab, *Adansonia digitata* separating from a representative of the Madagascan group around 12 Mya. The split between the genus *Hermannia* and remaining Malvaceae was given a prior at 60 Mya and this node is dated to  $\pm 59.68$  MY.



An overview of divergence dates within *Hermannia* shows that many of the deeper nodes at the rank of subgenus and section took place earlier than 10 Mya. All shallower taxonomic ranks with the exception of subsect. *Acicarpus* and subsect. *Cristatae* took place within the last 10 million years, with most speciation events taking place within the last 5 million years.

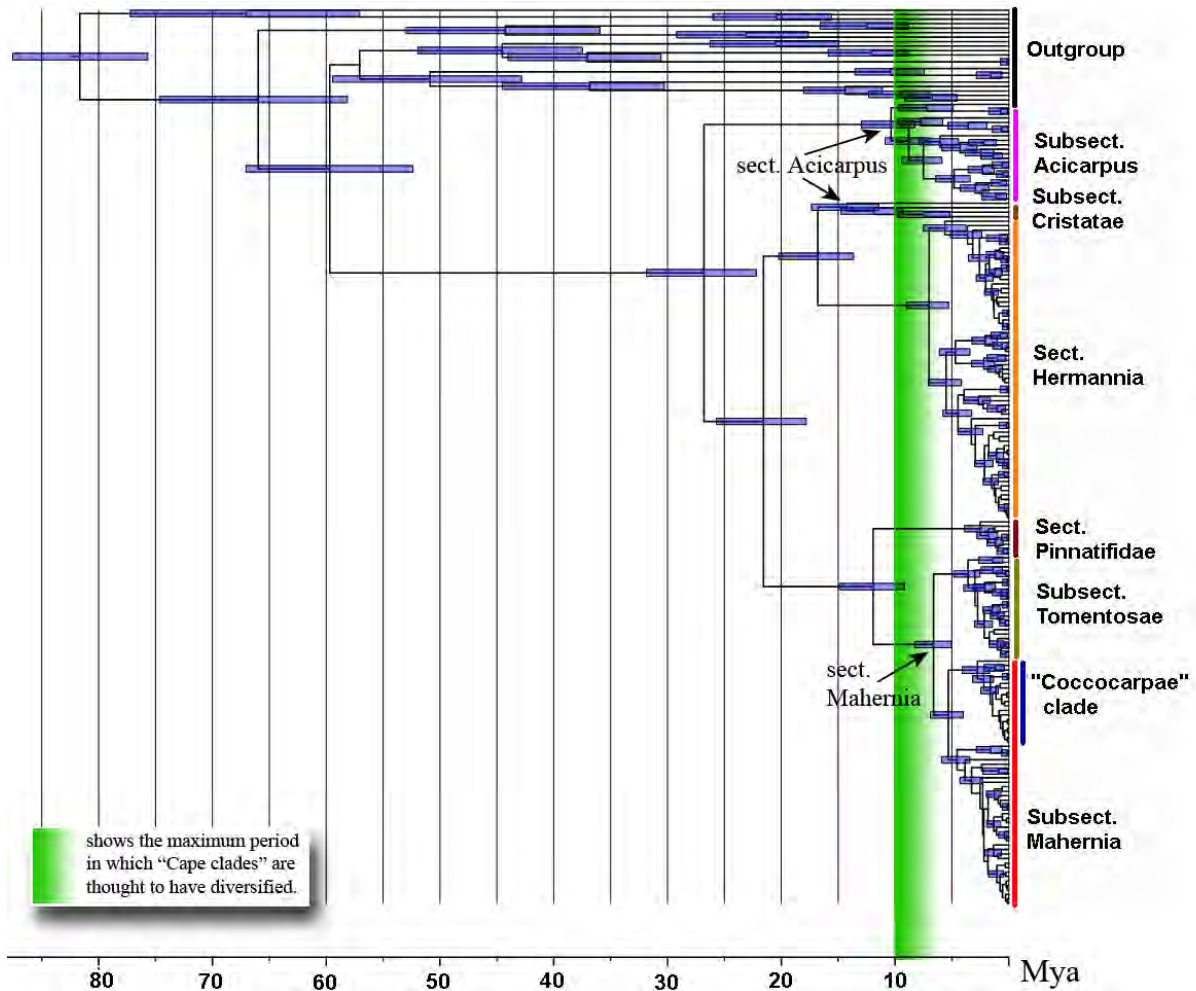
The overall pattern of the deeper ranks from subgenus to subsection are that they are dated at between  $\pm 26.8$  Mya and  $\pm 6.6$  Mya. More specifically, the stem node between the Namibian *Acicarpus* clade and the remaining *Hermannia* species is dated to  $\pm 26.8$  Mya. The node distinguishing the remaining subg. *Hermannia* from subg. *Mahernia* is  $\pm 21.56$  Mya. The Beast analysis that generates a phylogeny that was not constrained to the topology of the Bayesian analysis, places subsect. *Cristatae* as sister to sect. *Hermannia* instead of subsect. *Acicarpus*. The subsect. *Cristatae* has several relatively deep speciation events, with the summer rainfall *H. cristata*, splitting off from the E. African *H. uhligii* and American species at  $\pm 14.22$  Mya. The split between *H. uhligii* and the American taxa is  $\pm 11.82$  Mya. The American species *H. palmeri* and *H. texana* diverged about  $\pm 7.45$  Mya. Within subg. *Mahernia*, the *Pinnatifidae* split from the remaining *Mahernia* species by  $\pm 11.92$  My. The subsect. *Tomentosae* clade of summer rainfall species split from the winter-rainfall Cape Clade of subsect. *Mahernia* by  $\pm 6.6$  Mya. The *Coccocarpaceae*, a predominantly Karoo group with few summer rainfall species separated from the Cape Clade roughly  $\pm 5.3$  Mya.

Examining species patterns within clades, we find the sect. *Hermannia* has *H. linifolia*, a quarternary sand species from the around the Cape Peninsula at its base, at  $\pm 5.62$  MY. The remaining species in this portion of the clade are younger than  $\pm 3.63$  My, including Karoo, Namibian, E. Cape Karoo and sandstone species. Except for one other node dating to the Late Miocene at  $\pm 5.51$  Mya, the remaining nodes in the sect. *Hermannia* are all early to late Pliocene. All the species are Karoo or CFR species, with the exception of *H. bryoniifolia* which is a species from the Free State Karoo and is dated to  $\pm 3.3$  Mya.

The Namibian species within sect. *Acicarpus* have speciated regularly since  $\pm 10.35$  Mya, with that date marking the divergence between the annual species and the perennial species. The



progenitors of the summer rainfall species *H. boraginiflora* and *H. glanduligera* may have dispersed from Namibia  $\pm 6.03$  Mya. The progenitors of the South African Karoo species, *H. linearifolia* and *H. spinosa* are resolved as having dispersed from Namibia  $\pm 3$  Mya. The west-coast South African species, *H. trifurca* and *H. gariepina* arose  $\pm 3.58$  Mya.



**Fig. 3.7** Dated tree produced using a relaxed log-normal clock (see text for details). Blue lines are error bars. The green line is the period 8-10 Mya, which is the maximum period in which Cape clades are thought to have diversified.

**Table 3.3 Summary of the diversification of major clades (time given in Mya).**

Clade / Group	Earliest split from nearest major clade	Onset of diversification	Main radiation to age of youngest sister pair
<i>Acicarpus</i>	26	10.3	7.2–0.5
<i>Cristatae</i>	16.7	14.2	14.2–17.7
<i>Euhermannia</i>	16.8	7.0	3.6–0
<i>Mahernia</i>	11.9	4.5	3.5–0
<i>Pinnatifidae</i>	11.6	2.5	2.5–0.5
<i>Tomentosae</i>	6.6	3.6	2.3–0
Coccocarpae	5.3	2.6	2.7–0
Cape Clade	4.5	3.2	2.3–0

The major diversification events are highlighted in Table 3.3. The subg. *Mahernia* comprises the sect. *Pinnatifidae* that separates from the sect. *Mahernia*  $\pm 11.62$  Mya and subsequently radiates across multiple edaphic and climatic habitats within the last  $\pm 2.5$  My.

The sect. *Mahernia* has an early split dated to the end Miocene ( $\pm 6.61$  Mya) which separated the summer rainfall clade (subsect. *Tomentosae*) from the subsect. *Mahernia*. The species *H. quartiniana*, a Namibian species that occurs from northern Namibia through to northern South Africa, arose  $\pm 3.59$  Mya. All remaining species in the summer rainfall area (mainly *Tomentosae*) have speciated since then. The radiation of the subsect. *Mahernia* has taken place since the Miocene-Pliocene boundary  $\pm 5.31$  Mya. This led to two clades, the Coccocarpae which have speciated since  $\pm 2.6$  Mya, with the only summer rainfall endemic, *H. dissectifolia* arising recently. Sister to the Cape clade of *Mahernia* are two Drakensberg species dated to  $\pm 4.55$  Mya. The Australian representative separated from its Cape relatives some  $\pm 3.8$  Mya. At approximately  $\pm 3.27$  Mya, *H. linnaeoides*, a limestone endemic from the interior of South Africa occurs along with *H. bredaensis* of the west-coast Quarternary sands. The remaining species are all species that occur within or close to the CFR and are end-Pliocene or Quarternary in origin. This includes the limestone-, dolerite- and shale-loving species from Namaqualand through to the Eastern Cape.

## 3.4 Discussion

### 3.4.1 Taxonomic ranking, features of the significant clades and the validity of former taxonomic concepts.

There is strong support from the ITS data, that *Hermannia* is a monophyletic group that includes the American species, the tropical African species as well as the Australian species previously treated in the genus *Gilesia*. The phylogeny identifies several monophyletic groups and provides information for the placement of species within these groups allowing us to test the validity of previously proposed groups. Both subgenera encompass considerable genetic and morphological variation, so finding simple defining features for subgenera has not been successfully achieved in the past. Given the molecular-based phylogeny, it is important to attempt to reconcile the new groupings with morphology; in particular, where possible, to identify features unique to particular clades.

#### 3.4.1.1 An appraisal of subgenera

*Hermannia* constitutes two monophyletic groups, supported by both the Bayesian and parsimony analyses. These will be formalised in Ch. 4 as the subgenera *Mahernia* and *Hermannia*.

Historically there has been a debate about whether to place *Mahernia* and *Hermannia* at generic or subgeneric level. The only feature used to separate *Hermannia* from *Mahernia* has been the position of the expanded portion of the filament. However, both subgenera have species with linear filaments that cannot be placed using this character, a fact that was either overlooked or not acknowledged before. There are also two species in which the filament character incorrectly places them in the wrong subgenus. There is therefore an imperative to find other robust characters to distinguish these subgenera. A recent examination of high resolution scans of fresh floral material in December 2013 showed that two different filament textures were apparent: transparent and fleshy. Examination of around 100 species revealed that filament texture reliably distinguishes between subgenera. However, this feature is only reliably detectable on fresh specimens and has not included an examination of material from subsect. *Cristatae*. It appears that the defining features of subg. *Hermannia* are filaments that are

translucent and with a widened portion overlapping the base of the anther (with a few exceptions). In contrast, the filaments of subg. *Mahernia* are fleshy, with cruciform filaments. It is not always possible to use simple characters to define the subgenera and in cases where the taxonomic position of the species is particularly obscure, it is necessary to use a suite of characters. The defining characters of the groups are explored in Ch. 5, Ch. 6 and Ch. 7, including flower colour, geography, capsule orientation and capsule ornamentation.

### 3.4.1.2 Shortcomings of previous groupings within the genus *Hermannia*

Cladistic support exists for a number of groups within subg. *Hermannia*, proposed to fit in to the ranks of section and subsection. The groups utilized by de Candolle (1824), sect. *Hermannella* and sect. *Trionella* are based on an early and very limited understanding of the genus (green and black pentagons in Fig. 3.1). For instance, *Trionella* which is characterised by the calyx inflating after anthesis, includes a number of species that are polyphyletic. For instance, *H. hyssopifolia*, *H. decumbens* and *H. multiflora* are in different clades. Species lacking an inflated calyx previously placed in *Hermannella*, similarly form a paraphyletic group. De Candolle's groups are therefore disregarded in favour of examining the later and more considered groups erected by Harvey and Engler.

In the light of the molecular phylogeny, several of Harvey and Engler's groups/Reihe are untenable due to being polyphyletic, while other groups appear to be cohesive. However, within subg. *Hermannia*, Engler's treatment included the *Cristatae* and *Parvipetalae*. This latter group corresponds in part to Harvey's *Brachypetalae* within the currently recognised sect. *Acicarpus*. Furthermore, in the group *Lateriflorae* he included *H. gariepina* and *H. viscosa* (= *H. brachypetala* of Harvey's *Brachypetalae*) of the sect. *Acicarpus* and several other species of the sect. *Hermannia*, making his concept of the subgenus polyphyletic. The majority of Harvey and Engler's unranked groups additionally do not fit within a coordinate and ranked taxonomic system that suits the molecular phylogeny.

All subgeneric groups previously erected within the subg. *Mahernia* were erected by Harvey. Most of the species examined by him fall into the *Tomentosae*, *Lacerifoliae* or *Dentatae*. However, both the *Verticillatae* (*H. grandistipula* and *H. verticillata*) and the *Pinnatifidae* (*H.*

*cedarbergensis* and *H. pulchella*) are polyphyletic. The groups formalised in Ch. 4 are those erected by Harvey, but with the incorporation of molecular evidence and new insights into morphology, modified to include or exclude species that previously fell into other groups.

### 3.4.1.3 The newly defined sections within subg. *Hermannia*

A much simpler concept of subg. *Hermannia* than that given by Harvey and Engler is proposed here to include two sections at the higher levels, sect. *Hermannia* and sect. *Acicarpus*. The sect. *Hermannia* generally has more than one flower per axil. Most species have petals that are yellow, orange or red, with a few species having brown or white flowers. Section *Hermannia* is largely confined to the western parts of Southern Africa, i.e. the CFR (Cape Floristic Region), Karoo and N. Cape. A few species extend into Namibia, with only *H. erecta* being endemic to the summer rainfall region of South Africa.

#### 3.4.1.3.1 The subsect. *Acicarpus*

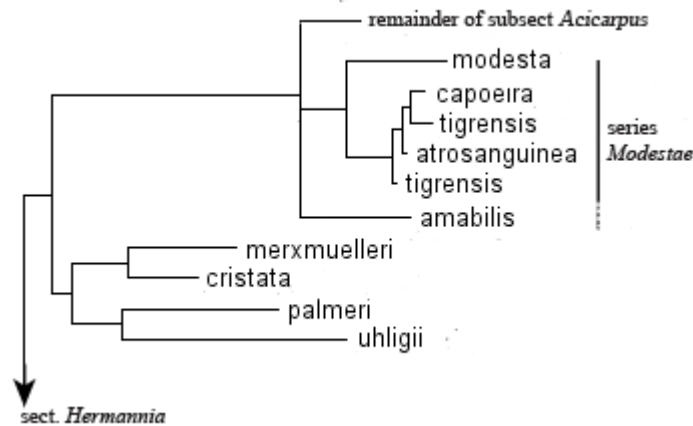


Fig. 3.8 A preview of molecular results for sect. *Acicarpus* and series *Modestae*.

The sect. *Acicarpus* comprises two disparate and very dissimilar subsections, subsect. *Acicarpus* and subsect. *Cristatae*. The subsect. *Acicarpus* is neatly defined by single flowers per axil, bearing typically pink and rarely red, orange or white petals. The capsules are also characteristic, bearing five or ten short to long horns apically. The highest diversity is in Namibia, with a few species extending to the Cape and across the summer rainfall parts of Southern Africa north of Gauteng. The sect. *Acicarpus* includes all annual species of *Hermannia*,

many of which extend into the summer rainfall parts of South Africa, with *H. modesta* extending to the Arabian Peninsula and *H. kirkii* occupying a latitudinal band from Cape Verde to Ethiopia. The Angolan species *Hermannia capoeira*, newly discovered by Adam Harrower is surprisingly included in the series *Modestae*, as it is a multistemmed perennial species. This is likely a reversion to the ancestral state for the group. It is uncertain whether the perennial *H. amabilis* should be included in the series *Modestae*, but I have chosen to include it based on the leaves being similar to *H. kirkii*.

#### **3.4.1.3.2 The subject. *Cristatae***

The subject. *Cristatae* encompasses two morphologically dissimilar groups - those with cristate capsules from America and southern Africa, the “*Cristatae*” and those without capsular ornamentation primarily from tropical Africa, “*Marehnia*”. The argument for their morphological similarities has been discussed in the introduction to the chapter. It is known from the molecular phylogeny (Fig. 3.1) that *H. uhligii*, the representative species from “*Marehnia*” is sister to the pair of American species, *H. palmeri* and *H. texana* that resolve as sister taxa. *Hermannia cristata* is also placed as sister to this set of species, but it is uncertain where *H. merxmulleri* is placed relative to *H. cristata*. Preliminary phylogenetic analysis (Fig. 3.8) unequivocally shows that *H. merxmulleri* and *H. cristata* are sister species. This means that *H. merxmulleri* is closer to the South African species than to either the tropical African representative or American representatives. The closeness of *H. uhligii* to the American species, together with the fact that its speciation occurred after the breakup of Gondwanaland, suggests that the species arose from a transcontinental event between a tropical African and American progenitor. However, without greater sampling of “*Marehnia*” in a phylogeny, or the inclusion of *H. inflata* that does not morphologically resemble the other American species, the nature of the relationship of the South African, tropical African and American species cannot be reconstructed with any degree of certainty.

#### 3.4.1.4 The sect. *Hermannia*

Section *Hermannia* includes species from Southern Africa that possess filaments that overlap with the anthers and have capsules without horns. Representatives of all seven of Harvey's groups are included in the phylogeny. Five of the seven previously defined groups within sect. *Hermannia* are polyphyletic (*Althaeoideae*, *Cuneifoliae*, *Velutinae*, *Glomeratae*, *Pinnatifidae*). The *Flammeae* could be monophyletic or paraphyletic, but would require greater resolution and the *Lateriflorae* has too few representatives in the phylogeny to draw conclusions.

#### 3.4.2 Species affinities of the red-flowered clade, “*Flammeae*”

The informal group “*Flammeae*” within the sect. *Hermannia* is generally characterised by having red flowers and has multiple species concentrated in the south-western Cape. An assessment of South African field guides detailed below shows that red flowers are relatively rare in nature and thus the origin, possible monophyly and pollination of this group is of interest. *H. hyssopifolia* is a species of uncertain affinity that De Candolle placed within the sect. *Trionella*, defined by having a calyx that inflates after anthesis, with an amply dilated filament. Pollen analysis resolves *H. hyssopifolia* together with the red-flowered species of the informal group *Flammeae*. The Bayesian phylogeny displays a clade with weak support, but that nonetheless encompasses all red-flowered species of the informal group “*Flammeae*” and also includes *H. hyssopifolia*. Several other yellow-flowered species fall within the “*Flammeae*” including *H. rudis*, *H. concinnifolia*, *H. ternifolia* and *H. trifoliata*. The latter two species as well as *H. hyssopifolia* were placed into the *Velutinae* by Harvey. Despite having yellow flowers, *Hermannia rudis* and *H. concinnifolia* have a calyx that is red, *H. ternifolia* has yellow-orange flowers with a reddish tinge and buds that are red and *H. trifoliata* has flowers that become dark red after fertilization. The combination of morphological features make for a group in which most of the species can be recognised as being closely related and in which some aspect of the flower is typically red. On this basis, it has been chosen to informally recognise the “*Flammeae*”.

If the species are closely related and differ primarily on flower colour, this could be useful group for the examination of pollination as a driver of speciation. An examination of field guides from four different regions of southern Africa including northern Botswana (Heath and Heath 2009), southern Namib (Mannheimer, Maggs-Kölling et al. 2008), Niewoudtville (Manning and

Goldblatt 2002); and Stellenbosch to Hermanus (Bean and Johns 2005), shows that red flowers are relatively rare in nature. The first three regions have less than 4% of species with red flowers, whereas the fynbos has less than 9%. Of these, the bird pollination syndrome was the most dominant syndrome within the red-flowered species (67%), followed by butterfly (10%), rodent (9%), monkey beetles (4%) and unknown (5%). *Hermannia hyssopifolia* is the only species that has a strong sweet scent at night. With a combination of pale cream flowers and the strong scent, it fits in with a moth pollination syndrome. As red flowers are relatively rare in nature and it is not obvious what the pollinators are of these red-flowered *Hermannia* species, the development of this entire clade may be worth focusing on in the context of phylogenetics and pollination.

#### **3.4.2.1 The subg. *Mahernia***

The sect. *Pinnatifidae* has species with pinnatifid leaves, and encompasses resprouting species that are confined to the Cape as exemplified by *H. grossularifolia*. The subsect. *Tomentosae* comprises species from the summer rainfall area with a sprawling and resprouting habit, with large, relatively broad leaves as exemplified by *H. transvaalensis*. The “Coccocarpace” comprises the widespread species complex of *H. coccocarpa* that occurs from the western Klein Karoo, to Namibia in the north to the upper reaches of the Lesotho Drakensberg in the east. The species within this section have primarily mauve flowers, though red, blue and white flowers also occur. The final clade, subsect. *Mahernia*, includes a duet of species from the Drakensberg and *H. biniflora* from Australia. It is essentially a clade comprising species that do not fall into the other clades and as such encompasses a wide range of morphological variation, with the degree of molecular variation approaching that of the subsect. *Acicarpus*. The series level ranking is based primarily on intuitive ideas based on morphological similarity that are loosely informed by molecular evidence. The partitioning of the series can be found in the taxonomic chapter [Ch. 4].

##### **3.4.2.1.1 Section *Pinnatifidae***

The revised sect. *Pinnatifidae* comprises ten species that are mostly multistemmed and have somewhat dissected leaves. Two informal groups with somewhat disjunct distributions can be discerned within sect. *Pinnatifidae* based on morphology. The proposed subsect. *Grossularifolia* has five resprouting species in the SW Cape, all with yellow flowers and strongly dissected



leaves. The second group, the proposed subsect. *Cedarbergensis* has five single-stemmed species with white or pink flowers growing in arid areas of the Northern Cape, Cedarberg or Klein Karoo. *H. virginalis*, *H. sisymbriifolia* and *H. cedarbergensis* are woody shrubs with white flowers growing along the range of mountains from the Cedarberg to the Bokkeveld escarpment. *H. barbiae* forms a dense, broad undercover beneath trees in the Oorlogskloof reserve in the Northern Cape, whereas *H. albiflora* is confined to shale valleys between Montagu and Barrydale in the Klein Karoo. Both species are narrow endemics with pink flowers.

#### **3.4.2.1.2 Subsection *Tomentosae***

There is no single unifying feature that characterises subsect. *Tomentosae*, but rather it is generally characterised by stellate indumentum and oblong, ovate or cordate leaves. The type species is *H. lancifolia* (previously *H. tomentosa*) and contains all the species previously in the group *Tomentosae* (Harvey and Sonder 1860). The subset of large-leafed species has the largest leaves in the genus and the largest flowers in the subgenus *Mahernia*. They have sub-entire leaves and yellow or white flowers. The subsect. *Tomentosae* also encompasses a number of species with smaller typically serrate, relatively glabrous leaves. This group of plants is reddish flowered (*H. oblongifolia*, *H. depressa*, *H. woodii* and *H. adenotricha*), white flowered (*H. parvula*, *H. parviflora* and *H. crassifolia*), or yellow flowered (*H. harveyi*, *H. saccifera*, *H. stellulata* and *H. quartiniana*). These species tend to occupy the most marginal areas of the overall distribution of the *Tomentosae*, extending to Namibia in the case of *H. quartiniana* and into the Cape in the case of *H. saccifera*.

#### **3.4.2.1.3 Subsection *Mahernia***

Subsection *Mahernia* encompasses more morphological variation including leaf form and flower colour than comparable groups within *Hermannia*. A moderately supported clade that includes *H. coccocarpa* has a PP of 94. This clade contains species with serrate leaves and red or blue pigments, which in *H. atrofulminalis* is masked to produce a white flower, with a bluish tint at the base. Red is atypical for the clade, occurring only in *H. cernua* and *H. dissectifolia*. The latter species is the only member of the clade to possess highly dissected leaves and occupies the north-eastern most position of the *Coccocarpa* clade. There are more representatives of *H. coccocarpa* in the phylogeny than any other species. The relative lack of molecular variation

amongst the variants of this species and closely allied species suggests that it is a recent and rapidly radiating complex. *H. coccocarpa* (*sensu lato*). has red, pink, blue, or purple flowers, that vary from open to tubular. The leaves vary from serrate to pinnatifid and from ovate to linear. It occurs from the arid Karoo to the mesic mountains of the Drakensberg.

The subsect. *Mahernia* also includes two species of near-endemics to the Drakensberg, *H. oligosperma* and *H. malvifolia*. Like the subsect. *Tomentosae*, these two species have yellow flowers and unlike the rest of the subsect. *Mahernia*, large hairy leaves. The similarity in leaves may be due to convergent evolution due to climatic conditions, or conserved morphology from a common ancestor that resembled species of the sect. *Tomentosae*.

*H. biniflora* is the only Australian species and is embedded within subsect. *Mahernia*. It is a species that is most similar to *H. erodioides*, but is the only *Hermannia* species that has upright flowers as depicted in Jessop (1986) and Harden (1990) (Jessop and Toelken 1986; Harden 1990).

The remainder of the *Mahernia* clade is composed of a composite of species from the Western Cape, Namibia, the Karoo and Free State and the south coast of South Africa. Many species have pinnatifid, bipinnatifid or even tripinnatifid leaves, while others have entire leaves. Flower colour includes red, pink, orange, yellow and rarely white (*H. argillicola*).

### **3.4.3 Patterns of speciation within *Hermannia***

#### **3.4.3.1 *Hermannia* as a “Cape Clade”**

The sect. *Hermannia* falls predominantly within the Cape as seen in Ch. 4, Fig. 4.7. It is reconstructed as having its origins in the Cape (Ch.5, Fig. 5.11) and has its centre of diversity in the Cape (Ch. 6, Fig. 6.9). Criteria for being a Cape clade (*sensu* Linder) are that the clade should have the majority of diversity in the Cape, most of the speciation should have taken place within the last 10 Mya and that it has its origins in the Cape. A sister species outside the Cape is considered desirable as well. The subg. *Hermannia* is a candidate as a Cape clade, although the subsect. *Acicarpus* is a considerable proportion of the subgenus, with much of the speciation of

subject. *Acicarpus* having taken place in Namibia. However, the sect. *Hermannia* appears to comfortably fit the criteria of a Cape clade.

Of the 53 species represented in the phylogeny of sect. *Hermannia*, 42 species occur in the Cape, five species (*H. vestita*, *H. macra*, *H. johansseni*, *H. pfeilii* and *H. onychotenax*) can be considered to be Greater CFR species and two species, *H. bolusii* and *H. bryoniifolia* occur in the Karoo in the Northern Cape beyond the GCFR. Several clades, for instance the "Flammeae", have all their species within the CFR.

In subg. *Mahernia*, the sect. *Pinnatifidae* comprises a yellow and a pink/white flowered clade. All species of the yellow flowered clade occur within the CFR, while the pink/white flowered clade is a combination of CFR (Cedarberg, Klein Karoo) and Greater CFR species (Niewoudtville).

The subsect. *Tomentosae* is entirely from outside the CFR with the exception of the derived species *H. saccifera*.

Within the subsect. *Mahernia*, there are two major clades, the "Coccocarpae" which can be considered primarily a great karoo clade and the remainder of subsect. *Mahernia*. This remainder comprises six groups informally recognised in this study. All of the groups have at least some representatives in the GCFR. The "Heterophyllae" and "Lacerae" have the majority of species in the CFR. The "Pulchellae" and "Candiflorae" have the majority of species within the GCFR. We can thus consider this entire clade which we shall call the "Cape clade of *Mahernia*" to fit Linder's criteria for diversification and timing. However, we shall explore in the chapter on phylogenetic reconstruction whether it has its origin in the Cape and in the diversity chapter, whether it has the majority of diversity in the Cape.

#### **3.4.4 Pollen as a phylogenetically informative character**

The pollen analysis is in broad agreement with the phylogeny produced by molecular analysis. A novel finding is that sect. *Hermannia* has significantly larger pollen than for either subg. *Mahernia* and subsect. *Acicarpus* (this is visible also in the reconstruction of pollen

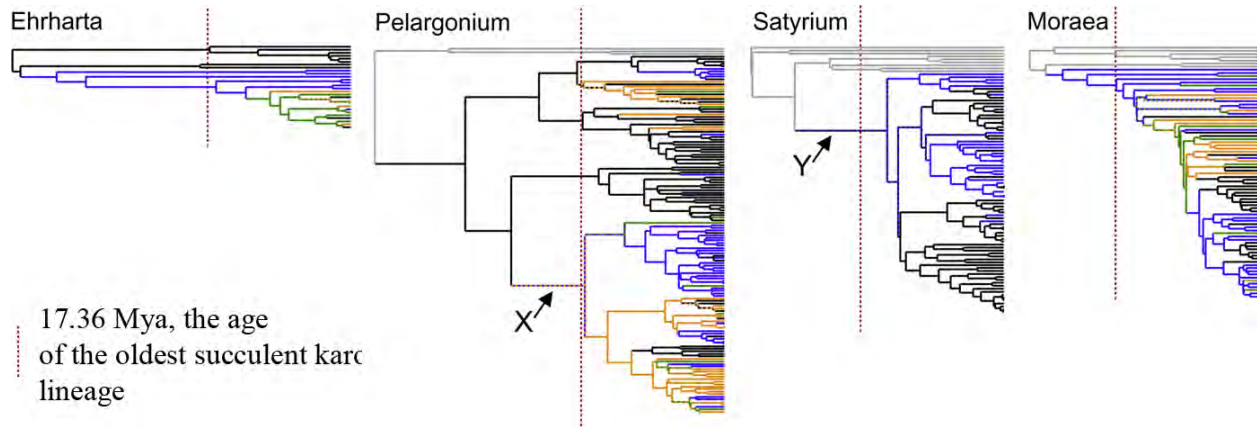
diameter in Ch. 5, Fig. 5.4). *Hermannia parviflora* and the two Drakensberg species, *H. malvifolia* and *H. oligosperma*, are resolved by nrDNA analysis as being within the Cape clade of subg. *Mahernia*, subsect. *Mahernia*. However, the pollen analysis places these species within sect. *Hermannia*. Morphologically the Drakensberg species, *H. malvifolia* and *H. oligosperma* bear floral resemblance to sect. *Hermannia*, thus the pollen morphology is consistent with the floral morphology. The primary character of pollen that is discriminating between these groups is pollen size. As *H. parviflora* and *H. malvifolia* share little in common besides small flowers, it is likely that the flower and pollen size are allometrically linked, i.e. as pollen diameter scales with flower size.

Species of the red-flowered clade “Flammeae” form a loose grouping within the phylogenetic tree (Fig. 5.4) but are undifferentiated from sect. *Hermannia* within the pollen consensus tree (Fig. 3.5). One of the few discrete differences within the pollen is the number of apertures, with the arid species having a greater likelihood of possessing four apertures. Although it may be expected that there is some phylogenetic value to this discrete character, Dajos et al. (1995) found that one-third of all angiosperm families contain genera or species that display pollen aperture polymorphism, with differing aperture number within a single plant being a widespread phenomenon. This explains why species with either three or four apertures are found spread throughout the phylogeny within sect. *Hermannia*. In conclusion, the qualitative pollen characters can be useful in distinguishing sect. *Hermannia* from other groups, but should be used with caution. The pollen data can be misleading, with discrete pollen characters providing insufficiently robust characters that do not adequately reflect phylogenetic processes.

### **3.4.5 Timing of divergences and radiations**

The pattern of diversification of *Hermannia* is similar to that of other groups studied in the CFR (Verboom, Archibald et al. 2009). This pattern shows the greatest similarity in terms of stem node ages with subsequent shallow radiations; this can be seen by comparing Fig. 3.7 for *Hermannia* to Fig. 3.9 for *Erharta*, *Pelargonium*, *Satyrium* and *Moraea*. However, *Pelargonium* has many deeper clades and most radiations tends to take place from closer to 17 Mya, whereas in *Hermannia* the main radiations are in the last 5 Mya. Although dates have now been

established for the diversifications within *Hermannia*, it is uncertain what influences may be associated to these dates. The climatic and edaphic factors are explored next to facilitate a deeper understanding of the processes that may have led to diversification. Dispersal is also discussed in the context of past climatic regimes.



**Fig. 3.9** Patterns of diversification in four selected genera that have mainly radiated within the CFR / GCFR. Beast chronograms have been coloured to reflect biome-reconstructions. Black lines are from outside the GCFR, green is a GCFR endemic, blue is a fynbos endemic and yellow is a succulent karoo endemic. Images modified and reproduced from Verboom et al. (2009) with permission.

### 3.4.5.1 The deeper nodes

A date of  $\pm 60$  Mya was retrieved for the split between *Hermannia* and the Malvoideae. This is markedly different from the date of  $\pm 40$  Mya by Forest et al. (2007). Additionally, the Malvaceae have been found to have the highest crown group diversification rate within the angiosperms and a high stem group diversification rate (Magallon and Castillo 2009). This would have the effect of overestimating the Forest et al. (2007) date, i.e. taking into account increased rate diversification would lead to a date for *Hermannia* of less than 40 Mya. How can this discrepancy be reconciled? Is the true date of the split of *Hermannia* from the remaining Malvaceae closer to 40 Mya, or 60 Mya? As the specified date for the Malvales-Brassicales split is similar, it is assumed that  $\pm 40$  Mya is an artefact of undersampling of the genus *Hermannia* represented by a single unidentified species in the Forest et al. study. This contrasts with this relatively comprehensive dataset and several calibration points with the current analysis, leading to a date of 60 Mya.

The next deepest node at c. 27 Mya distinguishes the Section *Acicarpus* from the remainder of *Hermannia*. This is around the start of the Oligocene (33.7-23.8 Mya), a time when many Cape

Clades started radiating (Linder and Hardy 2005), consistent with the expansion of arid, alpine and grassland biomes (Crisp, Arroyo et al. 2009). The Oligocene environment was dominated by a dry and cool climate, producing extensive regions of sand plains in South Africa (Zachos, Pagani et al. 2001). The late Oligocene (around 25 Mya) resulted in rising sea levels, with warmer and wetter conditions predominating (Tyson and Partridge 2000).

The divergence between subg. *Mahernia* and subg. *Hermannia* is dated to 21.56 Mya. This estimate is close to 22 Mya, the initiation of the Post-African I erosion cycle (Cowling, Proches et al. 2009) and the start of the Miocene (23.8-5.3 Mya). This early Miocene period is characterised by a considerable mixture of habitats and substrata becoming exposed as a result of upliftment. The shales and clay that *Hermannia* currently favours would have been exposed for the first time, with gravels and shallow loamy sands replacing wetlands in the valleys. Fresh quartzite, granite and sandstone were also exposed by the upliftment (Partridge and Maud 2003). The Miocene also heralded the initiation of a hothouse climate, with sea levels reaching around 150m above the current level, flooding much of the coastal plains that had been exposed (Cowling, Proches et al. 2009). The Late Miocene experienced renewed glaciation of Antarctica which led to rapid cooling (Tyson and Partridge 2000) and a drop in sea-level to 35m higher than at present. Importantly, these phases laid down calcareous substrata along the coastal plain (Cowling, Proches et al. 2009). All in all, three major transgressive events have been identified within this period which could have had sufficient impact to lead to a major diversification within *Hermannia*.

#### **3.4.5.2 The shallower nodes**

The Pliocene (5.3-2.6 Mya) and Quarternary (2.6 Mya to present) is when the majority of speciation has taken place. The Pliocene experienced a number of icehouse/hothouse cycles. The start of the Pliocene is earmarked by another massive upheaval in the eastern parts of Southern Africa due to mantle plumes. A rise of nearly 2000m in the east, translated to a lesser lift of 300m in the Eastern Cape and only 150m in the Western Cape. This relatively minor upliftment in the west was sufficient to expose extensive areas of coastal sands that extended till the edge of the coastal shelf some 60km to the west and around 200km to the south. Vast sandy and calcrete

habitats were exposed across the coast. This was coincident with extensive areas of shales (mudstones) and cretaceous sediments (conglomerates) in the lowlands which would have been favoured by early *Hermannia* species. In the Klein Karoo basin, shale ridges and quartz fields would have developed, with granite and inselbergs being exposed along the west-coast. This topographically and edaphically heterogeneous landscape would have been further dissected by this rejuvenating upliftment, producing highly sculptured topography with steep Cape mountains (Cowling, Proches et al. 2009). The increase in suitable lowland habitats separated by mountains, should have provided the ideal habitat for the rapid speciation of *Hermannia* that is visible in the molecular record. Schnitzler (2011) identified that for three out of four major groups studied within the CFR, soil type shifts were the most important cause of speciation. The transgressive phases are thought to have been characterised by strong wind regimes (Shi, Schneider et al. 2001), possibly suitable for the dispersal of some species of *Hermannia* across the landscape and over montane barriers.

Renewed glaciations of Antarctica led to rapid cooling with a resultant drop in sea-level rises during the late-Miocene (Tyson and Partridge 2000). Three transgressive events laid down an accumulation of calcareous substrata, although the sea-level rise was only 35m above present levels (*ibid.*). During the early Pleiocene, dropping sea-levels led to vast areas of coastal sands being exposed - the shoreline retreating up to 200km off the south coast (*ibid.*). The Quarternary (2.6-0 Mya) saw large areas of calcretes deposited along the coast and the leaching of sands creating acid-sand plains (Cowling, Proches et al. 2009). These calcareous and sandy deposits would have provided suitable habitat for the proliferation of the ancestors of the numerous *Hermannia* species that are present on coastal limestones and sand-plains today. The contraction and expansion of these habitats due to rising and lowering sea levels would have led to repeated fragmentation, isolation and expansion of plant populations, providing the right conditions for the speciation of calcareophilous and psammophilous species.

Evidence derived from Namibian sediments suggest that cycles of arid to semi-arid conditions interspersed with moist periods, have characterised the Namib since the Cretaceous around 80 Mya (Ward and Corbett 1990). The onset of the circum-polar current, some 10-15 Mya, is considered to have initiated a cooler and drier climate (Sanderson, Thorne et al. 2004). However,

resulting Mediterranean conditions in the Cape are considered to have only prevailed since the end of the Miocene ( $\pm 5$  Mya) due to the onset of the cold Benguela Current bringing polar waters past the Cape (Verboom, Archibald et al. 2009). The majority of species within the Cape appear to have radiated within the last 20 million years, coinciding with the predominance of these conditions (Verboom, Archibald et al. 2009). Along the West Coast, faunal fossils from Langebaanweg show a general aridification by the late Miocene (5-10 Mya), with a gradual change from forest and woodland to savanna (Hendley 1982). Pollen records of typically Cape taxa (Restionaceae and cf. *Stoebe*) from north of South Africa indicate a northwards expansion of the winter-rainfall vegetation during the last glacial period (Dupont, Behling et al. 2007). Dating of sect. *Hermannia* that encompasses most Cape species and a few Namibian species (Fig. 3.7) shows that most speciation events have taken place in the last 5MY. The onset and subsequent expansion northwards of Mediterranean conditions likely allowed for the dispersal of some members of the sect. *Hermannia* to Namibia, with a few representatives of their progeny surviving there today.

### **3.4.5.3 Vicariance or Dispersal? The non-Cape taxa.**

### **3.4.5.4 Higher level patterns: transcontinental dispersal and generic comparisons.**

The dating analysis (Fig. 3.7), shows a date of  $\pm 14$  Mya for the *H. cristata* - *H. uhligii* split. The second arisal and presumed dispersal of the annuals, *H. modesta* and *H. tigrensis*, is dated to  $\pm 10$  Mya. These dates therefore straddle that of trans-African species of *Indigofera* dated to  $\pm 11$  Mya (Schrire, Lavin et al. 2003), although they significantly pre-date the timing of dispersal of *Androcymbium* into North Africa. Vicariance seems unlikely as the Malvales are estimated as having diverged from the Sapindales some 80Ma, compared with the Proteales at around 140Ma (Wikström, Savolainen et al. 2001). A recent concerted effort at dating the Proteaceae more accurately using multiple fossil calibration points and seven gene regions, portrays the Cape taxa, including the Proteaceae, as wholly radiating within the last 90 million years (Sauquet, Weston et al. 2009). Thus the radiation of *Hermannia* is almost certainly more recent than Proteaceae, which postdates the Gondwanan breakup. The recent focus on molecular dating has demonstrated that the majority of inter-continental distributions are due to relatively recent long-distance dispersal since the Tertiary (Coleman, Liston et al. 2003; Renner 2004; Sanmartin and Ronquist 2004; de Queiroz 2005). The Malphiaceae appear to have dispersed from South



America to North America, through Laurasia, to northern Africa and then southwards into the southern subcontinent (Davis, Bell et al. 2002). The current distribution of *Hermannia* does not rule out this route, though analysis of the evidence favours alternative routes.

#### **3.4.5.5 The arid corridor as a channel for dispersal through Africa**

The presence of an arid corridor that contained distributions of a number of species and genera between south-western Africa (i.e. the Cape or Namibia) and north-eastern Africa via mountains of Eastern Africa has been termed the “arid track” by (Balinsky 1962). The arid-track seems to have been utilized by many taxa including *Zygophyllum* (Bellstedt et al., 2008), the Gnaphalidae (Bergh and Linder, 2008), *Androcymbium* (Hoyo et al., 2009), and multiple other taxa enumerated in Galley (2006) in which radiations appear to have taken place in the last 17 million years. Galley (2006) notes that the Drakensberg has been a stepping-stone for many unidirectional dispersal events from the Cape to tropical Africa. This is apparently not the case in *Hermannia* as the tropical “Marehnia” clade is of closer affinity to *H. cristata* and *H. merxmulleri* than the Drakensberg endemics, *H. malvifolia* and *H. oligosperma*. This accords with the finding of del Hoyo and Pedrola-Monfort (2006) in which *Androcymbium* was considered to have dispersed from Namibia to East Africa along the arid-track  $\pm 4$  Mya during the late Pliocene-Miocene. Levyns (1938 in Cowling, Proches et al. 2009) first proposed a directionality of Cape taxa from north to south, but *Hermannia* appears to have spread in the opposite direction, with *H. cristata* sister to the remainder of sect. *Hermannia*. The timing of the *H. cristata* – *H. uhligii* split coincides with the mid-Miocene expansion of the savanna in West and East Africa. This expansion continues, with the southern and northern tips of Africa becoming increasingly drier during the Pleiocene, leading to the proto-Namib desert (Burgoyne, van Wyk et al. 2005). Morphology of “Marehnia” indicates that most of the Tropical African species in this group are closely related suggesting that at least one dispersal event to this region resulted in significant radiation of species. This pattern of immigration with subsequent radiation is found also in *Pentaschistis* with five species radiating in East Africa (Galley, Bytebier et al. 2007). Galley et al. (2007) also found two larger separate radiations of 8 and 20 species within East Africa for *Disa* after immigration to the area.

The split between *H. uhligii* and the American species is dated at  $\pm 11.8$  Mya. The divergence of the genus *Waltheria* provides an oldest date of  $\pm 20$  Mya between Africa and South America. There are approximately 50 species of *Waltheria* (Saunders 1993), with arguably more than one species of *Waltheria* in Africa (pers. comm. Janice Saunders). Dating other *Waltheria* species in Africa and South America would likely reduce the age of the African-South American disjunction. These trans-continental disjunctions are more recent than the Gondwanan separation ( $\pm 100$  Mya) and thus it is necessary to examine means of dispersal.

#### **3.4.5.6 Patterns of dispersal between continents**

As the cristate capsules of the American species more closely resemble *H. cristata* and *H. merxmuelleri*, than the hornless East African species of *Marehnia*, it is suggested that the progenitor of the American taxa are most closely related to *H. merxmuelleri*, with dispersal around the end-Miocene. The Namibian Brandberg to which *H. merxmuelleri* is an endemic, is well-recognised both in fauna and flora as a taxic refugium (Nordenstam 1974; Burke, Jürgens et al. 1998).

An examination of plant dispersal across the Atlantic by Renner (2004) shows 111 genera that are candidates for intercontinental dispersal. She showed that several possibilities for dispersal exist, most noticeably wind currents and sea currents. Houle (1998) found floating islands largely comprising plant matter as large as 60m x 23m. These rafts have been shown to travel at least 3000km from Africa to North America. Satellite tracked drifters have been found to travel as fast as  $1\text{m}\cdot\text{s}^{-1}$  in the tropical regions (Houle 1999). The continental shelves such as the Rio Grande Rise off the coast of Brazil and the Walvis Ridge west of Africa, may have been exposed as late as the Oligocene, greatly narrowing the distances between the continents (Morley 2000). Westerly wind jets with surface speeds exceeding  $15\text{m}\cdot\text{s}^{-1}$  may be responsible for the transport of seeds between continents.

The vast dune-systems of the Kalahari also indicate substantially greater wind energy in the past than current conditions (Thomas, O'Conner et al. 2000). Four families have been linked to this possible route of aerial dispersal including Malvaceae (Renner 2004). In her conclusion,

Renner (2004) found that the four dated dispersals from America to Africa involved wind, whereas the contrasting studies from Africa to America all involved sea-currents. Molecular clock-based divergence times for sister clades that occur on both sides of the Atlantic suggest transoceanic dispersal during the Oligocene and Miocene (Renner 2005).

Mounting molecular evidence across a range of families occurring in the Cape, points to a decreasing likelihood of trans-Atlantic vicariance in favour of dispersal (Forest, Grenyer et al. 2007; Sauquet, Weston et al. 2009; Verboom, Archibald et al. 2009). Direct observations of long-distance plant dispersal events to islands (other than by oceanic-drift) are almost impossible to make (Carlquist 1967). Carlquist (1967) found that a “small but appreciable” proportion of plant arrivals to oceanic islands could be traced to seed that were transported in the feathers and on the feet of birds.

The seed of *Hermannia* has no particular adaptation to water or wind and is thus largely unsuited to free long-distance dispersal, therefore the alternative hypothesis of transoceanic avine transport from the west-coast of Africa to America is deemed more likely.

#### **3.4.5.7 An Australian dispersal**

The divergence for the Australian species, *H. biniflora* is dated to  $\pm 3.8$  Mya. This is a relatively recent dispersal compared with the American divergence. This perhaps explains its similarity to extant species from the African subcontinent, particularly *H. erodioides*. As the entire radiation within subsect. *Mahernia* dates to less than 5MY and *H. biniflora* is embedded within an otherwise Southern African clade, the dated phylogeny provides clear evidence of a transcontinental dispersal event from Africa to Australia.

#### **3.4.5.8 The Drakensberg as a refugium**

The species of “*Marehnia*” currently extant in North, West and East Africa could either be descendants of a proto-clade that dispersed into Southern Africa, a dispersal from Southern Africa northwards, or a splitting of a once widespread distribution of the genus from North to South Africa. The north-east region including the Horn of Africa has long-been deemed a

refugium for arid taxa of various ages (Schrire, Lavin et al. 2003) and is considered to be of considerable age (Jürgens 1997). DIVA analysis indicates unidirectional dispersal of four families from the Cape through to the Drakensberg (Galley, Bytebier et al. 2007). Two of these families are represented in East Africa and South Central Africa where optimization of the ancestral area [Ch. 5] indicated a northwards migration from the Cape or Drakensberg.

The outliers of the Cape clade from the Drakensberg, *H. malvifolia* and *H. oligosperma* are shown to have diverged from the Cape ancestors some 4.5 Mya. This is similar to the age obtained by Moore et al. (2010) for their Drakensberg species of *Thesium*. The Drakensberg is a known high-altitude refugium for Cape elements (Carbutt and Edwards 2001; Clark, Barker et al. 2007; Galley, Bytebier et al. 2007). The proposed mechanism for the survival of these two species of the Cape clade is that lower temperatures at around 3000m retard nutrient uptake, soils thereby effectively becoming as if nutrient-poor (Carbutt and Edwards 2001). It is the pre-adaptation to a nutrient poor environment, in combination with phylogenetic constraint that has been demonstrated to work at a biome level (Crisp, Arroyo et al. 2009), that likely explains the presence of these two Cape clade species in the Drakensberg. In a study by Galley et al. (2007), four clades in different families were examined for dispersal direction. An overwhelming directionality was found for species dispersal from the Cape to the Drakensberg, with only two *Disa* species (4%) being inferred as having a migration from the Drakensberg to the Cape.

### 3.5 Conclusion

The results of both Bayesian and parsimony molecular analysis support a reclassification of *Hermannia*, which forms a monophyletic group and includes the American taxa and Australian species formerly known as *Gilesia biniflora*. The primary distinguishing characters between the two subgenera *Hermannia* and *Mahernia* is the expansion of the filament below the anther, filament texture; capsule shape and pollen size. Although largely consistent, these characters appear insufficient to bisect an otherwise wholly recognisable genus. Engler's (1900) four subgenera cannot be recognised at that level, though his concepts were sound. Molecular analysis of ITS provides strong support for the recognition of subg. *Mahernia*, as proposed by Engler (1900), but his subgenera need to be recognised at a subsectional level to accommodate

the new phylogeny. No other characters examined such as habit, woodiness, trichome complement and flower colour, are diagnostic at subgeneric or sectional level.

Integration of morphological data was not able to improve the quality of the phylogeny, due to limitations in the available data. Nevertheless, interpretation of the phylogeny in view of known morphological features, as outlined in the Discussion, indicates that the phylogeny produced from molecular data alone reconciles well with both morphological and geographical features of the species making up the newly defined clades. Strong quantitative (albeit indirect) support for the phylogeny from reconstruction of characters will be provided in Ch. 5.

## **4. Towards a phylogenetically informed taxonomic framework of *Hermannia*, with biogeographic and associated climatic implications.**

### **4.1 Introduction**

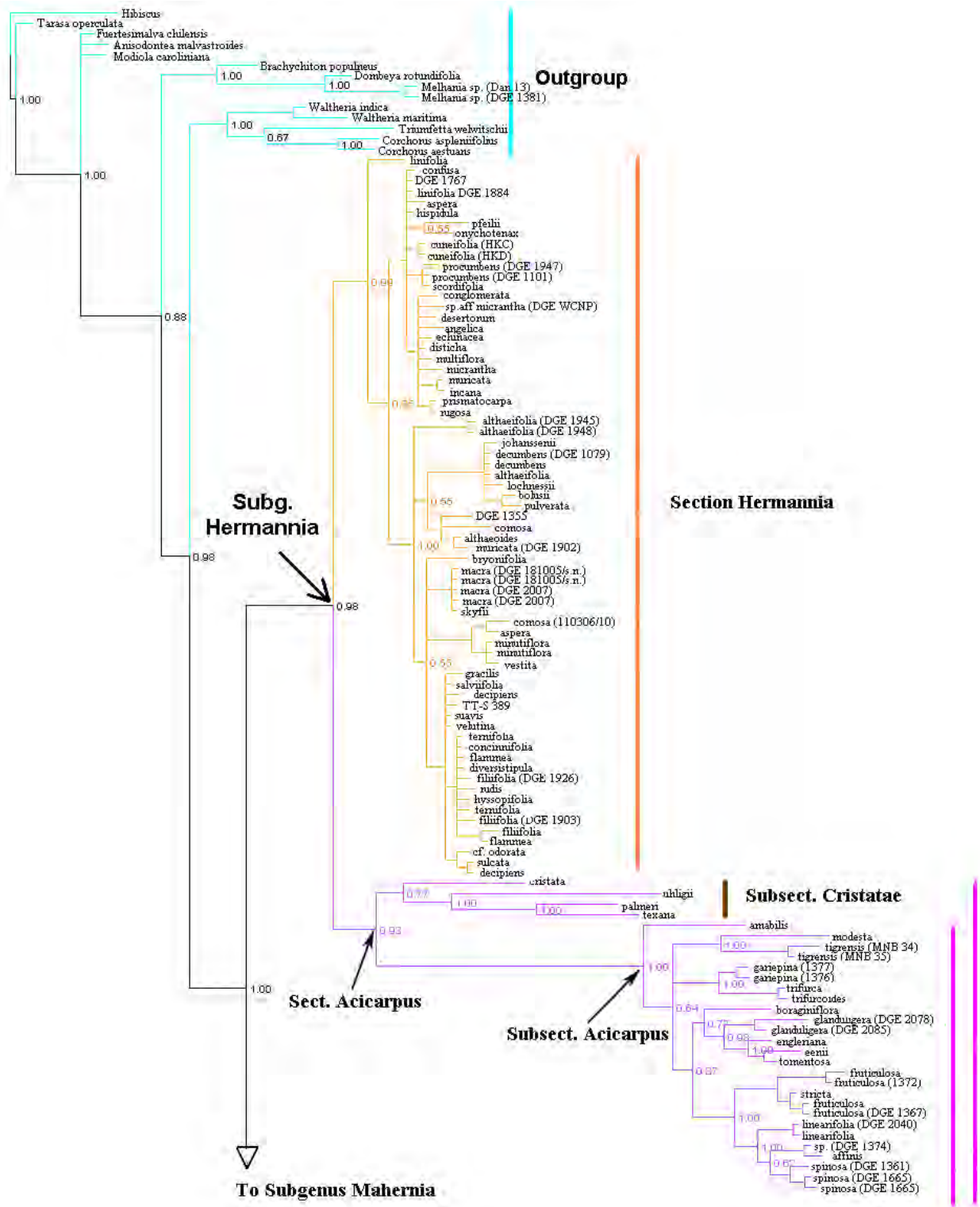
The previous chapter explored the phylogeny of *Hermannia* and demonstrated that the genus is divisible into a number of robustly supported groups. This chapter utilizes the phylogeny to separate *Hermannia* into hierarchically and phylogenetically structured groups [Ch. 3]. A number of co-ordinate levels are here formally adopted or erected from subgeneric to subsectional level. This and the synonymy of previous systems has been formalized in the paragraph below Fig. 4.1. Distribution maps are then shown of species organised into these groups, revealing the association between spatial distribution and relatedness of species. As the species composition of the higher level clades is necessarily opaque (one cannot adequately view both an overview and detail at the same time on a static page), distribution maps of lower level groups including informal groups are provided. Where distributions are deemed particularly nested, or distributional outliers noted, a Köppen-Geiger climatic map is used to explore the climatic tolerances of each species and the group in which it occurs. This is used to identify the relationship between the species relatedness, distributional patterns and climatic zones. This theme is taken up again in the final chapter, in which phytochoria and climatic influences are considered.

#### 4.1.1 *Hermannia* and *Mahernia*: generic vs. subgeneric rank.

As discussed in the previous chapter, *Hermannia* and *Mahernia* have been recognised at subgeneric rather than generic level for the following reasons:

- 1) *Hermannia* including *Mahernia* is easily recognisable as a whole and is united by a number of characters such as stamens opposite the petals, small pendulous flowers typically with whorled petals and capsules containing many seeds.
- 2) The distinguishing features between *Hermannia* and *Mahernia*, i.e. the position of the expanded portion of the filament, cannot be discerned in those species that have linear or nearly linear filaments. This includes *H. biniflora* in subg. *Mahernia* and several species in subg. *Hermannia*.
- 3) This distinguishing feature appears to have two contradictions: *H. waltherioides* has a filament typical of *Mahernia*, but otherwise fits the description of a typical species of *Hermannia* within subg. *Hermannia*; *Hermannia stricta* has filaments that resemble a *Mahernia*, but the capsules and molecular characters unequivocally place it within subg. *Hermannia*. Thus there is no absolute character separating the two subgenera.
- 4) I have examined approximately 100 species of *Hermannia* and have found that a fleshy versus membranous filament always distinguishes between *Hermannia* and *Mahernia*. However, neither all the species, or even all the major groups have been sampled for this character yet. Thus the robustness of this character is still in question. This character also requires floral dissection and is difficult to discern on desiccated specimens. It is therefore practically inconvenient.

I would therefore hesitate to split *Hermannia* and *Mahernia* into separate genera unless there is a better rationale to do so.





To subgenus *Hermannia*

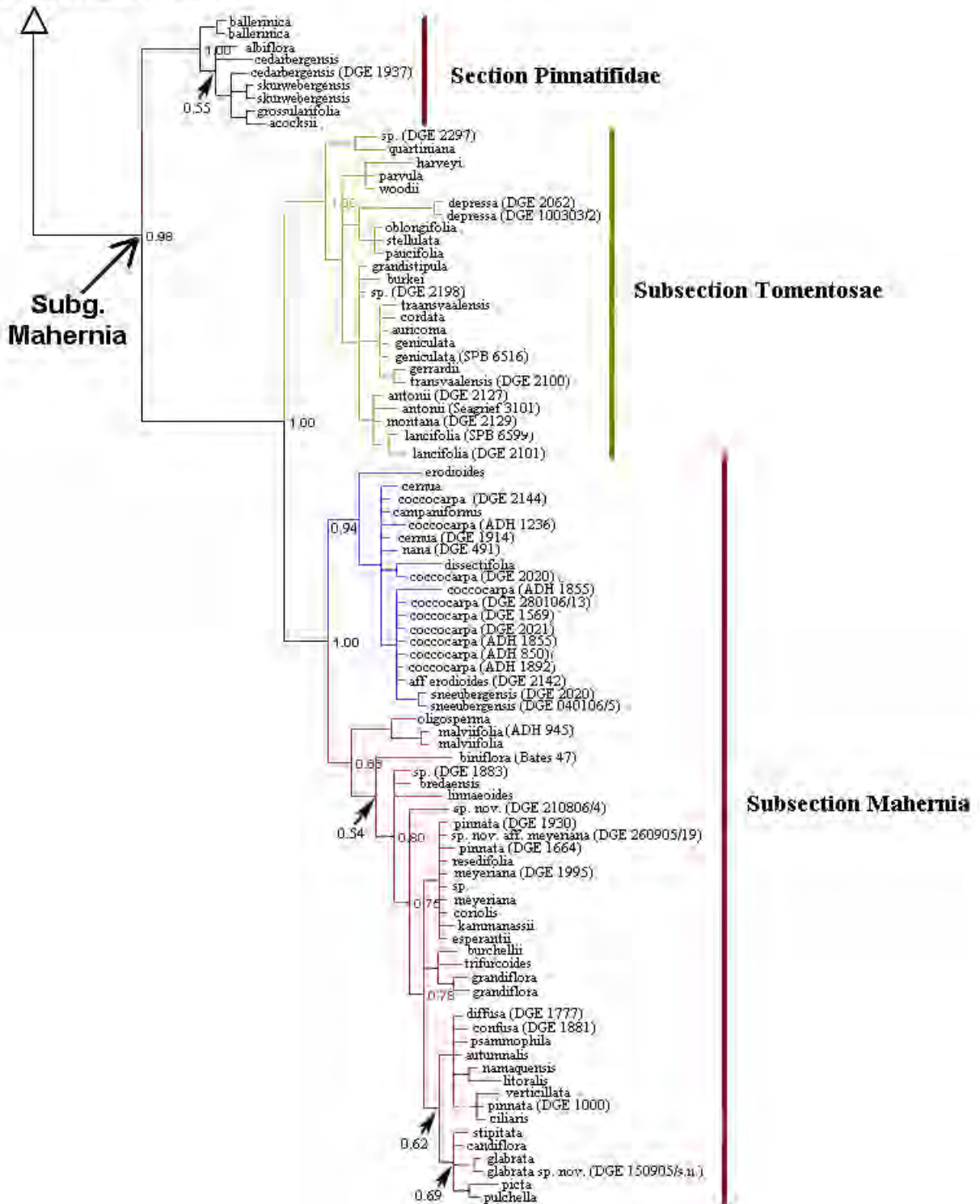


Fig. 4.1 A repeat of Fig. 3.1 as a quick reference for the supra-specific taxonomic treatment (below), showing the revised generic and infrageneric classification of *Hermannia*.

#### 4.1.2 Maps depicting taxonomic groups and their component species.

To contextualize the distribution maps, we can consider a set of hypotheses:

**H<sub>0</sub> μ = species are evenly or randomly spread within the potential species space.**

i.e. species are not constrained by dispersal and have had sufficient time to adapt to a broad range of environmental conditions and are therefore evenly spread throughout the “potential species space”.

**H<sub>1</sub> μ = species are unevenly spread or clustered throughout the potential species space.**

i.e. species are constrained by dispersability and phylogenetic conservatism / momentum and thus are spread unevenly throughout the “potential species space”.

The “potential species space” is here defined as that area which any species of *Hermannia* could potentially occupy given the range of environmental and spatial variability occupied by the genus. The PSS is confined to a portion of southern Africa with closely contiguous distribution points and thus excludes the somewhat disjunct tropical species, the north American species and the Australian species.



**Fig. 4.2** Known distribution of *Hermannia*, with the outline representing the “potential species space” that any species of *Hermannia* can occupy given the genetic variation and adaptability within the genus.

The null hypothesis implies that species are spread evenly / randomly throughout the potential range of *Hermannia*. Due to factors such as competition from other species, barriers to dispersal, extreme variation in climate within Southern Africa between desert and tropical

conditions, and summer- and winter-rainfall, it is absurd that any one species should occupy this total space. This chapter highlights how distributions within a clade differ from the null hypothesis and that any deviation from the null hypothesis is due to a combination of a) limitations of dispersal; b) a limited climatic envelope that does not allow a species to extend beyond its existing distribution; c) geological or edaphic constraints; and d) catastrophes that wipe out entire species or geographic portions of a species. These catastrophes may be current or historical, be of a long-term or short-term duration, and of a man-made or natural nature. The following chapter explores the alternative hypothesis, and the factors that appear to limit each clade from expanding across the full “potential species space”. Subsequent chapters explore different components of these factors.

### 4.1.3 Limits of the “potential species range”

The “potential species range” of Fig. 4.2. only represents a proportion of the total distribution and excludes much of tropical Africa, the Middle East, America and Australia. Distribution records within the Middle East are few and the localities have not been located. The map of tropical Africa is separately presented in Fig. 4.2; and Australia in Fig. 4.35. It is highly likely that the extent of the contiguous portion of the “potential species range” could be expanded by collecting in undercollected areas such as Angola and Zambia and by documenting herbarium specimens from those countries. As “*Marehnia*” is a distinct clade, it may also better represent the real distribution of subg. *Mahernia* and sect. *Hermannia* to contract the “potential species range” to exclude this northern section, cutting it at the northern point of Mozambique. The “potential species range” also treats the northern extent of members of the sect. *Acicarpus* as outliers and thus does not take into account those species that occur sporadically north of Malawi.

Distributional Endemicity (DE) has a number of caveats that prevent rigorous statistical analysis. A hypothetical example is presented (Fig. 4.3) to better illustrate the implications of species distributions. Three different scenarios that highlight different aspects of distribution accompany this example. What is being examined is not simply a matter of area, but also of climate type. This makes the areas qualitatively different, which makes comparisons between

areas more interesting and meaningful, as it is not simply a matter of dispersal to a different area, but of the species being pre-adapted or adapting to a different climate as well.

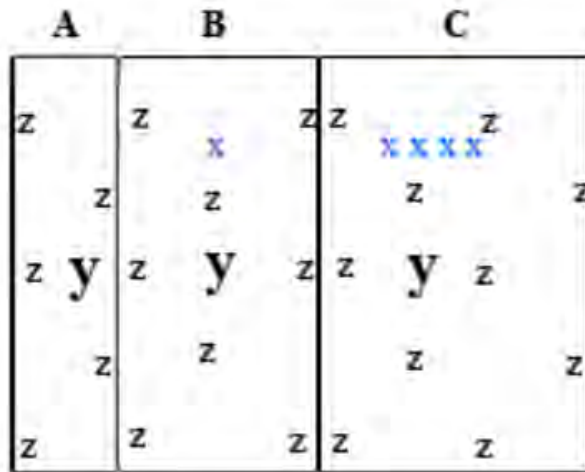


Fig. 4.3 Hypothetical model of species (x, y and z) distribution across three areas (A, B, C).

Initially and throughout this chapter I have simply stated the Association of Distribution to Climate (ADC) as a percentage for each. For instance, in scenario 1, species 'x' has an ADC to area A, B and C of 0%, 75% and 25% respectively. This assumes that these occurrences are actual occurrences rather than based on collecting effort. These measures show that the majority of species x is found in area C and does not occur at all in area A. If A, B & C were simply areas, we would infer that species x has most of its distribution in C and for unknown reasons hasn't occupied A. However, because they are climatic types, we can infer that it is likely that area B is the most suitable for this species, area C less so and that area A is wholly unsuitable. If this scenario was an actual example of a broad scale map that has been plotted for the world and shows a climate model, then the boundaries are not hard, but would gradually merge from one climate type to the next. Thus distributions appearing close to the border in one climatic type, could be occurring on an adjacent climatic type that is too fine for the model to represent, the model may have the boundary in the incorrect place, or the species may have a slightly greater climatic envelope than that given by the boundaries of the climate type.

In scenario 2, species Z is evenly distributed across the landscape to demonstrate area effects. From a simple value such as DE, one finds ADC is  $5/23 = 21.74\%$  for area A;  $8/23 =$

34.78% for area B; and  $10/23 = 43.47\%$  for area C. So despite the fact that they all have the same density, Area A appears to have a lower endemism than Area C because it is smaller and thus can fit in less individuals of species Z. If area A has an area of 1 of a total area of 6 i.e.  $1/6$ th, area B an area of  $2/6$ th and area C an area of  $3/6$ th, then dividing the ADC by  $1/6$ th,  $2/6$ th and  $3/6$ th for area A, B and C respectively gives us an average ADC (ADE) for: area A of  $21.74/1/6=3.62$ ; area B of  $34.78/2/6=2.90$ ; and area C has a value of 2.42. Thus area A has the highest average endemism because it has a greater proportion of species for the area. A shift of only a few millimetres to the left in the set of points in the model of area A would exclude more than half the points. Producing an example with a higher density of distribution in this example would minimize this kind of error.

Adapting scenario 1 with the area as found in scenario 2, the ADE of species  $\underline{x}$  is  $0/1/6 = 0$ ;  $75/2/6 = 6.25$ ; and  $25/3/6 = 1.38$ . However, unlike the population of species  $\underline{z}$  in the previous example, species  $\underline{x}$  is not evenly spread, only occupies a fraction of area B and fits into area C. It does not make sense to penalize the ADC of  $\underline{x}$  for area B based on its full size, when only a small portion of it is being occupied. Additionally there is a logical dilemma when calculating ADC as to whether to take into account area A because it could occur there (i.e. area B would be penalized  $2/6$ ), or to only take into account the areas in which it is actually found (i.e. a penalty of  $2/5$ )? This illustrates the point of the PSS, which seeks to limit the total search area of extent.

There is a final complicating factor. In scenario 3, species Y has an equal ADC (33.3%) for all areas. However if we were to derive an ADE for each area, we would get values of  $33.3/1/6 = 5.55$ ;  $33.3/2/6 = 2.76$ ; and  $33.3/3/6 = 1.85$  for area A, B and C respectively. Penalizing area C for being larger would give it an endemism value nearly  $1/3^{\text{rd}}$  that of area A, yet there is no difference in concentration of species  $\underline{y}$  between these areas.

The conclusion from this model, is that there is very little that can be derived from endemism without rigorous sampling and methodology, other than a simple proportionality (DE) between one climate type and the next. Also because of differing collecting intensities in which one species is more frequently collected than the next because it is more striking, it is difficult to compare between species. The number of collections within a quarter degree square is also not

taken into account, which may provide a truer sense of a species presence in the landscape, or may simply reflect collecting intensity. Additionally, because each discrete area represents a different climate, one climate may be more difficult to access or less desirable as a botanical destination and hence the sampling of species between areas could be very different.

#### 4.1.4 Climatic map for comparisons

Several broad vegetation/climatic maps were investigated for their ability to represent the broad vegetation and climate across Africa, in order to assess the distributions of tropical African species. The Weimarck (1941) map that was utilized by Linder(2001) in a study that sought patterns within sub-Saharan African flora was found to have relatively low explanatory power and to be too coarse. The Köppen-Geiger vegetation scheme ((Peel, Finlayson et al. 2007) was ultimately chosen despite various criticisms, as it: covers the whole of Africa; has proven robust as a research and teaching tool since 1923; has been found to link to natural vegetation patterns; has been updated in the last decade; utilizes modelling based on precipitation and temperature; and was found in several studies to perform adequately in relation to more complex global climate models (Peel, Finlayson et al. 2007). Three dominant climate types (A, B & C) are present in Africa (Fig. 4.4). By proportion of total land area, they are arid B (57.2%); tropical A (31.0%); and temperate C (11.8%).



**Fig. 4.4** The climate types in Africa. Categorised into tropical (A); arid (B); and temperate (C). Af = Tropical rainforest climate; Am = Tropical monsoon climate; Aw = Tropical savanna climate; BWh = Hot desert climate; BWk = Cold desert climate; BSh = Hot semi-arid climate; BSk = Cold semi-arid climate; Csa = Hot-summer Mediterranean climate; Csb = Warm-summer Mediterranean climate; Cwa = Humid subtropical climate; Cwb = Subtropical highland climate; Cfa = Humid subtropical climate; Cfb = Oceanic climate.

## 4.2 Methods

The maps are derived from all  $\pm 17,000$  georeferenced African herbarium records. The species have been selected and depicted using DivaGIS v5.2 (Hijmans, Guarino et al. 2004). Symbols utilized in the maps have been chosen to maximize the visibility of overlapping species, generally with the symbol corresponding to the first letter of the species name. This facilitates more rapid determination of the species compared with traditional symbols

As Southern African herbaria had few records of tropical African species, a query was run on the African Plants database (2013) to generate distribution maps of these species ([www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php](http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php)). This database mostly comprises georeferenced points based on statements of locality in taxonomic literature. The images of these maps were opened with Photoshop 6.0 and scaled to closely fit over a map showing the updated Köppen-Geiger climatic zones (Peel, Finlayson et al. 2007). A new blank layer was created and dots made using the brush tool to create neat circles representing the species occurrences. For the species with more than c. 20 data points, a different technique was required to isolate the points. As the original distributional dots were red, the green channel was selected rendering black dots on a lighter grey background. A new layer was created from a full colour layer and adjustments made to the levels of the highlights till only the red dots and some of the boundaries were visible. The noise and features not germane to the distribution points were cleaned up using the eraser tool. Layers could then be hidden or shown to highlight the distribution of certain species and combinations of species.

To determine which vegetation types were best representing the different tropical African species, the points were visually assigned to underlying vegetation types based on the Köppen-Geiger vegetation scheme. The distribution map was placed using Photoshop as a separate layer, the opacity changed to ‘\_multiply’ and the layer scaled to match the underlying map. Where some overlap occurred between two vegetation types, the point was assigned to the greater vegetation type. Where it lay halfway between the two points, the point was assigned to both vegetation types. Where map points were too dense to be discerned, the number of points was estimated based on the size and density of the area.

To test the association of a species with a habitat, the species occurrence within a vegetation type was counted and assigned to a vegetation type using the method above. These were then entered into a table to assign relative percentage occurrences within each climatic type. However, because the surface area of each vegetation type is different, there is a greater chance of a species falling into a larger surface area. The percentage of surface area for each climatic type was therefore determined by using a modified method of user Hellick

([http://conworld.wikia.com/wiki/User:Hellerick/How\\_to\\_calculate\\_map\\_area\\_in\\_Photoshop](http://conworld.wikia.com/wiki/User:Hellerick/How_to_calculate_map_area_in_Photoshop) ).

Each portion of land was selected using the magic wand tool with a threshold of 55. This was pasted to a new layer. The layer was then converted to pure black by adjusting the image threshold to 255. The image was flattened and Filter>Blur>Average used to create a uniform colour (Col). The eyedropper tool was then used to obtain the average colour value. The total area as a proportion of image size was calculated by the formula:

$$\text{Area of climatic type} = \text{image L} \times \text{image W} \times (255 - \text{Col}) \div 255$$

ADC – Association of Distribution to Climate - is defined here as the number of quarter degree square (QDS) records for a species that are confined to a particular climate type or set of climate types and is expressed along with the climatic type as a percentage. If expressed as  $ADC = x/y = z\%$ , then x is the number of distribution QDS that are endemic, y the total number of QDS for that species or set of species and Z the proportion. As the distribution records are extracted from herbarium records and literature, the distribution is not rigorously sampled across the landscape, so cannot be realistically analysed statistically. Additionally it is simply a presence measure for a QDS and does not include number of collections per locality. i.e. an ADC of 25% for hot-arid climatic type means that 25% of the distributional QDS records for that species are found in the hot-arid climatic type.

**Quarter Degree Square – QDS**

	X°	15"	30"	45"	X+1°
Y°	AA	AB	BA	BB	
15"	AC	AD	BC	BD	
30"	CA	CB	DA	DB	
45"	CC	CD	DC	DD	
Y+1°					

In the geographical QDS system illustrated above, each degree of latitude and longitude can be divided into 16 squares. Although the north-south distance of a cell varies on the latitude, within South Africa cells cover an area of around 25 × 25km long.



## 4.3 Results

### 4.3.1 A proposed supra-specific taxonomic treatment for *Hermannia*

A taxonomic framework is provided here in which the placement of species within ranks from subgeneric to subsectional level are formalized. In some cases, informal groups are proposed, these names appearing in inverted commas eg. –*Marehnia*”. These informal groups are based on morphological observation of the species, their distribution and informed, where resolution allows it, by the molecular phylogeny. A future more comprehensive phylogeny and improved analysis of characters should allow for the formal erection of species groups at series and subseries rank. Currently there is little resolution in the phylogeny of sect. *Hermannia* and subsect. *Acicarpus*. Erection of groups have only been made where significant morphological knowledge is available. Taxa upheld by the author are written in bold. Subsequent taxa not in bold are considered synonyms. Informal groups or taxa at unspecified ranks are enclosed by inverted commas. Here follows the proposed taxonomy.

***Hermannia*** L. Sp. pl.: 673 (1753); Fl. Cap. ed. Schultes: 501 (1823); Genera Plantarum ed. 5 (1754); Benth. & Hook., Gen. pl. 1: 223 (1862-7); Harv., Gen. S.A. Pl. 1: 32 (1838); Type species: *H. hyssopifolia* L., lectotypified by M.L. Green in Prop. Brit. Bot.: 172 (1929).

*Mahernia* L. Mant. Pl. 8 & 59 (1767). Type species: *M. verticillata* L. = *H. verticillata* (L.) Hochr. [This mantissa is a combined book of genera and species, with *Mahernia* on p. 8 of genera, with *M. verticillata* on p. 59 of species].

Subg. ***Hermannia*** – K. Schum. In Engl. Monogr. Afr. Pflanzfam. V.: 53 (1900); Verd. In Bothalia 13, 1&2: 1-63 (1980). Type: *Hermannia alnifolia* L., here designated.

Subg. *Euhermannia* Harv. in Flor. Cap. 1: 180 (1860).

Subg. *Acicarpus* Harv. in Flor. Cap. 1: 205 (1860).

Subg. *Marehnia* K. Schum., Stercul. Afr. in Engl. Monogr. Afr. Pflzfam. V.: 49 (1900).

Sect. *Marehnia* K. Schum. —as*Mahrenia*”, in Engl. Monogr. Afr. Pflzfam. V.: 354 (1919).

–Group” *Althaeoideae* Harv. in Flor. Cap. 1: 184 (1860).

*Cristatae* Engl. in Engl. Bot. Jahrb. 55: 362 (1919).

–Group” *Cuneifoliae* Harv. in Flor. Cap. 1: 188 (1860).

*Exstipulatae* Engl. in Engl. Bot. Jahrb. 55: 361 (1919).

–Group” *Flammeae* Harv. in Flor. Cap. 1: 194 (1860).

–Group” *Glomeratae* Harv. in Flor. Cap. 1: 192 (1860).

–Group” *Lateriflorae* Harv. in Flor. Cap. 1: 200 (1860).  
*Parvipetalae* Engl. in Engl. Bot. Jahrb. 55: 362 (1919).  
*Patellicalyces* Engl. in Engl. Bot. Jahrb. 55: 358 (1919).  
–Group” *Pinnatifidae* Harv. in Flor. Cap. 1: 203 (1860).  
–Group” *Scaberrimae* Harv. in Flor. Cap. 1: 190 (1860).  
–Group” *Velutinae* Harv. in Flor. Cap. 1: 197 (1860).  
Tribe *Hermannieae* Engl. Die Planz. Ost-Afr. und der Nachb.: 270 (1895).  
Sect. *Euhermannia* Harv. Die Planz. Ost-Afr. und der Nachb.: 270 (1895).  
Sect. *Acicarpus* Harv. Die Planz. Ost-Afr. und der Nachb.: 270 (1895).

Sect. ***Hermannia*** – K. Schum Stercul. Afr. in Engl. Monogr. Afr. Pflzfam. V.: 53 (1900).  
Type as for subg. *Hermannia*.

Subg. *Hermannia* K. Schum. Stercul. Afr. in Engl. Monogr. Afr. Pflzfam. V.:53 (1900).  
Sect. *Hermannella* DC. Prod. Syst. Nat. 1: 494 (1824).  
Sect. *Trionella* DC. Prod. Syst. Nat. 1: 493 (1824).

**Sect. *Acicarpus*** (Harv.) Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 364 (1919). Lectotype species: *H. trifurca* L., here designated.

Subg. *Acicarpus* Harv. in Flor. Cap. 1: 205 (1860).  
Sect. *Scaphiostemon* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 363 (1919).

Subsect. ***Acicarpus*** (Harv.) Gwynn., **stat. nov.** Type as for sect. *Acicarpus*.

Subg. *Acicarpus* Harv. in Flor. Cap. 1: 205 (1860).  
Series *Brachypetalae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 369 (1919).  
Series *Fruticulosae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 366 (1919).  
Series *Garipeianae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 364 (1919).  
Series *Helianthemifoliae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 364 (1919).  
Series *Macropetalae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 364 (1919).  
Series *Modestae* Engl. Stercul. Afr. VI. in Engl. Jahrb. 55: 367 (1919).

Subsect. ***Cristatae*** (Engl.) Gwynn., **stat. nov.** Lectotype species: *H. cristata* Bol., here designated.

*Cristatae* Engl. in Engl. Bot. Jahrb. 55: 362 (1919).  
Sect. *Marehnia* (K. Schum.) K. Schum. Stercul. Afr. VI. in Engl. Jahrb. 55: 354 (1919).  
*Waltherioideae* Engl. in Pflanzenwelt Afrikas 3,2: 433 (1921).

Subg. ***Mahernia*** K. Schum In Engl. Monogr. Afr. Pflzfam.: 61 (1900); L.f. Mant. Pl. 8: 59 (1767). Type species: *H. pinnata* L.

Sect. *Mahernia* – K. Schum. Stercul. Afr. VI. in Engl. Jahrb. 55: 372 (1919). Type as for subg. *Mahernia*.

–Group” *Dentatae* Harv. in Flor. Cap. 1: 215 (1860).

–Group” *Lacerifoliae* Harv. in Flor. Cap. 1: 213 (1860).

–Group” *Verticillatae* Harv. in Flor. Cap. 1: 209 (1860).

Subsect. *Mahernia* Gwynn., **subsect. nov.** Type as for subg. *Mahernia*.

Subsect. *Tomentosae* (Harv.) Gwynn., **stat. nov.** Lectotype species: *H. lancifolia* Szyszyl., here designated.

–Group” *Tomentosae* Harv. in Flor. Cap. 1: 218 (1860).

Sect. *Pinnatifidae* (Harv.) Gwynn. Lectotype species: *H. grossularifolia* L., here designated.

–Group” *Pinnatifidae* Harv. in Flor. Cap. 1: 203 (1860).

Subsect. *Grossularifolia*

Subsect. *Cedarbergensis* Gwynn.

### 4.3.2 Classification of the species of *Hermannia*

As above, groups in bold are those I have formally recognised. Inverted commas indicate informal groups that due to being unresolved in the phylogeny, have no taxonomic status nor rank. I choose to recognise these as potential groups based on morphology and biogeography.

An asterisk denotes that it is a new and as yet unpublished species.

A + indicates a species from the Cape Floristic Region (>115 spp.).

A ⌋ indicates a species from the Greater Cape Floristic Region.

Here follows the list of names.

**subg. Mahernia** K. Schum.

**sect. Pinnatifidae** (Harv.) Gwynn.

**subsect. Grossularifolia**

- \* *acocksii* De Winter ex. Gwynn. +  
*grossularifolia* L. +
- \* *grossularoides* Gwynn. +
- \* *hanselandgretelia* Gwynn. +
- \* *lanterna* Gwynn. +
- \* *waltonii* Gwynn. +

**subsect. Cedarbergensis**

- \* *albiflora* De Winter ex. Gwynn. +
- \* *ballerinica* Gwynn. +
- \* *cedarbergensis* De Winter ex. Gwynn. +  
*sisymbriifolia* (Turcz.) Hochr. +
- \* *virgata* Gwynn. +

**sect. Mahernia** (L.) K. Schum.

**subsect. Tomentosae** (Harv.) Gwynn.

“Sinensis”

- \* *crassifolia* Gwynn.  
*depressa* N.E.Br.  
*grosseserrata* Schinz  
*harveyi* K. Schum. +
- \* *molina* Gwynn. +
- \* *mortifera* Gwynn. +  
*parviflora* (Eckl. & Zeyh.) K. Schum.  
*parvula* Burt Davy  
*rautananii* Schinz ex K. Schum.  
*saccifera* K. Schum. +  
*schlechteriana* Schinz ex K. Schum.  
*veronicifolia* K. Schum.  
*woodii* Schinz

“Stellulatae”

- adenotricha* K. Schum.  
*grosseserrata* Schinz  
*oblongifolia* Harv.  
*quartiniana* A.Rich.  
*stellulata* (Harv.) K. Schum.

“Grandifoliae”

- auricoma* (Szyszyl) K. Schum.  
*burkei* Burt Davy  
*cordata* (E. Mey. ex Phillips) De Winter
- \* *ichthyoskeletos* Gwynn.  
*geniculata* Eckl. & Zeyh.  
*gerrardii* Harv.  
*grandifolia* N.E.Br.

*grandistipula* (Buching.) K. Schum.

- \* *middelburgensis* De Winter ex. Gwynn.
- \* *porcumen* Gwynn.  
*sinuata* Burt Davy  
*transvaalensis* Schinz

“lancifolia”

- antonii* Verdoorn  
*brachymalla* K. Schum.  
*lancifolia* Szyszyl.  
*montana* N.E.Br.  
*rogersii* Burt Davy  
*staurostemon* K. Schum.
- \* *triumfettifolia* Gwynn.
- \* *verdoorniae* De Winter ex. Gwynn.

**subsect. Mahernia** Gwynn.

“Coccocarpace”

- \* *atrofulminalis* Gwynn. +
- \* *azurea* Gwynn. & van den Berg
- \* *biniflora* (F. Muell.) Gwynn.  
*cernua* Thunb. |  
*coccocarpa* Kuntze
- \* *cyanellus* Gwynn. |
- \* *deus* Gwynn. +
- \* *dissectifolia* De Winter ex. Gwynn.  
*erodioides* (Burch. ex DC.) Kuntze  
*nana* (Eckl. & Zeyh.) Hochr. +
- \* *octopussyae* Gwynn. +
- \* *sneeubergensis* Gwynn.  
*violacea* (Burch.) K. Schum.

“Drakensberg”

- malvifolia* N.E.Br.  
*oligosperma* K. Schum.  
*umbratica* Verdoorn
- \* *umbraticoides* Gwynn.

“Calcareophilae”

- argillicola* Dinter ex Holz.
- \* *bredaensis* De Winter ex. Gwynn. +  
*linnaeoides* (Burch.) K. Schum.  
*linnaeopsis* Dinter & Engl.

“Grandiflorae”

- burchellii* (Sweet) Verdoorn  
*elliottiana* (Harv.) K. Schum  
*grandiflora* Ait.
- \* *supernova* Gwynn.

“Heterophyllae”

- \* *abbreviata* Gwynn.
- \* *abutiloides* Gwynn.
- \* *adamas* Gwynn.
- \* *anisodontii* Gwynn. +
- \* *angustibracteata* De Winter ex. Gwynn. +
- \* *bredaensis* De Winter +
- \* *dichroma* Salter +
- \* *heterophylla* (Cav.) Thunb. +
- \* *humifusa* (Eckl. & Zeyh.) Hochr. +
- \* *humilis* Thunb. +
- \* *larustipularis* Gwynn.
- \* *pinnata* L. +
- \* *psammophila* Gwynn. +
- \* *rocherpanensis* Gwynn. +
- \* *ruskiflora* Gwynn. +
- \* *odoratissima* Gwynn.

“Pulchellae”

- \* *aramontana* Gwynn.
- \* *diffusa* L.f. +
- \* *dinkyflora* Gwynn. +
- \* *glabripedicellata* De Winter ex. Gwynn. +
- \* *leucantha* Schltr.
- \* *micromammosa* Gwynn.
- \* *pulchella* L.f.
- \* *pulchelloides* Gwynn.
- \* *stipitata* De Winter ex. Gwynn.

“Candiflorae”

- \* *akkersdamensis* Gwynn. |
- \* *batmaniana* Gwynn.
- \* *bicolor* Dinter & Engl.
- \* *candiflora* Gwynn.
- \* *felicifolia* Gwynn.
- \* *glabrata* L.f. |
- \* *haemata* Gwynn. |
- \* *imperialis* Gwynn. +
- \* *kenii* Gwynn.
- \* *latimontana* Gwynn.
- \* *linearis* (Harv.) Hochr.
- \* *marginata* (Turcz.) Pillans
- \* *meyeriana* R.Glover
- \* *pedata* Gwynn.
- \* *picta* (Schltr.) ex. Gwynn. & De Winter
- \* *resedifolia* (Burch. ex DC.) R.A.Dyer
- \* *rosea* Gwynn. & Harrower +
- \* *simulans* De Winter ex. Gwynn.

- \* *supplicans* Gwynn. |
- \* *tanquam* Gwynn. |
- \* *towerkopensis* Gwynn. +
- \* *trisecta* Gwynn. +

“Lacerae”

- \* *coriolis* Gwynn. |
- \* *herpetiformis* Gwynn. +
- \* *lacera* (E. Mey.) Fourc. +
- \* *scabricaulis* Salter +
- \* *sperata* Gwynn. +

UNKNOWN POSITION within subg. *Mahernia*

- \* *mysteriosa* m.s.

**subg. *Hermannia*** K. Schum.

**sect. *Hermannia*** K. Schum.

- \* *abrotanoides* Schrad.
- \* *alnifolia* L. +
- \* *althaeifolia* L. +
- \* *althaeoides* Link. +
- \* *aspera* J.C.Wendl. +
- \* *bolusii* Szyszyl.
- \* *bryoniifolia* Burch.
- \* *citrina* Gwynn. +
- \* *comosa* Burch. ex DC.
- \* *confusa* Salter +
- \* *conglomerata* Eckl. & Zeyh. |
- \* *cordifolia* Harv. +
- \* *curiosa* Gwynn.
- \* *cylindrifolia* Gwynn. +
- \* *decipiens* E. Mey. ex Harv. +
- \* *decumbens* Willd. ex Spreng. +
- \* *denudata* L.f. +
- \* *echinocapsulare* Gwynn. +
- \* *erecta* N.E. Br.
- \* *castellana* Gwynn.
- \* *flabellifolia* Gwynn. +
- \* *frangelica* Gwynn. +
- \* *fourcadii* Pillans ex Gwynn. +
- \* *floribunda* Harv.
- \* *fulmenalis* Gwynn.
- \* *gracilis* Eckl. & Zeyh. +
- \* *hederacea* Gwynn.
- \* *helicoidea* Verdoorn +
- \* *hispidula* Rechb. +
- \* *hoarensis* Gwynn. +
- \* *holosericea* Jacq. +
- \* *hyssopifolia* L. +
- \* *incana* Cav. +
- \* *draconis* Gwynn.

*involucrata* Cav. +  
*johansseni* N.E.Br. |  
*joubertiana* Harv. +  
*juttiae* Dinter & Engl.  
*lavandulifolia* L. +  
*linifolia* Burm. f. +  
*litoralis* Verdoorn +  
\* *lochnessii* Gwynn. +  
*macra* Schltr.  
\* *mcdowellii* Gwynn. +  
*minutiflora* Engl.  
*mucronulata* Turcz. +  
*muirii* Pillans +  
*multiflora* Jacq. +  
*muricata* Eckl. & Zeyh. +  
*odorata* Ait. +  
\* *opuntioides* Gwynn.  
\* *orgasmiodorata* Gwynn. +  
*paucifolia* Turcz.  
\* *phasma* Gwynn.  
*pillansii* Compton +  
*prismatocarpa* E. Mey. ex Harv. +  
*procumbens* Cav. +  
*procumbens*  
subsp. *myrrhifolia* (Thunb.) De Winter +  
*pulverata* Andrews +  
\* *reeferi* Gwynn. +  
*rehobothensis* Holz.  
*repetenda* Verdoorn +  
*rigida* Harv. +  
*rugosa* Adamson +  
*salviifolia* L.f. +  
*salviifolia* var. *grandistipula* Harv. +  
*salviifolia* var. *oblonga* Harv. +  
*sandersonii* Harv.  
*scabra* Cav. +  
*scordifolia* Jacq. +  
\* *simia* Gwynn.  
\* *skyfii* Gwynn. +  
*stipulacea* Lehm. ex Eckl. & Zeyh. +  
*suavis* C.Presl ex Harv. +  
*sulcata* Harv. +  
\* *talpida* Gwynn. +  
\* *urceolata* Pillans ex Gwynn. +  
*velutina* DC. +  
*vestita* Thunb.  
\* *vuvuzeloides* Gwynn. +

“Amoenaes”

*amoena* Dinter ex Holz.  
\* *bungholensis* Gwynn.  
*disermifolia* Jacq.  
\* *eruca* Gwynn.

“Angelicae”

\* *angelica* Gwynn. +  
\* *cherubim* Gwynn. +  
*disticha* Schrad. +  
\* *puttii* Gwynn. +

“Cuneifoliae”

*cuneifolia* var. *cuneifolia* (Jacq.) Verdoorn +  
*cuneifolia*  
var. *glabrescens* (Harv.) Verdoorn +  
*desertorum* Eckl. & Zeyh. +  
\* *harpaga* Gwynn. +  
*micrantha* Adamson +  
\* *microtesticulare* Gwynn. +  
\* *onychotenax* Gwynn.  
*pfeilii* K. Schum.  
\* *tritoniana* Gwynn. +

“Flammeae”

*angularis* Jacq. +  
*asteroidea* Gwynn. +  
*bifaria* Lindb. +  
\* *castra* Gwynn.  
*concinifolia* Verdoorn +  
*diversistipula* C.Presl ex Harv. +  
*diversistipula* var. *graciliflora* Verdoorn +  
*filifolia* L.f. var. *filifolia* Verdoorn +  
*filifolia* var. *grandicalyx* Verdoorn +  
*filifolia* var. *robusta* Verdoorn +  
*flammea* Jacq. +  
*flammula* Harv. +  
\* *martita* Gwynn. +  
\* *mumia* Gwynn. +  
\* *poseidonii* Gwynn. +  
*rudis* N.E.Br. +  
\* *satanica* Gwynn. +  
*ternifolia* C.Presl ex Harv. +  
*trifoliata* L. +

**sect. *Acicarpus*** (Harv.) Engl.

**subject. *Cristatae*** (Engl.) Gwynn.

—***Cristatae*** (International group)

*cristata* Bolus

*inflata* Link & Otto

*merxmulleri* M. Friedrich

*palmeri* Rose  
*pauciflora* S. Watson  
*texana* A. Gray

“Marehnia”

*athiensis* K. Schum.  
*boranensis* K. Schum.  
*conradsiana* Engl.  
*erlangeriana* K. Schum.  
*exappendiculata* K. Schum.  
*fischeri* K. Schum.  
*macrobotrys* K. Schum.  
*oliveri* K. Schum.  
*paniculata* Franch.  
*pseudathiensis* Cheek  
*pseudofischeri* Cheek  
*stuhlmannii* K. Schum.  
*uhligii* Engl.  
*volkensis* K. Schum.  
*vollesenii* Cheek  
*waltherioides* K. Schum.

**subsect. *Acicarpus*** (Harv.) Gwynn.

Series *Modestae*

*amabilis* Marloth ex K. Schum.  
*atrosanguinea* Dinter  
\* *capoeira* Gwynn.  
*filipes* Harv.  
*holubii* Burt Davy  
*kirkii* Mast.  
*modesta* (Ehrenb.) Mast.  
*testacea* Vollesen  
*tigrensii* Hochst. ex Rich.

“Glanduligeræ”

*boraginiflora* Hook.  
*glanduligera* K. Schum.  
*glandulossisima* Engl.  
*viscosa* Hiern.

“Namhernia”

*affinis* K. Schum.  
*angolensis* K. Schum.  
\* *camella* Gwynn.  
*complicata* Engl.  
*damarana* Baker  
*eenii* Baker  
*engleri* Schinz  
*fruticulosa* K. Schum.  
*gariepina* Eckl. & Zeyh.  
*grisea* Schinz  
*glandulossisima* Engl.  
*guerkeana* K. Schum.  
*helianthemum* K. Schum.  
*hereroensis* Schinz.  
*linearifolia* Harv.  
*micropetala* Harv.  
*minimifolia* Holz.  
*pearsonii* Exell & Mendonça  
*seineri* Engl.  
*solaniflora* K. Schum.  
*spinosa* E. Mey. ex Harv.  
*squarrosa* Dinter ex Range  
*stricta* (E. Mey. ex Turcz.) Harv.  
*tomentosa* Schinz ex Engl.  
*torrei* Wild  
*trifurca* L. +



### 4.3.3 Distribution at subgenus level

Maps in the following pages depict the known distribution of species groups and their component species. The species have been placed within their groups in order of decreasing rank to highlight the nested nature of their geographic distribution. The species are also depicted in order to demonstrate the cohesiveness of the groups in both their phylogenetic and distributional component, as well as to illustrate the component species that make up a group.

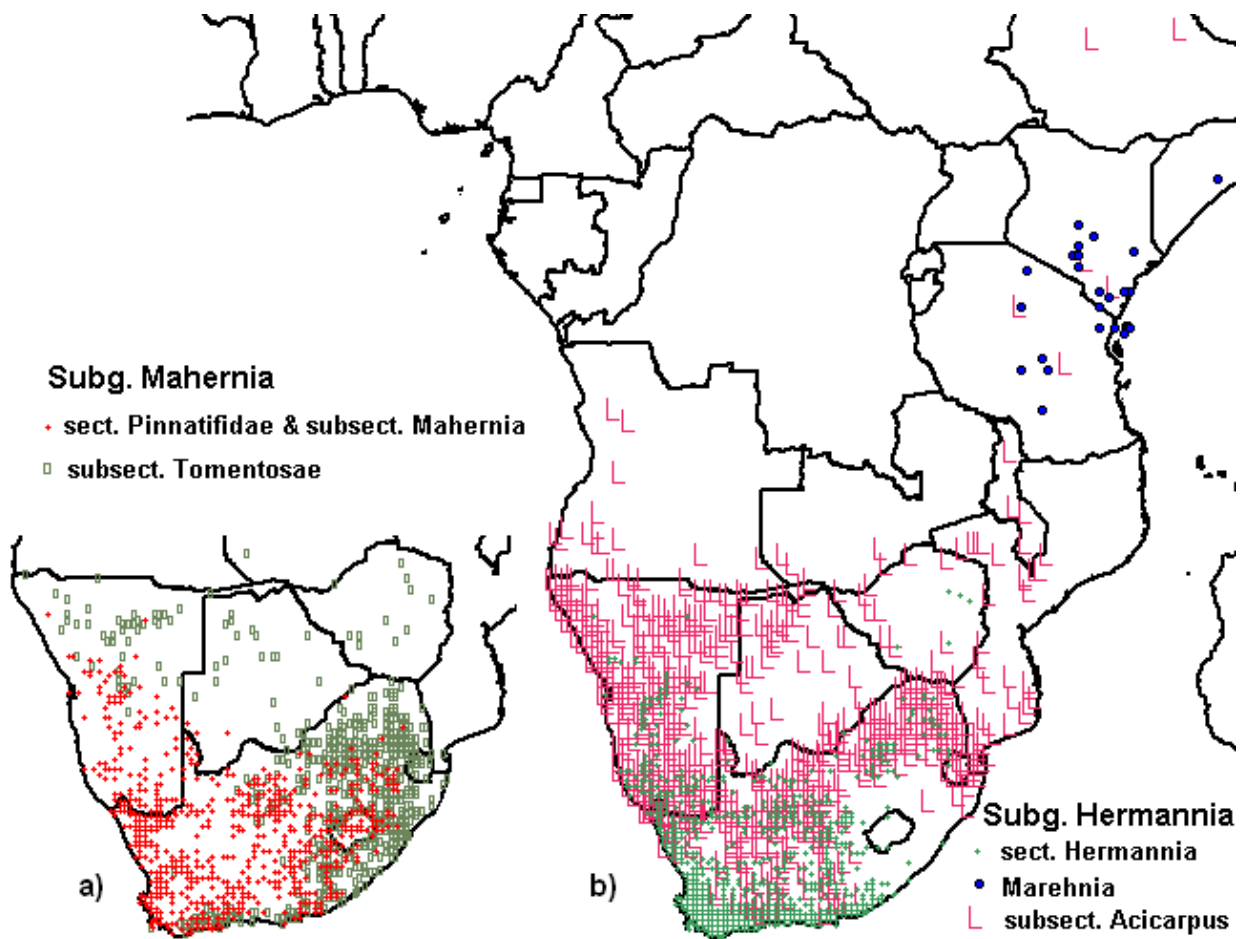
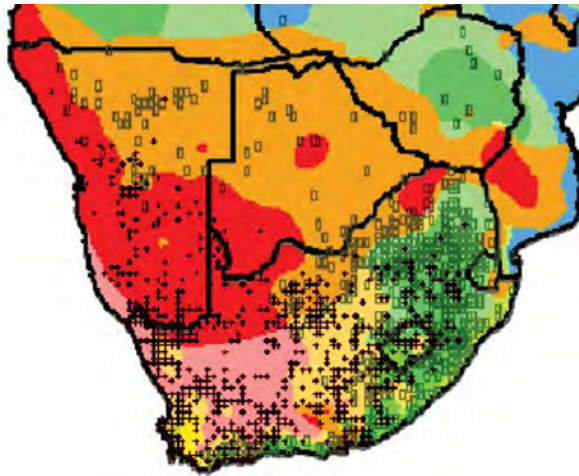


Fig. 4.5 Distributions of the major sections of *Hermannia*: a) the western group of subg. *Mahernia* with sect. *Pinnatifidae* and subsect. *Mahernia* combined, and distinguished from the summer rainfall subsect. *Tomentosae*; and b) subg. *Hermannia*, with sect. *Hermannia*, “*Marehnia*”, and subsect. *Acicarpus* separated.



**Fig. 4.6** The distribution of Subg. *Mahernia* in Fig. 4.6a overlaid on the Köppen-Geiger climate map.

It can be seen in Fig. 4.6a and Fig. 4.6b that there is substantial geographic structuring even at the coarse level of subgenus. The subg. *Mahernia* (Fig. 4.6a) is fairly evenly dispersed throughout South Africa, with a lower density in Namibia, Botswana and the central karoo than subg. *Hermannia* (Fig. 4.6b). The subg. *Mahernia* is essentially absent from Mozambique and north of Zimbabwe. It is somewhat structured, with the subsect. *Tomentosae* more prevalent in the northern and eastern portions of the total distribution of subg. *Mahernia*; and sect. *Pinnatifidae* and subsect. *Mahernia* predominant in the Cape, central Karoo, and southern portions of Namibia.

The subg. *Hermannia* (Fig. 4.6b) occupies most of Southern Africa, but is conspicuously absent from a broad area around Pondoland and Lesotho. There is considerable structuring within this subgenus, with sect. *Hermannia* mainly occupying the Cape as far as central Namibia, and the Zimbabwe, with a conspicuous absence in Botswana, Mozambique, and eastern portions of South Africa around Lesotho. “*Marehnia*” only occupies a narrow portion of the tropical region (although it does extend further north and west in the tropic of Africa than shown in the map).

The Subsect. *Acicarpus* occupies most of the distributional area of the “potential species range”, including being the only clade other than “*Marehnia*” to occupy tropical Africa, Angola and Mozambique. It has its densest area in Namibia, and occurs across Southern Africa with two notable exceptions, the South-Western Cape and a large area around Lesotho and Pondoland. In Fig. 4.6 the subsect. *Tomentosae* is strongly associated with the hot semi-arid climate and the

tropical climates, and negatively associated with the desert climates. This is the inverse pattern to subg. *Hermannia*. There is considerable mixing of the subgenera in the cold semi-arid climate type.

From this initial examination of the high level clades, it can be seen that there are considerable differences in distribution between the taxa. Adaptation to desert or more mesic environments explains much of the distributional differences between the subgenera. At this taxonomic level it is difficult to discern what other factors might be limiting the overall distributions within a clade, and whether there is a pattern to distribution within the cold semi-arid area where the subgenera co-occur. Also at this level there is no sense of species diversity, and the areas individual species occupy. To resolve this the clades are now presented at a lower level, highlighting the important species components that make up the clade, and identifying outliers from the general pattern.

#### 4.3.4 The distribution of the formal groups within *Hermannia*

##### 4.3.4.1 The Section *Hermannia*

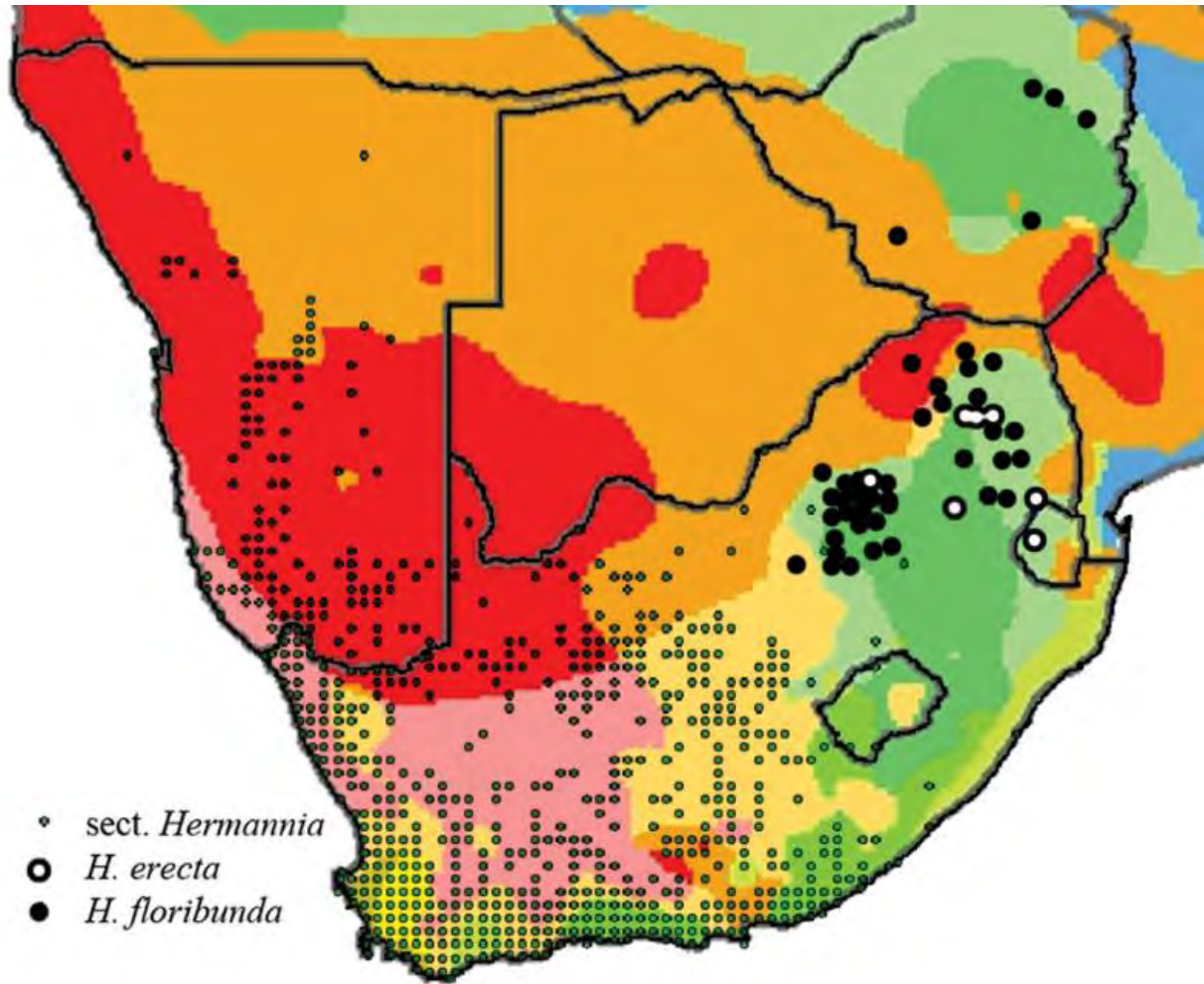


Fig. 4.7 The sect. *Hermannia* with the summer rainfall endemics differentiated, superimposed over a Köppen-Geiger climate map.

The sect. *Hermannia* predominantly occupies the South-Western Cape and coastal areas within 150km of the coast, losing contiguity in the eastern Cape, southern Namibia and in the Karoo. It would appear that species within this section favour more mesic winter-rainfall conditions. Two outliers are considerably separate from the bulk of the distribution (Fig. 4.7): *H. floribunda* that extends into Zimbabwe, and *H. erecta* (formerly *H. denudata* var. *erecta*). These species both occupy a highveld summer rainfall area that is prone to frost. These conditions may be what has excluded other members of the sect. *Hermannia* that have their centre of diversity in

within 150km of the coast in the winter-rainfall area. Comparison with the climatic types shows that *H. floribunda* has an Association of Distribution to Climate (ADC) of  $35/40 = 87.5\%$  to the humid sub-tropical climate and the subtropical highland climate. *H. erecta* has an ADC of  $7/7 = 100\%$  to these same climatic zones. Less than  $8/\pm 400 = 2\%$  of the c. 100 of the remaining species in the sect. *Hermannia* in the clade occur on this vegetation type, demonstrating that the adaptation to this climate type is a rare event and not readily accomplished.

4.3.4.2 The section *Acicarpus*, excluding “Marehnia”

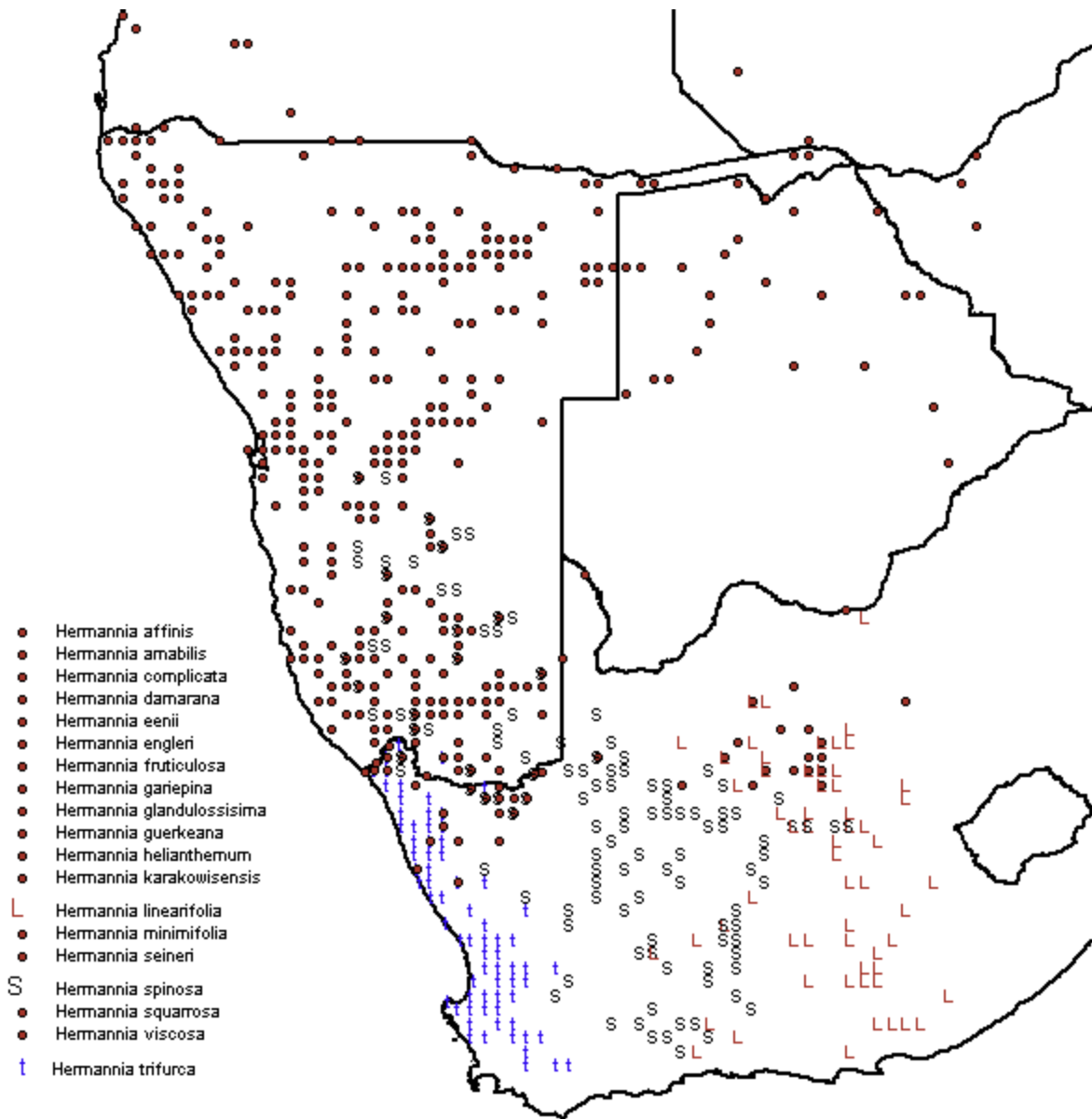
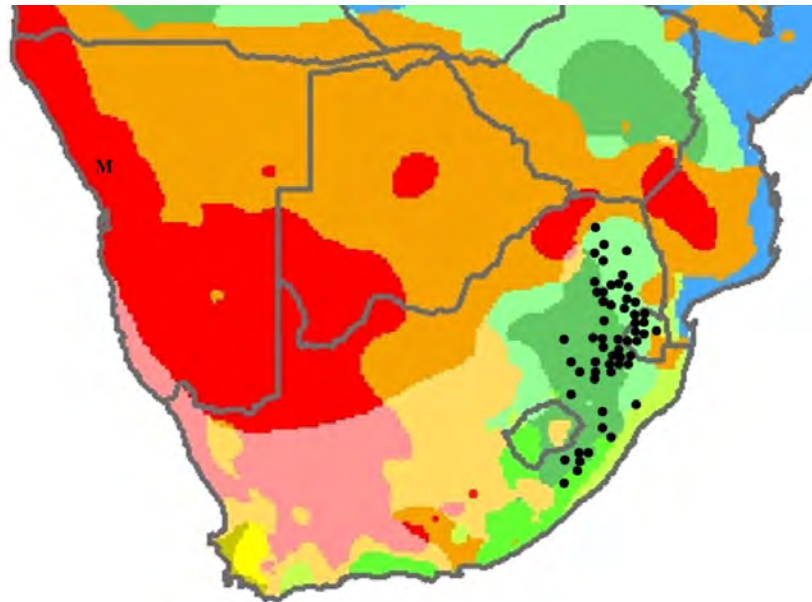


Fig. 4.8 Distribution of the core subject. *Acicarpus* (excluding annual and eastern spp.), with the South African outliers distinguished.

The subject. *Acicarpus* comprises the horned species of two clades. The species with complex horns (fringed processes) in the subject. *Cristatae* occur in Namibia, the summer rainfall region, and America. The clade with simple horns, subject. *Acicarpus*, occurs primarily in Namibia, but has three species that extend to the southern portions of South Africa (Fig. 4.8, above). There are three salient species that extend from a latitude around southern Namibia to a latitude around

Cape Town. These species occupy complementary and adjacent geographic distributions: *H. trifurca* occupies the western side of South Africa to around 150km inland; *H. spinosa* occupies an intermediate position from near central Namibia to the Klein Karoo, and likely experiences the driest position of the three species; *H. linearifolia* is the eastern-most species, and occurs from the Kimberley district to the Eastern Cape. This species is distributed across a more mesic summer rainfall area. Three closely related species that occupy the north-eastern summer rainfall areas of Southern Africa, *H. micropetala*, *H. boraginiflora*, and *H. glanduligera*, have been excluded from Fig. 4.8 as they fall into different groups and are shown in Fig. 4.11 and Fig. 4.18. *Hermannia glanduligera* extends to Kenya.



**Fig. 4.9** Distribution of *H. cristata* (dots) in South Africa and *H. merxmuelleri* (M) in Namibia, superimposed over a Köppen-Geiger climate map.

*Hermannia cristata* occurs predominantly in the Subtropical highland climate (Cwb, ADC = 33/61), to a lesser extent in the Humid subtropical climate (Cwa, ADC = 24/61), and with a few localities marginally located within the Oceanic climate (Cfb, ADC = 5/61). *Hermannia merxmuelleri* occurs on the south slopes of the Brandberg within the Hot desert climate (BWh, ADC = 1/1).



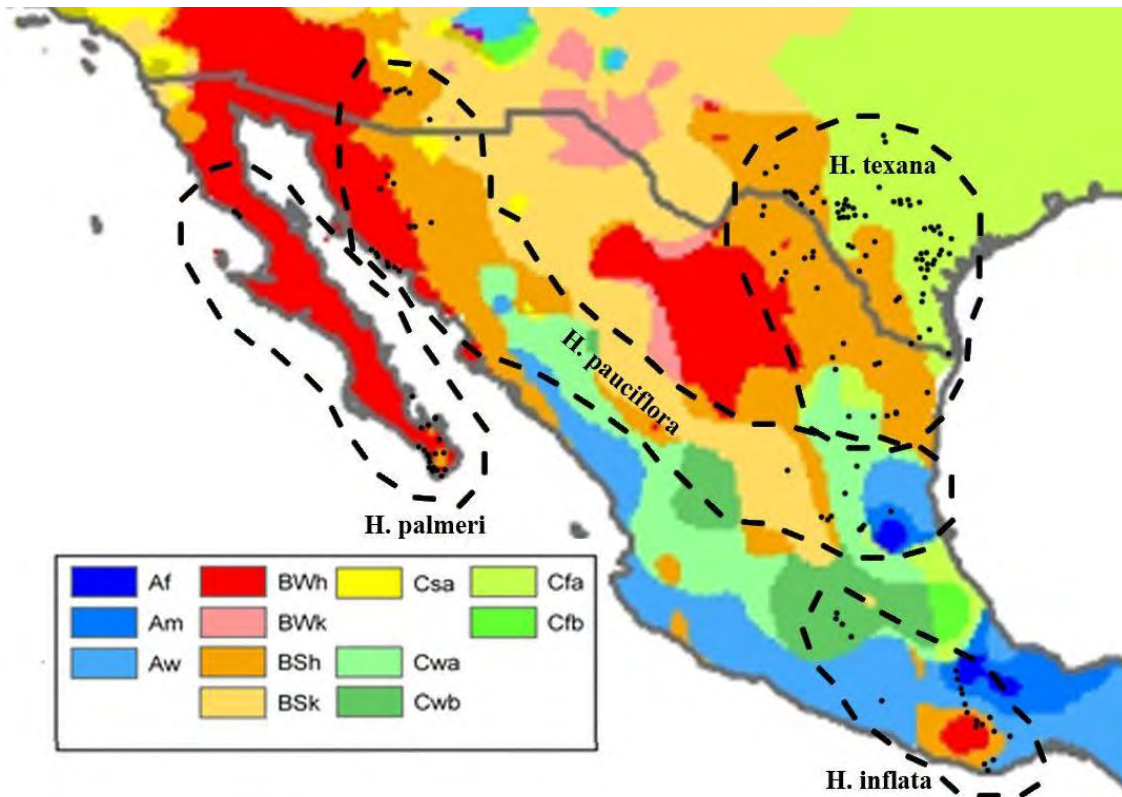


Fig. 4.10 The distribution of the four American species. The key is defined in Fig. 4.4.

Three of the four American species can be considered to be significantly associated with an arid climate. *H. palmeri* with an ADC of 22/22 appears to occur exclusively in the Hot desert climate. *H. pauciflora* has an ADC of 12/31 in BWh, 11/31 in the BSh, 4/31 in the Cwa, 2/31 in the BSk, and 1/31 in the Am. *H. texana* is mainly associated with BSh of 37/89, Cfa of 49/89, and Cwa of 3/89. *H. inflata* occupies the BSh of 3/21, Aw of 7/21, Am of 3/21, and Cwb of 4/21.

Although much of *H. palmeri* appears to be associated with the Hot desert climate, the two separate populations all occur along the coast except a portion of the southern population which is designated as Hot semi-arid climate. An inspection of the localities of *H. pauciflora* falling within the Hot desert climates shows that they too are either associated with the coast, or border the BSh. The same can be said of *H. inflata* which also has marginal populations in the Hot desert climate, and *H. texana* which narrowly avoids this climate type. The general optimal habitat of the three northern species is therefore a Hot semi-arid climate. A significant portion of the distribution of *H. texana* and a minor portion of the eastern population of *H.*



*pauciflora* is as associated with the temperate climate, particularly the Humid subtropical climate. *H. inflata* is most closely associated with the Tropical savanna climate and to a lesser extent the Subtropical highland climate and is likely to be a species inhabiting more mesic areas.

Integrating the climate information for the sect. *Cristatae*, we see that *H. merxmuelleri* has a climate most similar to that of the northern American species. *H. inflata* has non-cristate septa, and is therefore less related to *H. merxmuelleri* than either *H. texana* or *H. pauciflora*. Climatically it is also the odd one out of the American species. As the only American species with reflexed petals, *H. palmeri* is more similar to *H. paniculata* and *H. stuhlmannii* than the rest of the sect. *Cristatae*. Although *H. tigrensis* may seem a biogeographically likely connection to American continent, it is from the sect. *Acicarpus* and thus not represented in America. Combining the biogeography, phylogeny, morphology and climate information, and given that the timing post-dates the breakup of Gondwanaland, it is therefore most likely that a relative of *H. merxmuelleri* crossed the Atlantic setting seed around the area occupied by *H. texana*. It then speciated to *H. texana* and *H. paucifolia*. The origins of *H. palmeri* and *H. inflata* are still unknown, but possibly represent independent dispersal from Africa.

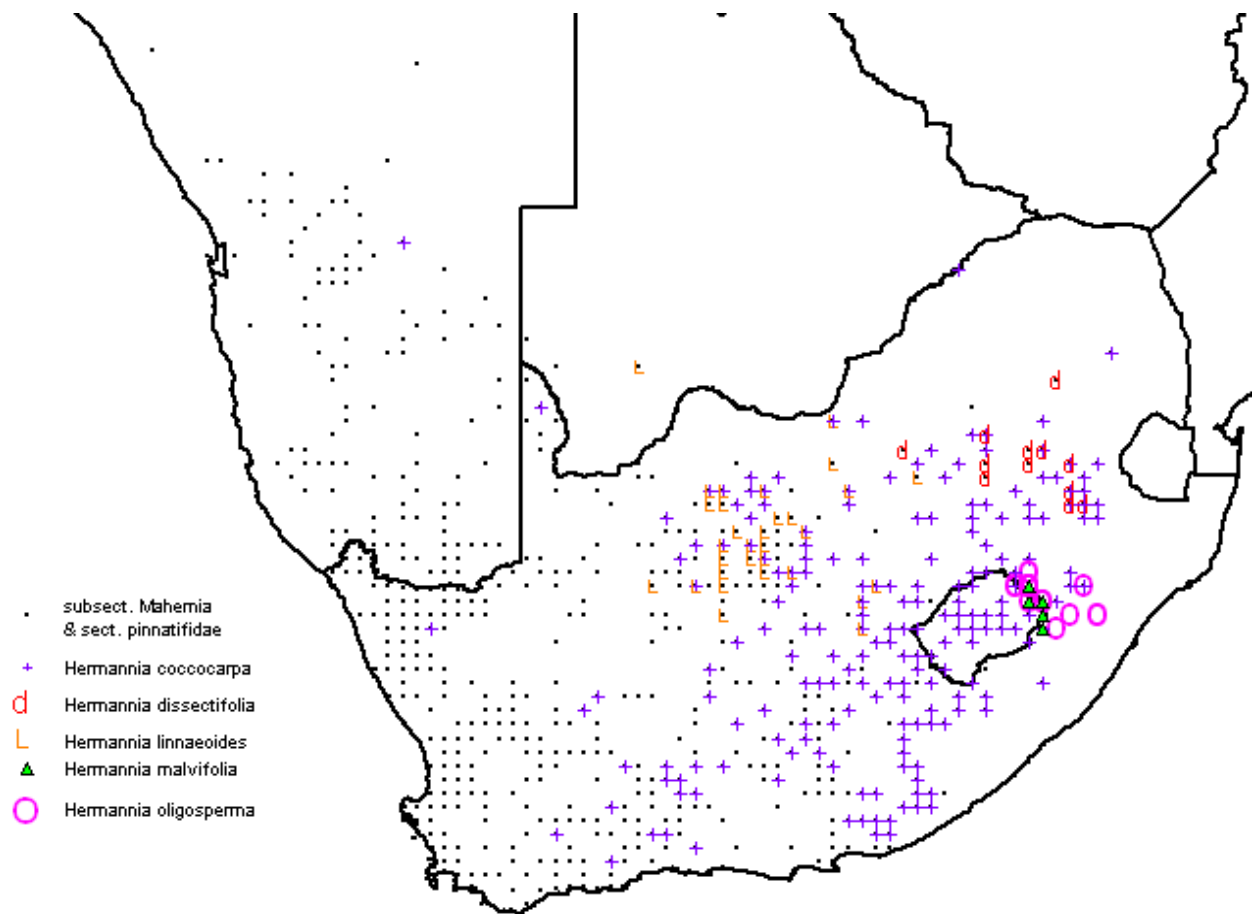


Fig. 4.11 The subsection *Mahernia* and section *Pinnatifidae* clades, with the summer-rain adapted species differentiated from the rest of the clade.

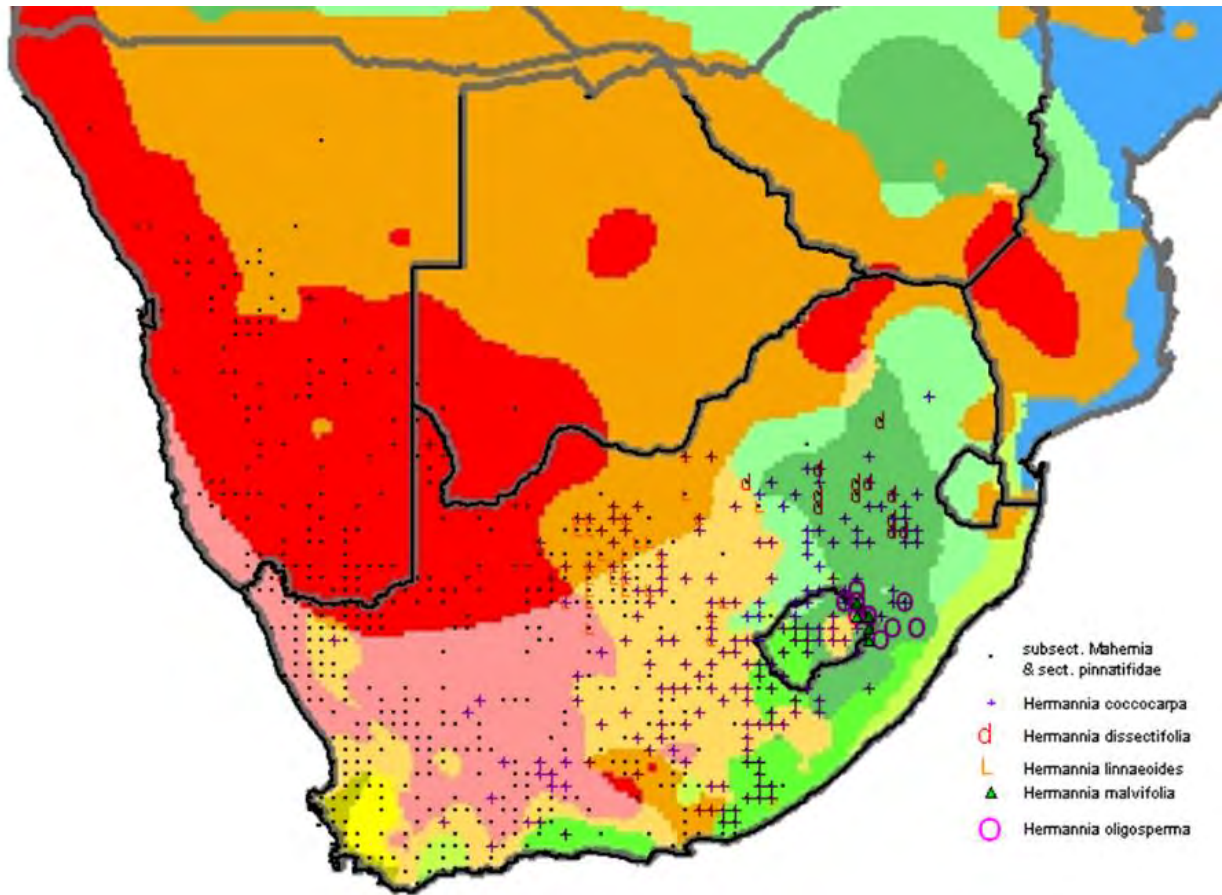


Fig. 4.12 The subset. *Mahernia* and sect. *Pinnatifidae* clades, with the summer-rain adapted species differentiated from the rest of the clade, and their distribution superimposed on the Köppen-Geiger climate map.

#### 4.3.4.3 The subg. *Mahernia*: subset. *Mahernia* and sect. *Pinnatifidae*

Overall, *Mahernia* could be considered a South African subgenus, as only six species, are endemic to areas beyond South Africa: *H. elliottiana*, *H. grosseserrata*, *H. rautanenii*, *H. linnaeopsis* and *H. argillicola*, all from Namibia, and *H. biniflora* from Australia. A number of species from the northern parts of South Africa extend to the neighbouring countries. The subg. *Mahernia* is well represented in the summer rainfall areas of South Africa (Fig. 4.13) by the subset. *Tomentosae*. The Cape species of subset. *Mahernia* and the sect. *Pinnatifidae* contribute substantially to the species diversity of the Cape. Several major clades occur within subg. *Mahernia*, of which species of the subset. *Mahernia* and the sect. *Pinnatifidae* are mostly confined to the Cape and Namibia. The contribution of species to the summer rainfall area is not solely from the subset. *Tomentosae*, but also includes two species from the Cape clade of the subg. *Mahernia* that are found in the Drakensberg area, *H. malvifolia* and *H. oligosperma* (Fig.

4.11, above). The subg. *Mahernia* has mainly radiated along the West Coast, and the arid Karoo areas of South Africa. *H. linnaeoides* and *H. coccocarpa* are both distributed primarily within the summer rainfall regions of the Karoo. In Ch. 3 it was demonstrated that the latter likely speciated to form a neo-species, *H. dissectifolia* (Fig. 4.11, above) within Gauteng.

Examining the distributions superimposed over the Köppen-Geiger climatic map shows that the majority of the genus occurs in arid climatic types (BWh, BWk, BSh, or BSk) or temperate climate types (Csa, Csb, or Cfb). The tropical climate types are relatively sparsely occupied, with only 5 species of this clade typifying this area. ADC values for these species to the sub-tropical highland climate are:  $11/12 = 91.6\%$  for *H. dissectifolia*;  $9/9 = 100\%$  for *H. oligosperma*;  $5/5 = 100\%$  for *H. malvifolia*. *H. linnaeoides* has an ADC of  $25/28 = 89.3\%$  to the semi-arid climates. *Hermannia coccocarpa* has no particular climatic type pattern, and this may in part be explained by it being a widely distributed species complex.

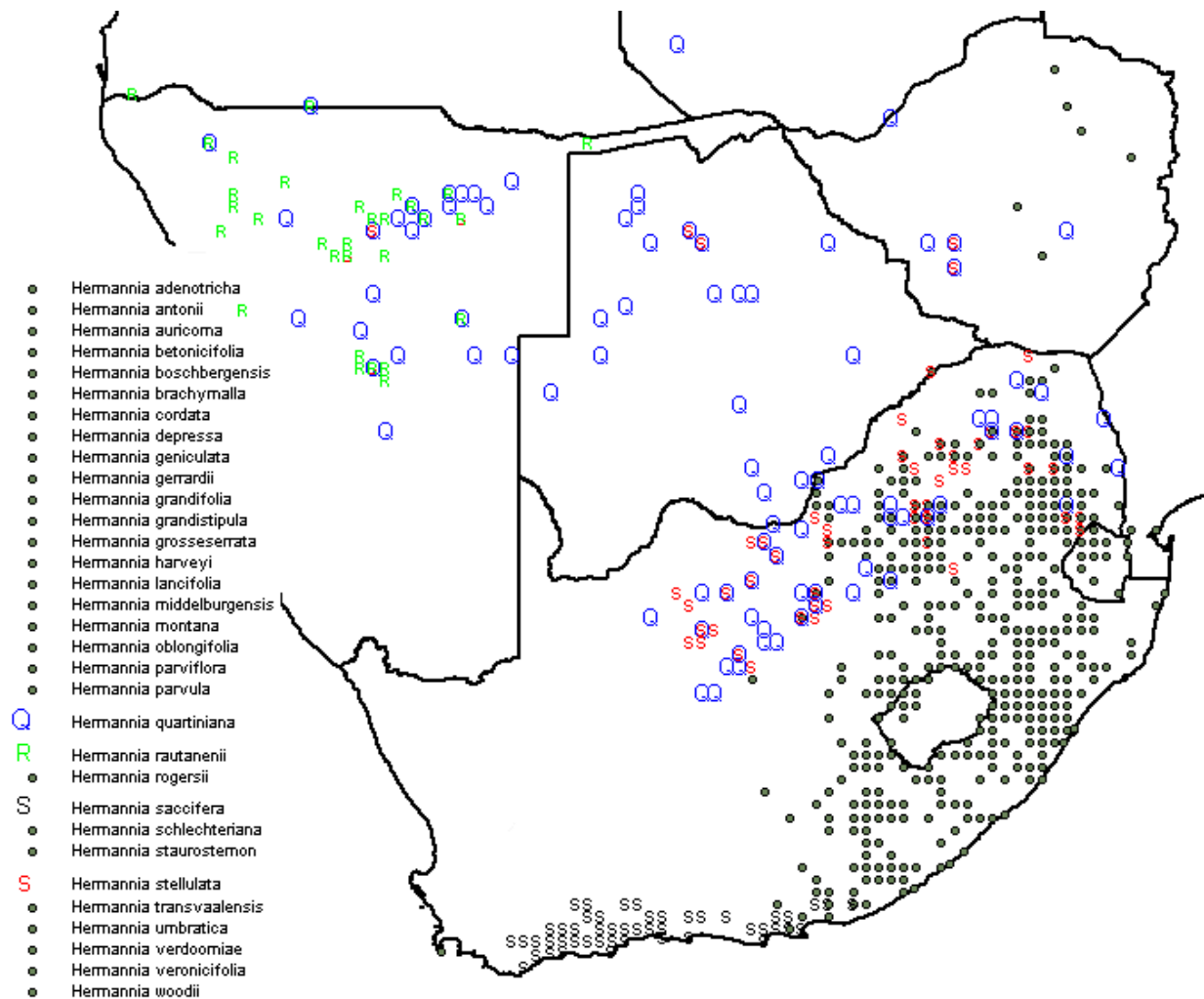


Fig. 4.13. The summer rainfall clade, subject. *Tomentosae*. The western species are here differentiated from the core species of the clade.

#### 4.3.4.4 The subject. *Tomentosae* (subg. *Mahernia*)

The subject. *Tomentosae* is confined to the high rainfall areas of the summer rainfall portion of South Africa, with some notable exceptions (Fig. 4.13, above). *Hermannia saccoifera* has extended down the south coast to the Cape, both along the coast and into the Klein Karoo. There is significant variation within this species suggesting substantial isolation and speciation across its range. *H. quartiniana* and *H. stellulata* are the northern most species which extend to Namibia, with *H. rautanenii* being confined mostly to Namibia. These species occupy the most arid climatic envelope (7.3.2.2, 323), with the former two species occupying a position sister to the rest of the sect. *Tomentosae*.

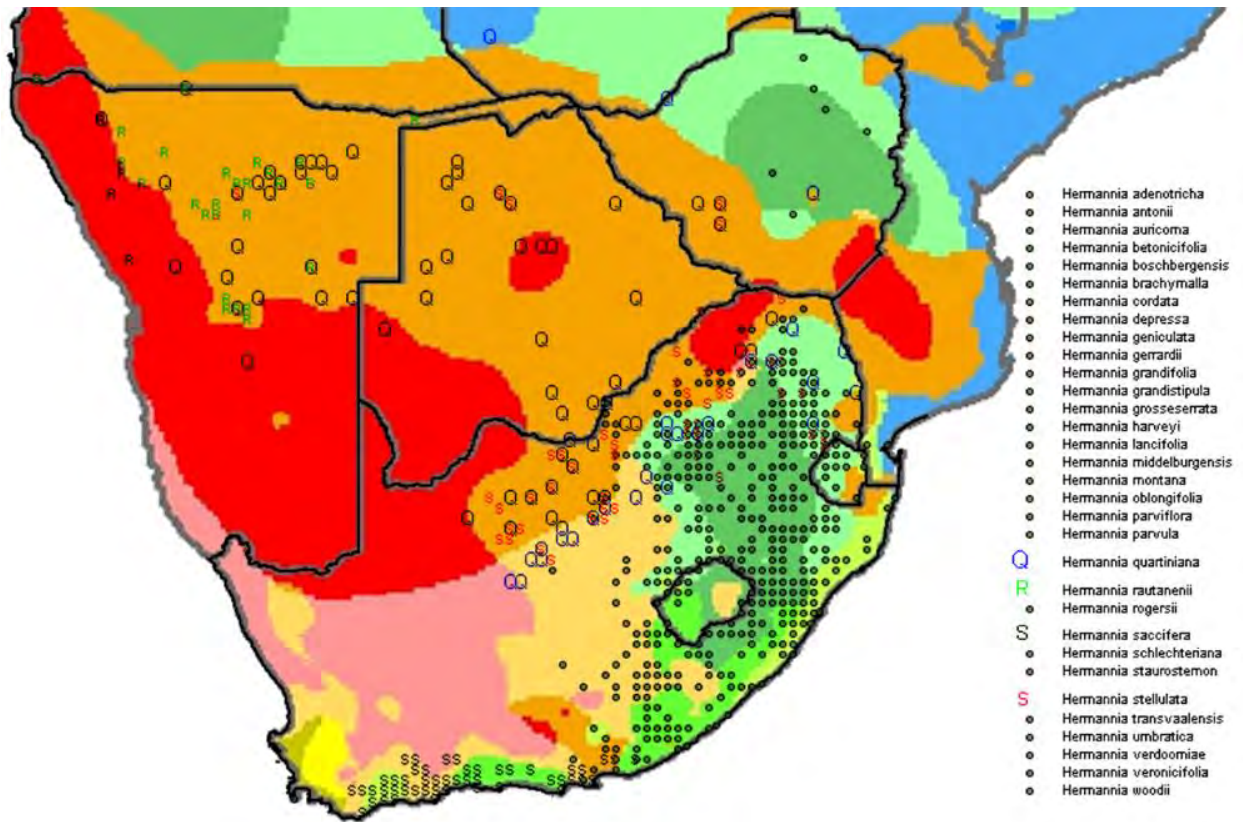


Fig. 4.14 The summer rainfall clade, subsect. *Tomentosae*. The western species are here differentiated from the core species of the clade. These distributions are superimposed on the Köppen-Geiger climate map.

Superimposing distributions of the subsect. *Tomentosae* onto the climate map (Fig. 4.14) shows that the majority of the clade is strongly associated with the sub-tropical (Cwa, Cwb, Cwc) and temperate (Cfa, Cfb) climate types. There is some spread evident from this core area into adjacent semi-arid climate types (BSh and BSk). The outlying species show an inverse pattern, being confined to the semi-arid climates with some spread close to the boundaries into the sub-tropical climate. The respective values of species to the arid and semi-arid areas are: *H. quartiniana* with an ADC of  $79/90 = 87.9\%$ ; *H. stellulata* with  $37/50 = 74\%$ ; and *H. rautanenii* with  $27/27 = 100\%$ . *H. saccifera* has  $47/47 = 100\%$  of records occurring off of the core sub-tropical climate types.



### 4.3.5 The informal groups of *Hermannia*

*Hermannia* has been broken down into a number of informal groups that morphologically link together, but lack sufficient sampling of species or the molecular support to formally recognise them with confidence. These groups are interesting in reflecting the distributional diversity of a group that comprises limited genetic variation. This theme could potentially be explored further, with respect to phylogenetic constraint determining their climatic adaptability. The distributional observations and maps for these informal groups are given below.

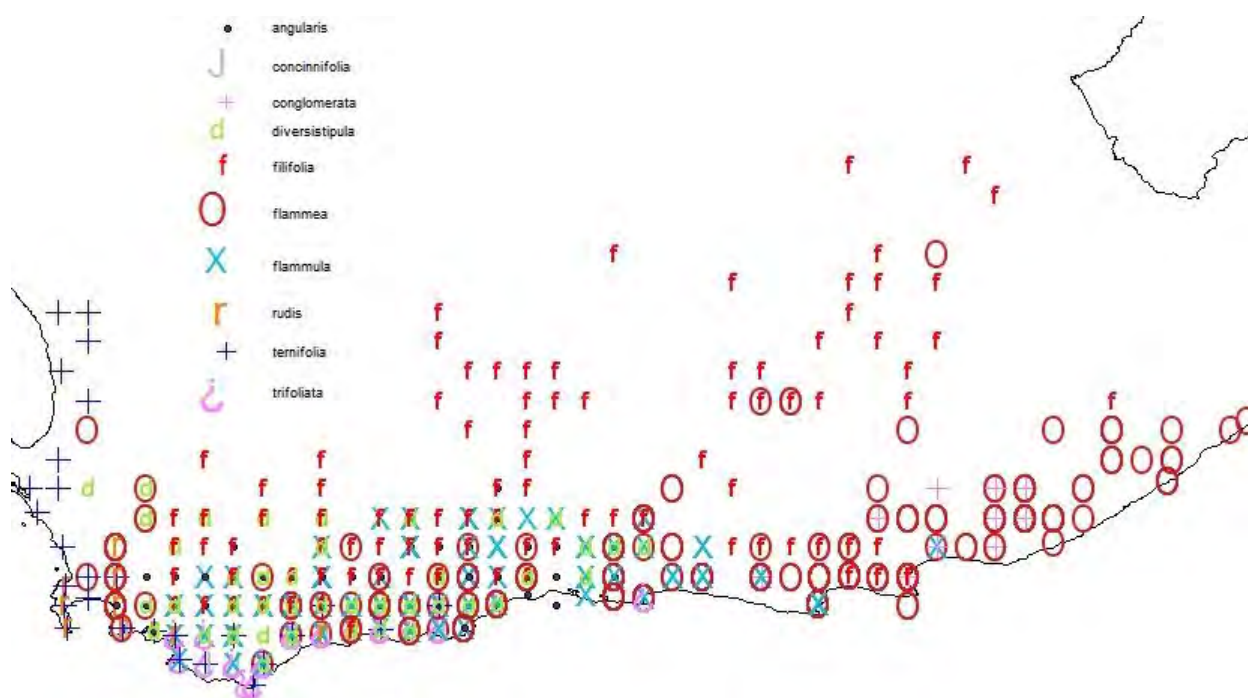


Fig. 4.15 Distribution of species of sect. *Hermannia*, "Flammeae", mostly with red flowers.

#### 4.3.5.1 The sect. *Hermannia*, "Flammeae"

The "Flammeae" (Fig. 4.15, above) is a group containing mainly red-flowered species and a number of coastal limestone endemics. These species are primarily from the South Coast and Klein Karoo, with *H. ternifolia* expanding up the West Coast on the coastal limestones. *H. flammea* and *H. filifolia* are both species that occur from the South Coast well into the interior of the Karoo, and to the Eastern Cape. The remaining species are confined to the coastal limestones (*H. trifoliata*, *H. concinnifolia*), the eastern Klein Karoo (*H. conglomerata*), or the general Klein

Karoo area. Despite molecular and pollen work showing that *H. hyssopifolia* likely belongs in the “Flammeae”, it is excluded from this group on account of having pale cream flowers. However its distribution is similar to that of *H. flammula*, extending from the Cape Peninsula eastwards along the South Coast and Klein Karoo.

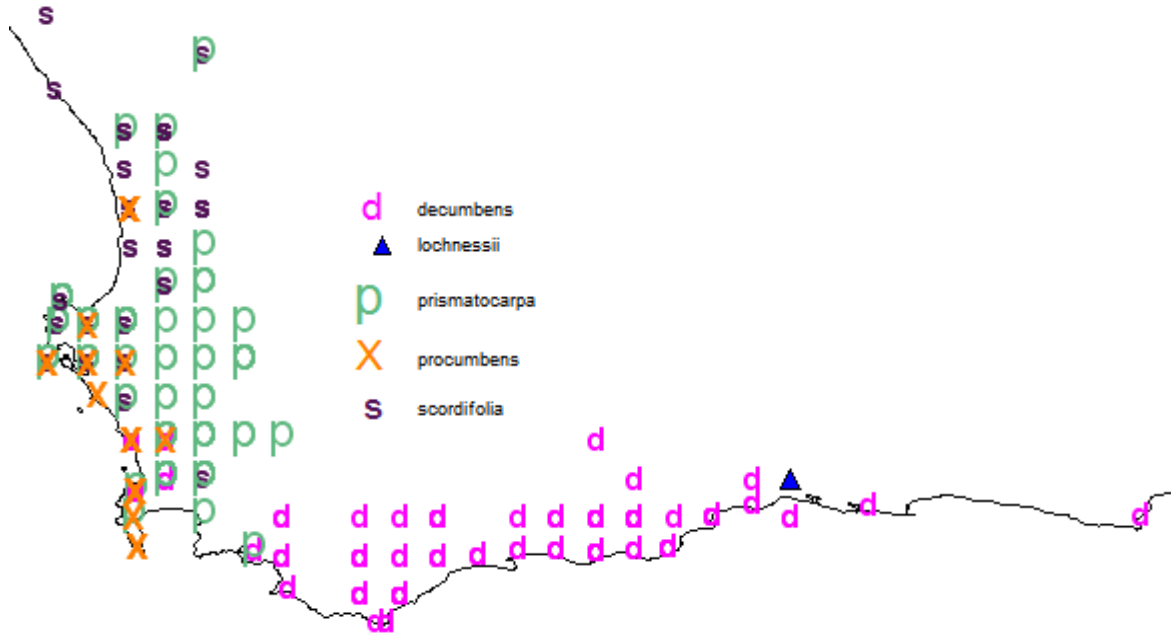


Fig. 4.16 Distribution of the sprawling species of the informal group, “Decumbens”.

#### 4.3.5.2 The sect. *Hermannia*, “Decumbens”

The “Decumbens” group (Fig. 4.16, above) comprises species that sprawl, possess large stellate hairs, and tubular yellow flowers. *H. decumbens* is a species complex that encompasses forms both on sandstone and limestone, and is very similar to *H. nessii*. It is confined largely to the Southern Cape, extending as far west as the Cape Flats around Cape Town. The remainder of the group is confined to the West Coast where it has speciated into at least three species. *H. procumbens* in the map includes the former subsp. *myrrhifolia* and subsp. *procumbens*, now raised to species level.



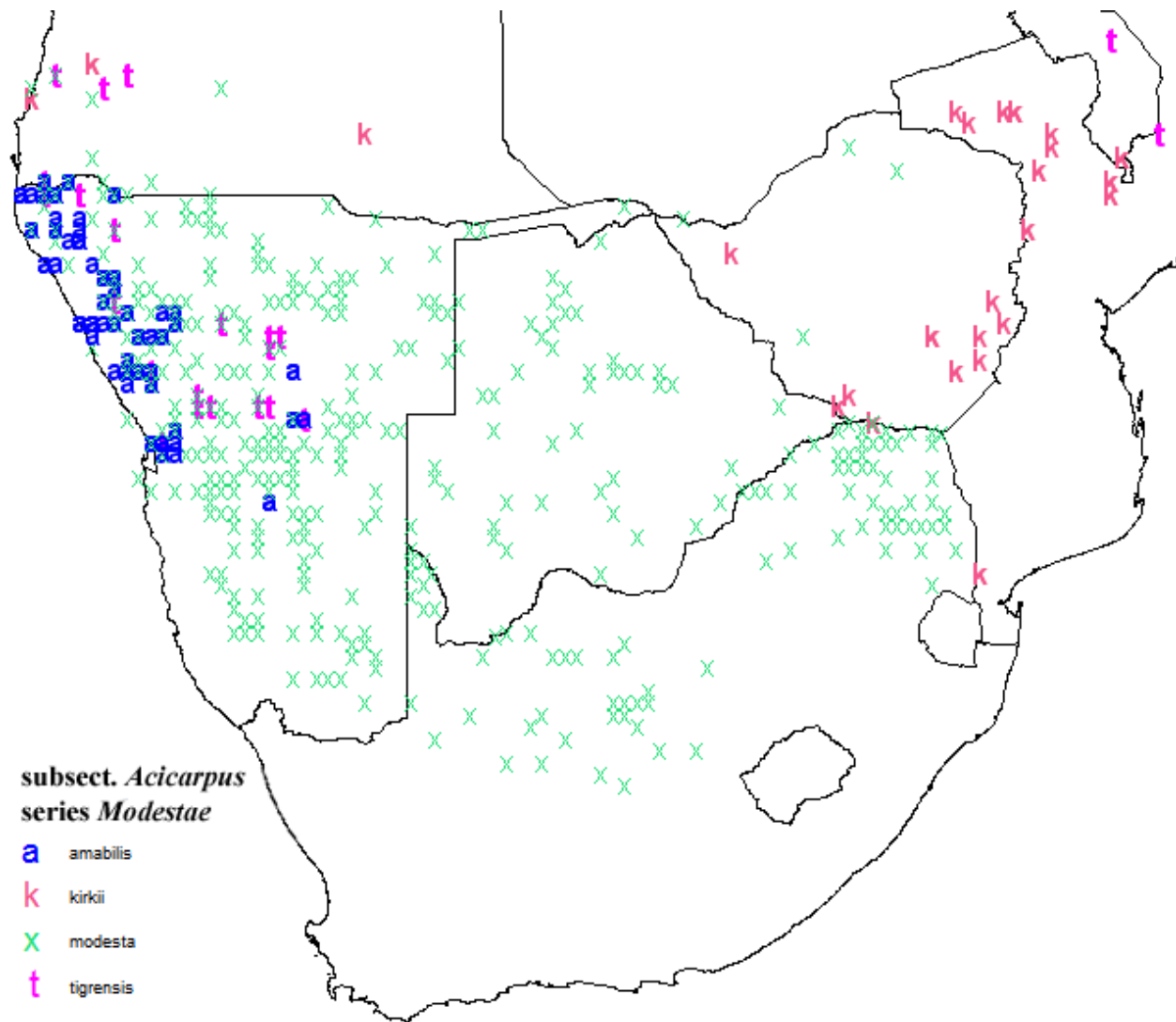


Fig. 4.17 Annual species of the sect. *Acicarpus*, ser. *Modestae*

#### 4.3.5.3 The subject. *Acicarpus*, ser. *Modestae*

The series *Modestae* (Fig. 4.17, above) comprises the annual species within subject. *Acicarpus*. *H. amabilis* is sister to the remainder of the subject. *Acicarpus*, and seems to morphologically fit in most closely with these annual species. *H. modesta* reaches northern Africa and Arabia, and *H. tigrensis* extends along the tropics from the Cape Verde islands to East Africa, where the latter appears to have diversified into *H. testacea* (not shown) in Ethiopia on limestone (see Fig. 4.40 for tropical African distributions). *H. modesta* is a species complex, which may partially explain its broad distribution.

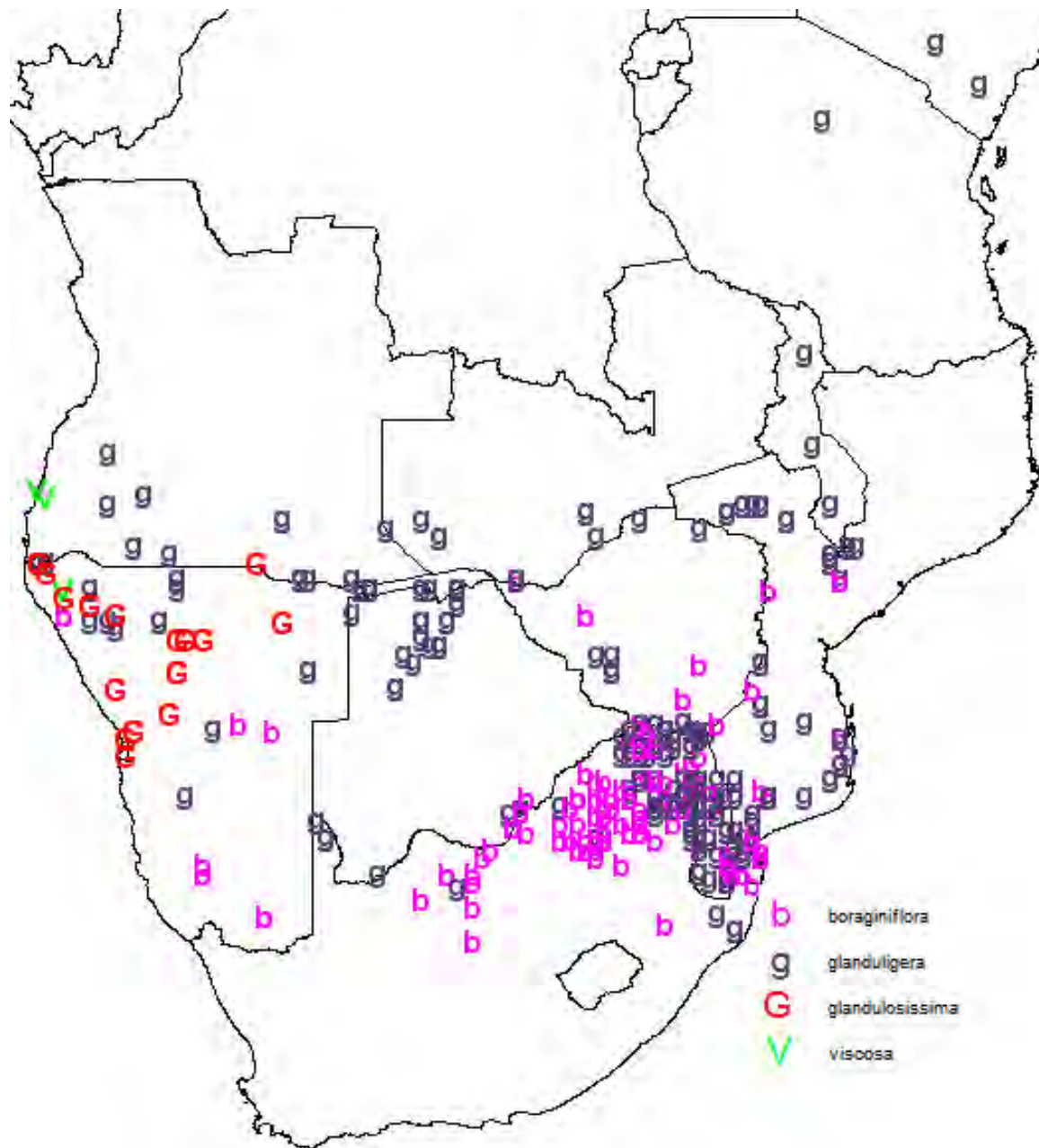
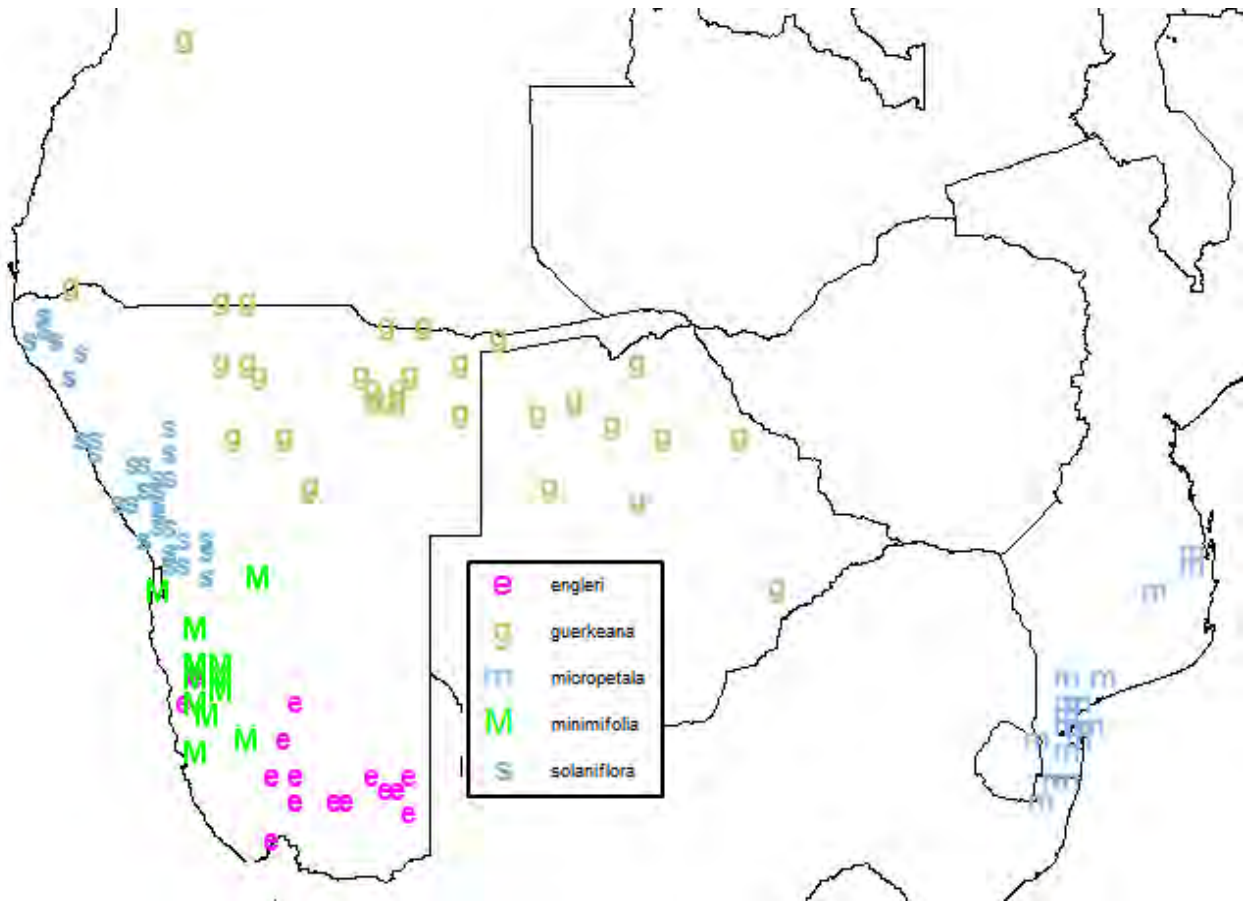


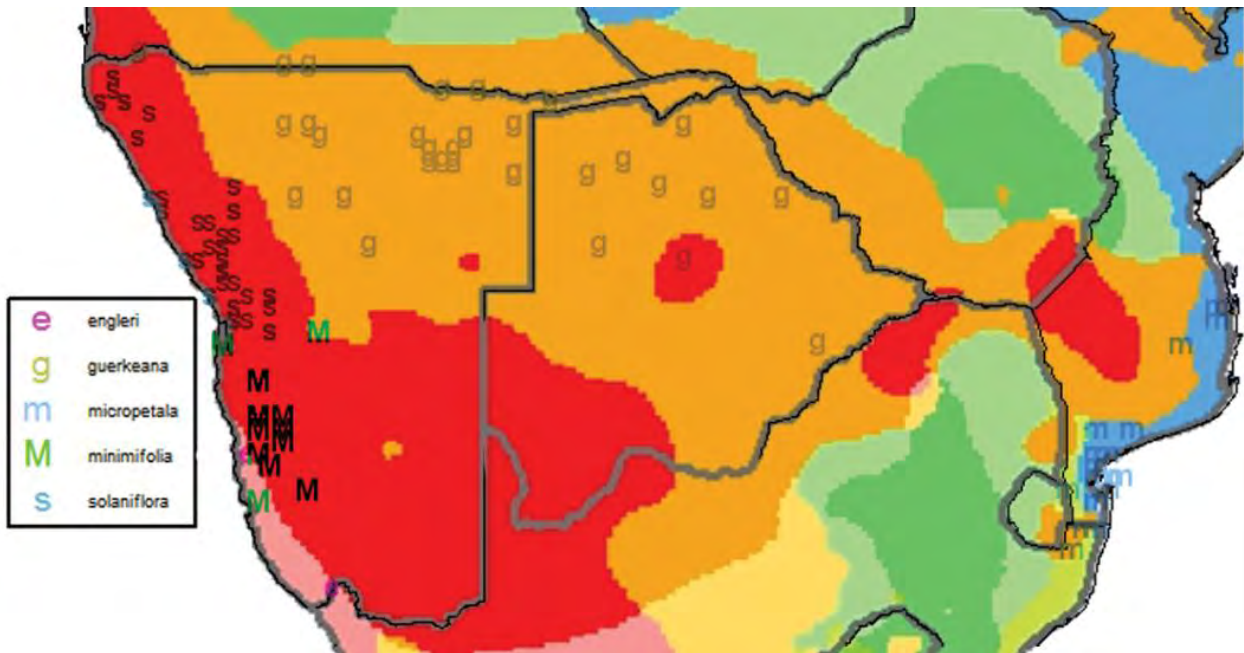
Fig. 4.18 Members of the “Glanduligerae” within subsect. *Acicarpus*.

The “Glanduligerae” (Fig. 4.18, above) are united by being somewhat clammy due to the presence of sticky glandular hairs, and are confined to a summer rainfall regime. This group appears unable to tolerate extreme aridity or a winter-rainfall regime. *Hermannia glanduligera* is one of the few species to extend to tropical Africa.



**Fig. 4.19 Members of the subject. *Acicarpus* with calyces longer than the petals.**

The species allied to *H. micropetala* (Fig. 4.19, above) are united in having short petals. These typically form an open chalice-shaped flower, with the calyx longer than the petals, and the stamens forming a prominent conical cluster. Flowers are pink and occasionally white. I have photographed moths visiting the flowers of *H. eenii*. *Hermannia eenii* and *H. tomentosa* are not depicted, but likely belong in this group. The concentration of species in Namibia suggests that this is its centre of origin, with *H. micropetala* dispersing to the east of the country from a Namibian ancestor.



**Fig. 4.20** Members of the subject, *Acicarpus*; distribution overlaid on the Köppen-Geiger climate map.

This is primarily an arid clade, with *H. minimifolia* and *H. solaniflora* being almost entirely confined to the hot arid climate type. *Hermannia guerkeana* is similarly restricted to the hot semi-arid climate type. *Hermannia micropetala* is anomalous in it not only being possibly the only *Hermannia* to occupy the tropical savanna climate type, but also in being largely confined to it, with an ADC of  $15/17 = 88.2\%$ . This represents a considerable disparity from the rest of the clade, both in distance, some 600km to the nearest *Hermannia guerkeana* population and nearly 1,600km to the remainder of the clade. Climate types differ significantly in attributes, with the tropical climate type being on the other end of the spectrum from the hot arid climate type in terms of moisture.

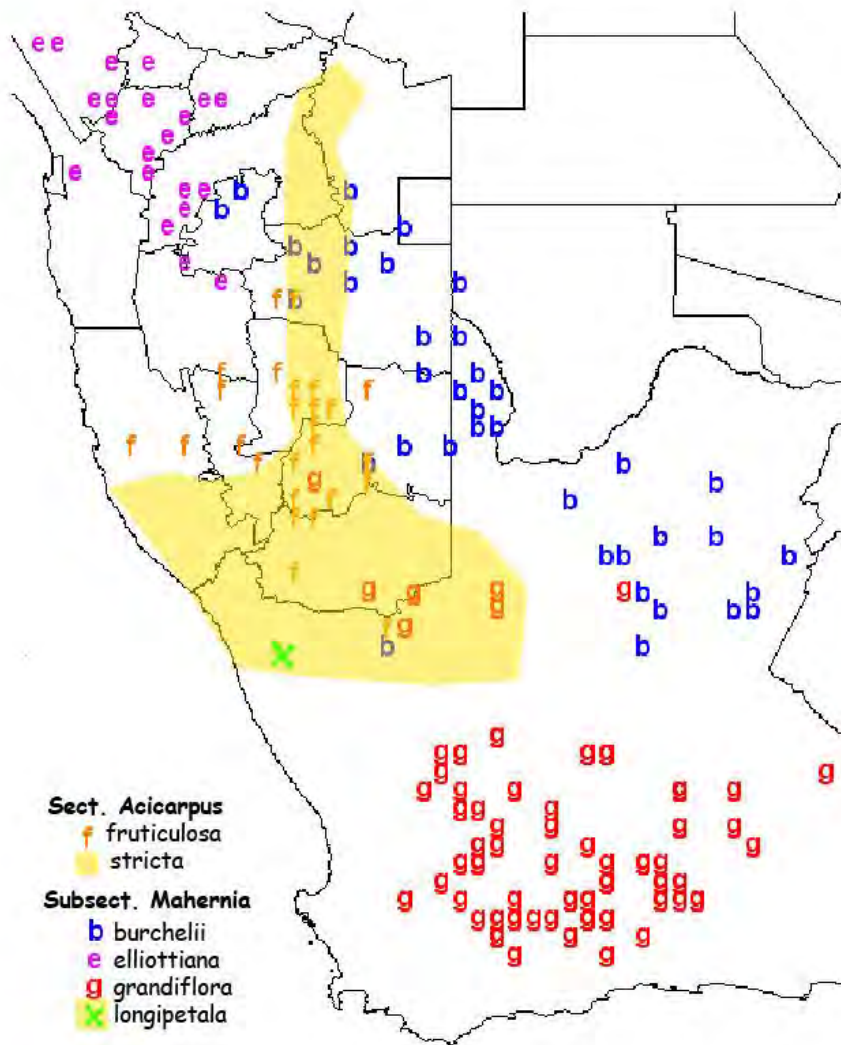
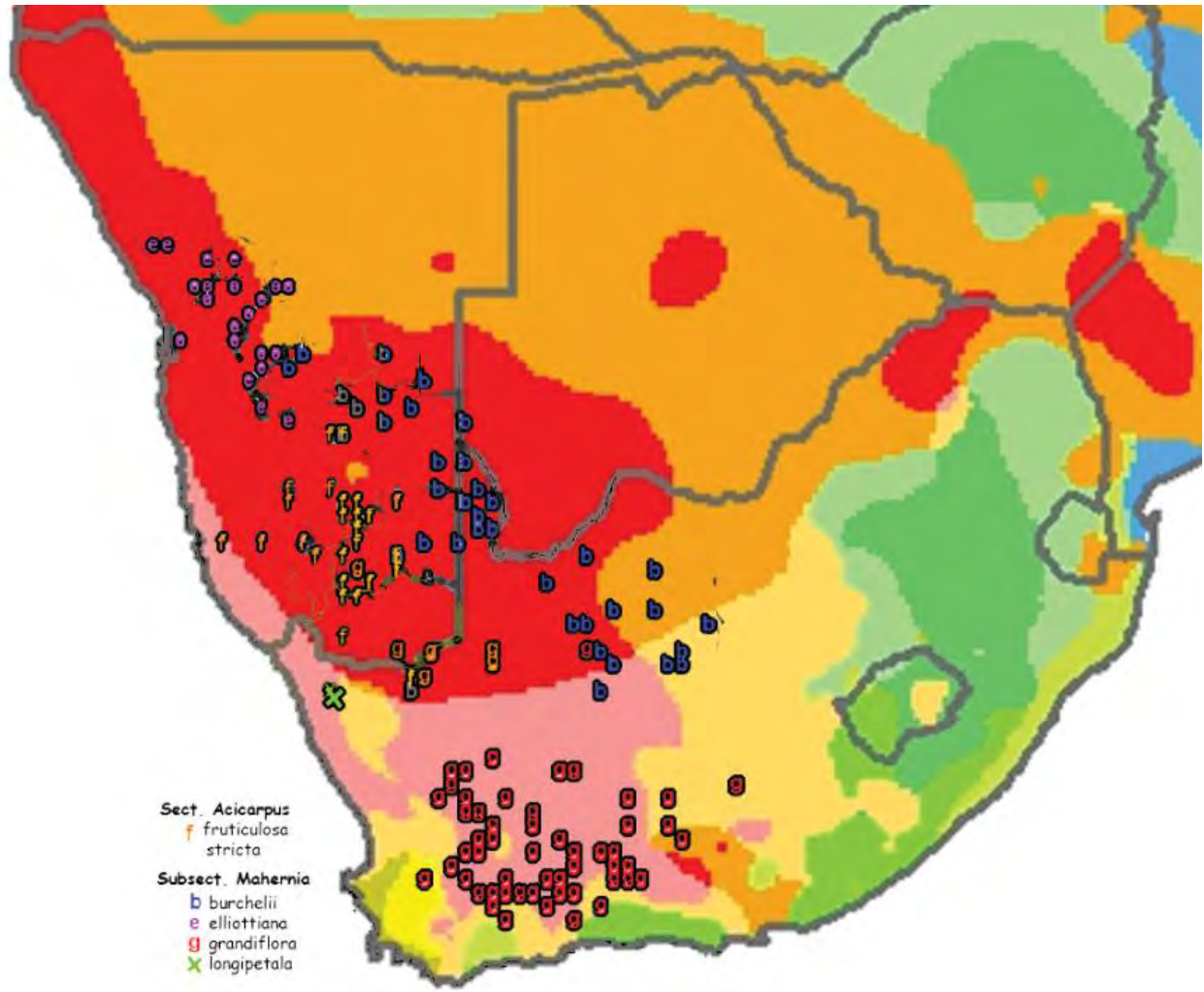


Fig. 4.21 The “Grandiflorae”, *H. fruticulosa*, and *H. stricta*: resinous species with flaring petals.

The “Grandiflorae” (Fig. 4.21, above) and the morphologically similar *H. fruticulosa* and *H. stricta* are mainly woody species (*H. elliotiana* is herbaceous), with resinous branches (*H. burchellii* is stellate-tomentose and *H. elliotiana* is glandular), relatively large petals close to 3X the length of the spreading and recurved pink petals. *H. fruticulosa* is included in the map as it is vegetatively similar looking to *H. grandiflora* but has flowers with orange non-reflexed petals that are only twice the length of the calyx. It would appear that all species are adapted to arid summer rainfall conditions, although *H. grandiflora* can tolerate partial winter-rainfall around the northern Klein Karoo in the south of its distribution range. The distribution of *H. burchellii* undoubtedly relates at least in part to it being confined to deep red Kalahari sands. It is



undoubtedly more widespread within Botswana, but there are no collections from this undercollected area.



**Fig. 4.22** The “Grandiflorae”, *H. fruticulosa*, and *H. stricta*: resinous species with flaring petals. Distribution overlaid on the Köppen-Geiger climate map.

The “Grandiflorae” are largely tied to a desert climate (BWh, BWk) with some representation in the semi-arid climate types. ADC values are for the desert climates are: *H. fruticulosa*: 100%; *H. elliotiana*: 19/21 = 90.5%; 30/37 = 81.1%; and *H. grandiflora* with 41/50 = 82%. Interestingly, *H. grandiflora* is the only species that is significantly disjunct from the remaining species, and it is largely confined to the cold desert climate (BWk) type. Overlaying *H. burchellii* onto the overlay of the sands of the Kalahari (not shown) shows that 28/35 = 80% entirely overlap the mapped region of the dunes, and only one of the 35 records is more than 30km from a plotted dune.

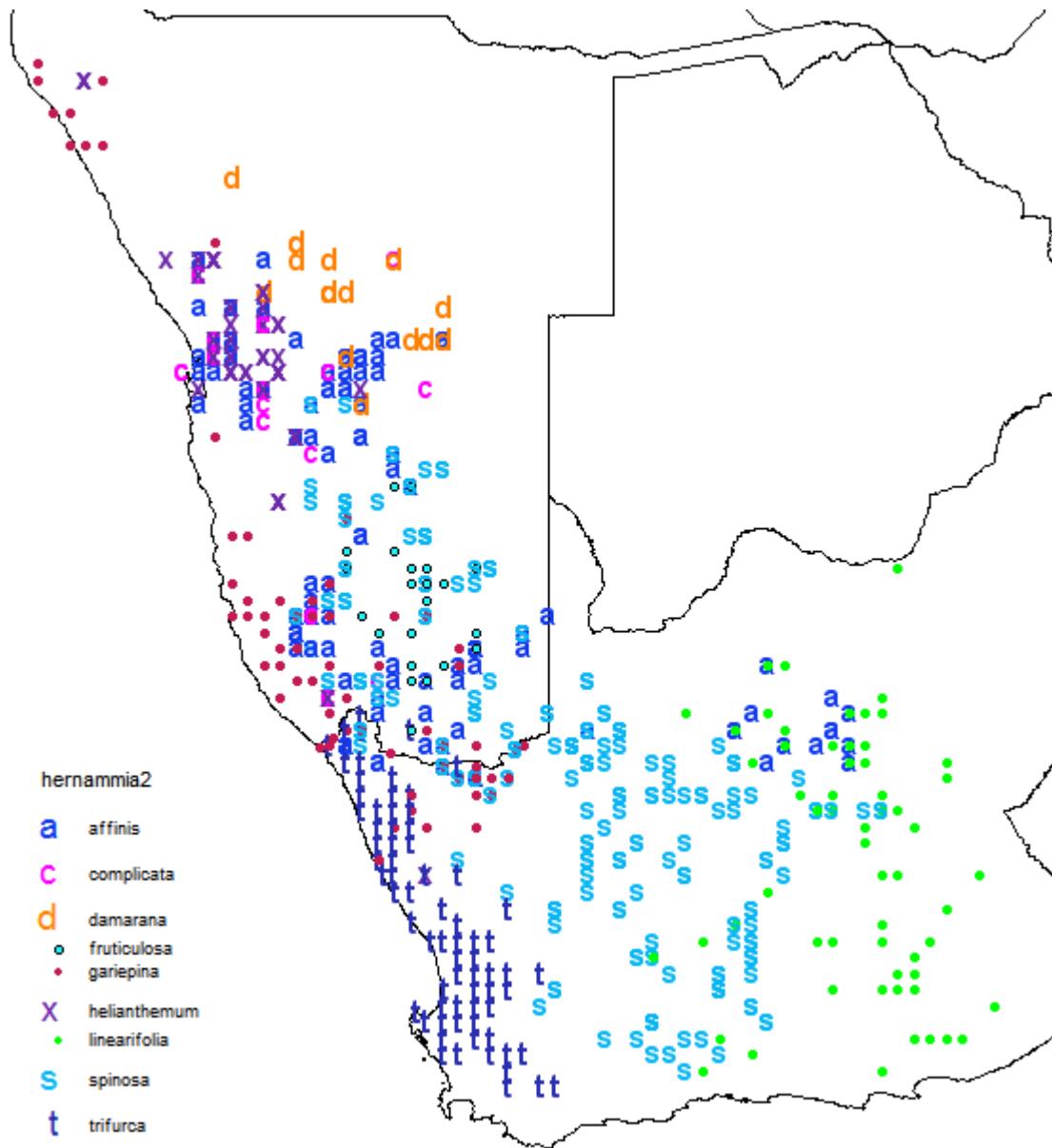


Fig. 4.23 Woody species of the subject. *Acicarpus*.

These maps (Fig. 4.23, above, and Fig. 4.25, below) depict various woody species from the *H. spinosa/affinis* group. *H. trifurca* and *H. linearifolia* are unique within this group in being almost exclusively South African groups. These have been discussed previously, but with species of subject. *Acicarpus* unresolved. This figure also reveals that there are only four species in this group that are both in southern Namibia and South Africa: *H. gariiepina* which occurs within the distribution of *H. trifurca* and *H. spinosa*; *H. affinis* that occupies primarily the arid dolerite

substrates, occurring from around Kimberley to central Namibia; and *H. affinis*; and *H. spinosa* that occupies gneiss and shale in the Karoo and southern Namibia. It is uncertain whether the gap in the distribution within *H. affinis* between the Karoo and Namibia represents a true disjunction, a lack of collecting between the two populations, or whether the South African cluster represents a unique species. It is also dubious whether *H. gariiepina* actually occurs in the north-east of the distribution, and that this is likely belongs to a morphologically similar entity that has not been taxonomically distinguished. The remainder of this clade occurs in Namibia, with some grouping due to climatic requirements.

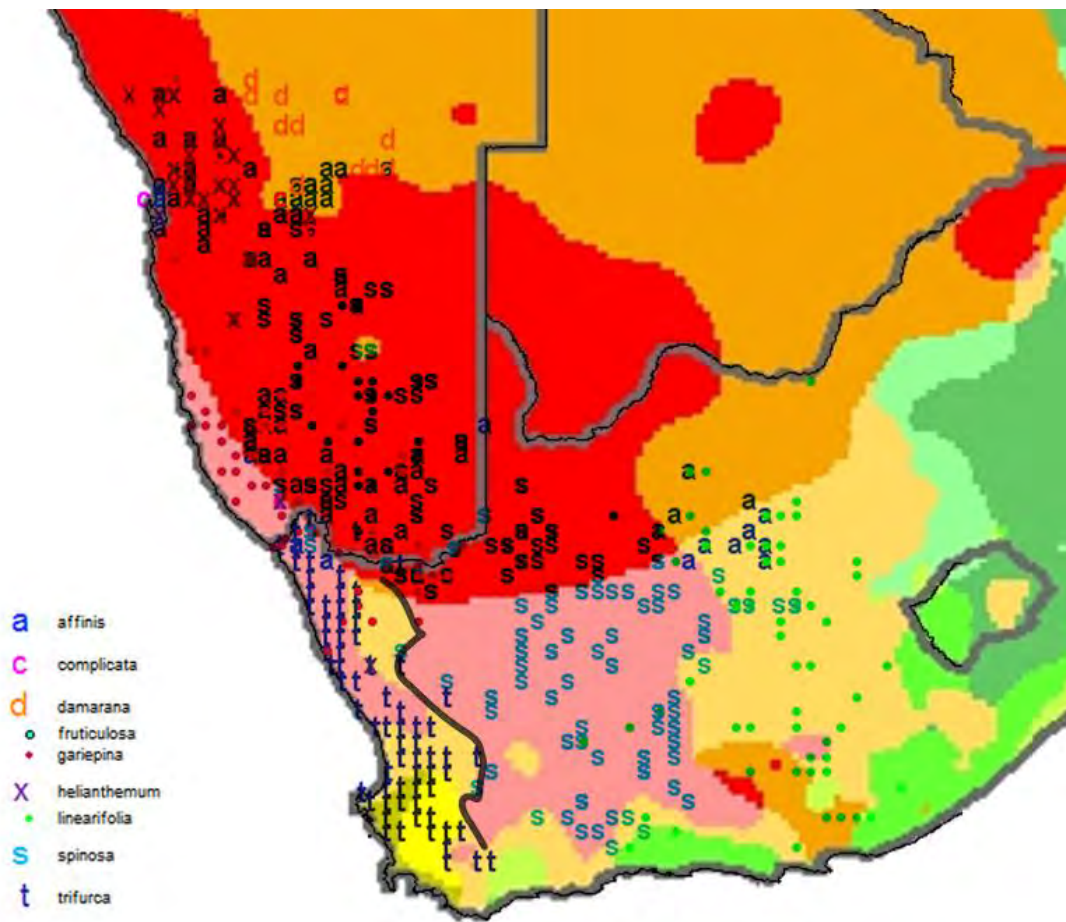


Fig. 4.24. Distribution of the southern members of subsect. *Acicarpus* superimposed on the Köppen-Geiger climate map. The boundary line shows the interface between BWk coastal and BWk inland.

Examining the distribution of these species from sect. *Acicarpus* in relation to the Köppen-Geiger vegetation map reveals some very strong correlations, especially if the coastal cold desert



climate (in pink) is distinguished from the inland portion of it. This I have indicated in Fig. 4.24 by a wavy line outlining the western border of the inland BWk; henceforth designated BWk-coast and BWk-inland respectively. Similarly the cold semi-arid climate (BSk) was assigned to BSk-west and BSk-east relative to the same boundary line. The results of the number and percentage of each species that occur within a vegetation type, and the relative land cover is given in Table 4.1. As would be expected for a predominantly Namibian group, 342 records (92.9%) occur within six modified arid climatic types; with 26 (7.1%) found in 3 temperate climatic types. The most commonly occupied climatic types are the arid types: BWh (139 QDS records); followed by BWk-coastal (90); and BSk-east (47). These make up 75.1% of the total area.

**Table 4.1** The species of sect. *Acicarpus* from Fig. 4.24 with the records of each species plotted by climatic types. Climatic types have been grouped as to whether they are arid or temperate types. The colours that appear on the map are stated. The calculated area of each climatic area is given as a percentage of the total land area of climatic types in which the species are found.

Species	<u>Vegetation Types</u>									Total
	<u>Arid</u>			<u>Temperate</u>						
Map colour	BWh	BWk-inland	BWk-coastal	BSh	BSk-west	BSk-east	Csa	Csb	Cwa	
Area as %	Red	Pink	Pink	Orange	Cream	Cream	Yellow	Beige	Green	<b>100</b>
<i>complicata</i>	12	0	1	1	0	0	0	0	0	14
<i>damarana</i>	3	0	0	12	0	0	0	0	0	15
<i>fruticulosa</i>	21	0	0	0	0	0	0	0	0	21
<i>gariepina</i>	27	20	1	0	3	0	0	0	0	51
<i>helianthemum</i>	24	0	0	0	0	0	0	0	0	24
<i>linearifolia</i>	2	0	4	9	0	38	0	0	4	57
<i>spinosa</i>	50	2	56	0	2	9	0	0	1	120
<i>trifurca</i>	0	2	28	0	15	0	10	11	0	66
<b>Total</b>	<b>139</b>	<b>24</b>	<b>90</b>	<b>22</b>	<b>20</b>	<b>47</b>	<b>10</b>	<b>11</b>	<b>5</b>	<b>368</b>
Total of climate type as a % of total	37.8	6.5	24.5	6.0	5.4	12.8	2.7	3.0	1.4	100
Total records by dominant climate type				342				26		
Total of dominant climate type as % of total				92.9				7.1		

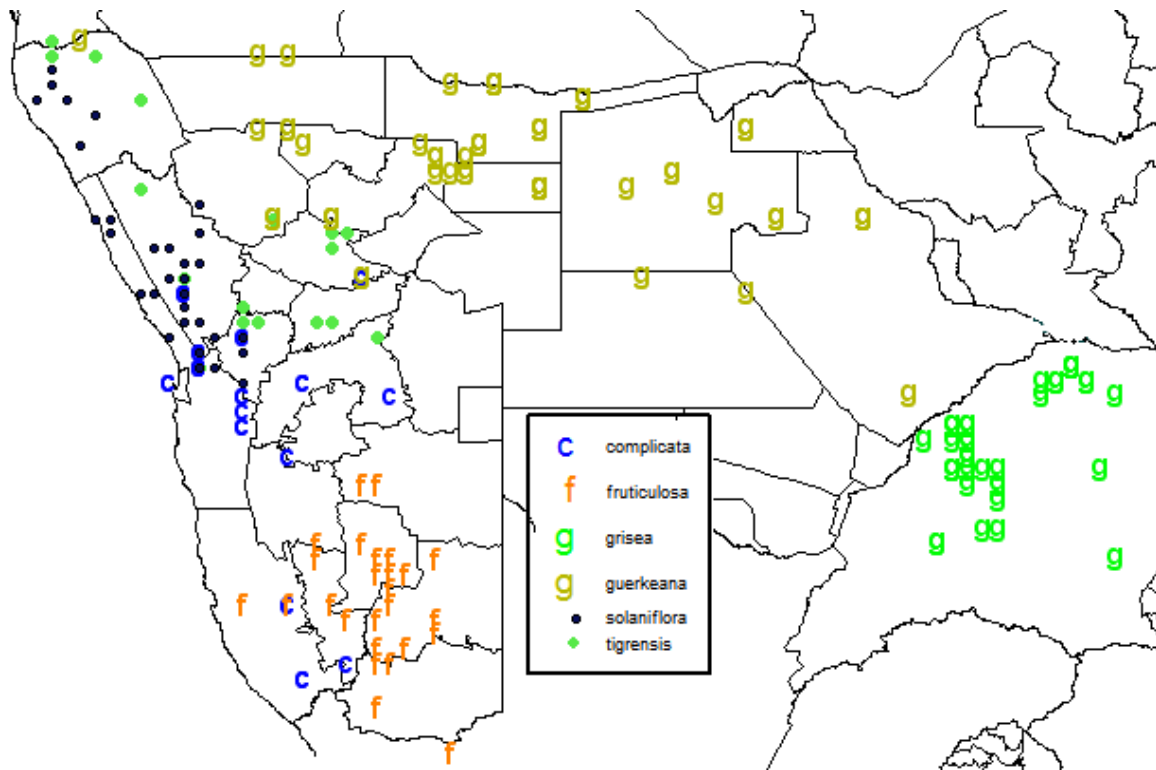


Fig. 4.25 Selected members of the subject. *Acicarpus*

*Hermannia grisea*, *H. guerkeana* and *H. micropetala* (Fig. 4.19) are the only three species of this subsection north of South Africa that occur to the east of Namibia, and are outliers compared to the rest of this group. By overlaying the distribution over the Köppen-Geiger climate map, it can be seen that *Hermannia guerkeana* is almost exclusively associated with a hot semi-arid climate (ED = 28/29 = 96.5% map to a hot-desert climate), and likely can tolerate the particular conditions associated with deep Kalahari sands. Seventy-two of the 76 distribution points of the in-group are divorced from the dune system, indicating that this might be quite a formidable barrier to these species. It is also a consideration that the dunes may form considerable barriers to collecting, although this does not seem to be the case if so many points of *H. guerkeana* were collected amongst the dunes. This is shown in Fig. 4.26 (*Acacia* subproject E1, University of Cologne), where 20 out of 25 (80%) of points overlap the mapped distribution of the dune system, and taking minor errors in dune mapping and locality georeferencing, four of the five remaining points may also occur on dune soils. *Hermannia grisea* on the other hand occurs entirely off the dune system, mainly in hot semi-arid climate (ED = 17/24=71%) , and partially in a humid sub-tropical climate (ED =7/24=29%).

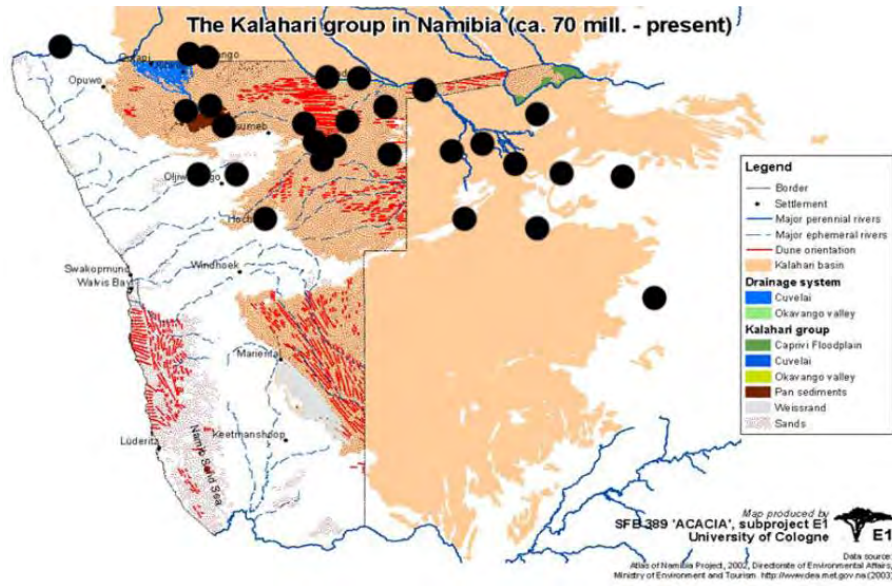


Fig. 4.26 Map of the extent of the Kalahari dune system with *Hermannia grisea* overlaid showing its close association with this substrate.

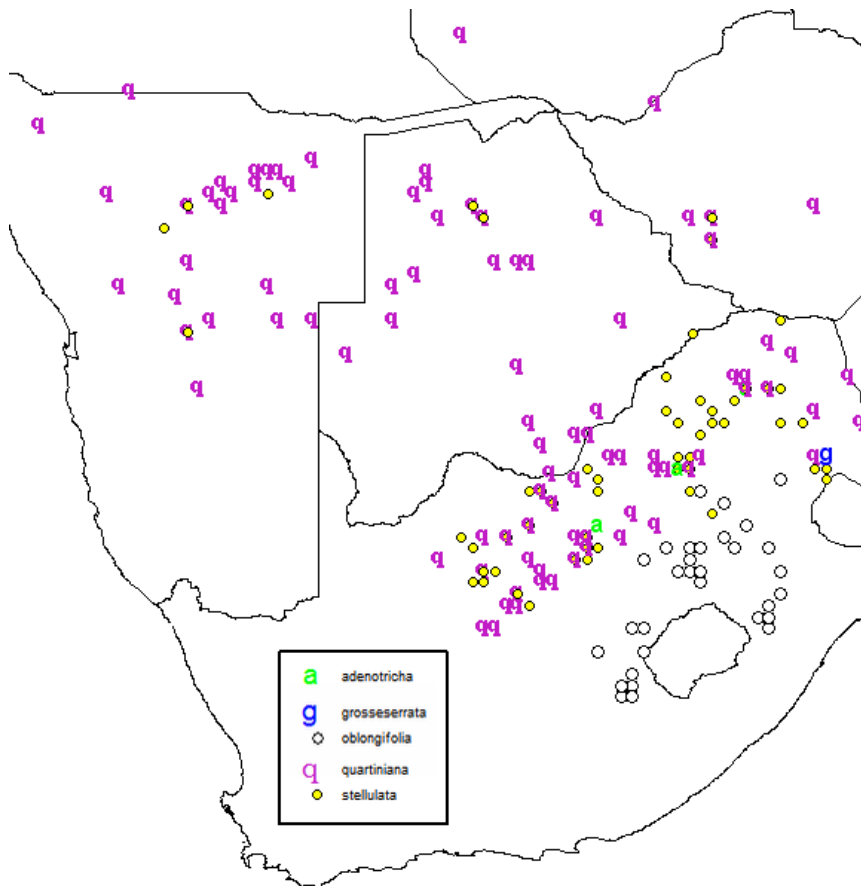
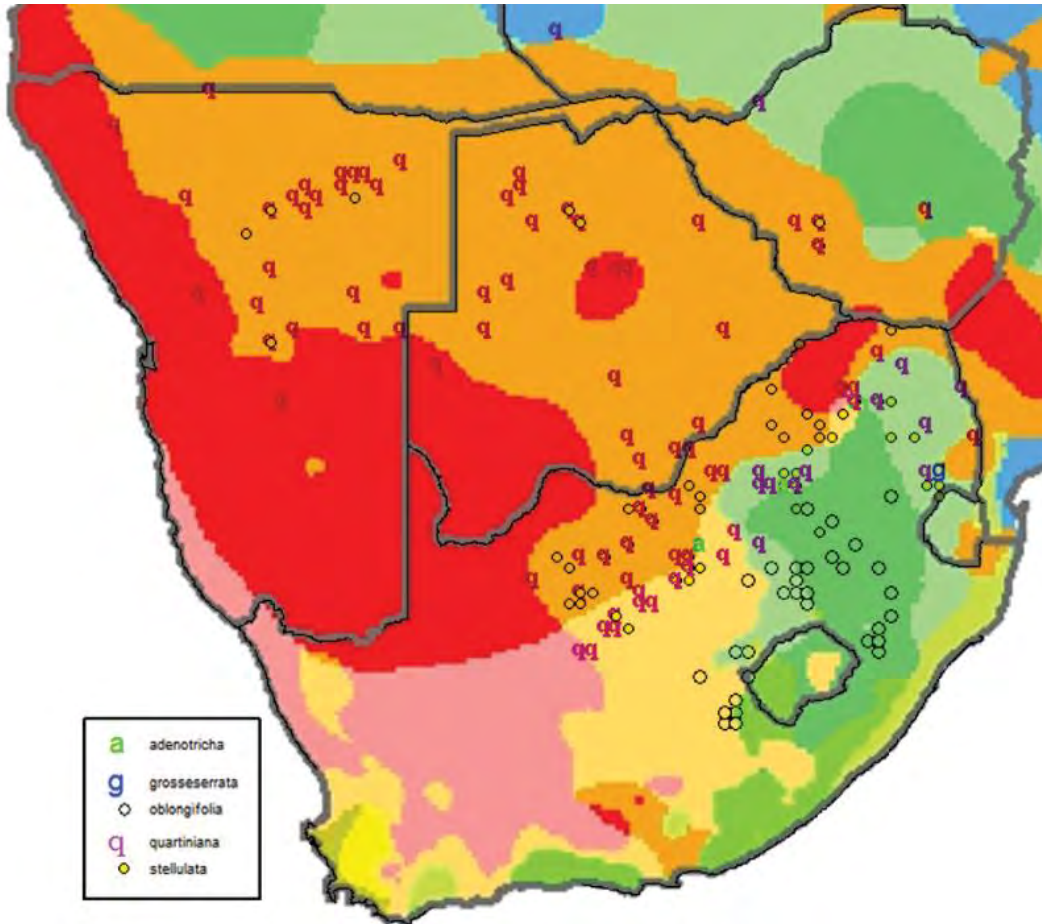


Fig. 4.27 The “Stellulatae”- the small-leaved members of the subject. *Tomentosae*.

This group –Stellulatae” (Fig. 4.27, above), comprises the atypical summer rainfall species that have small leaves relative to the –Grandifoliae”. They are generally less hairy, and frequently possess glandular indumentum. From their distribution and habitats they also appear to favour more arid areas than the remainder of the subsect. *Tomentosae*. The core of the subsect. *Tomentosae* (Fig. 4.29, below) has a more southerly and hence mesic preference.



**Fig. 4.28 Distribution map of the “Stellulatae” superimposed onto the Köppen-Geiger climate map.**

*Hermannia quartiniana* is closely associated with a hot semi-arid climate (Fig. 4.28), with outliers seldom exceeding the boundaries of this climate type by much. It is suggested that this species has a slightly larger tolerance than the boundary set for this climate type. *Hermannia stellulata* occupies the general area between the hot semi-arid climate, the cold semi-arid climate, and the humid sub-tropical climate. *Hermannia oblongifolia* is strongly associated with the subtropical highland climate.

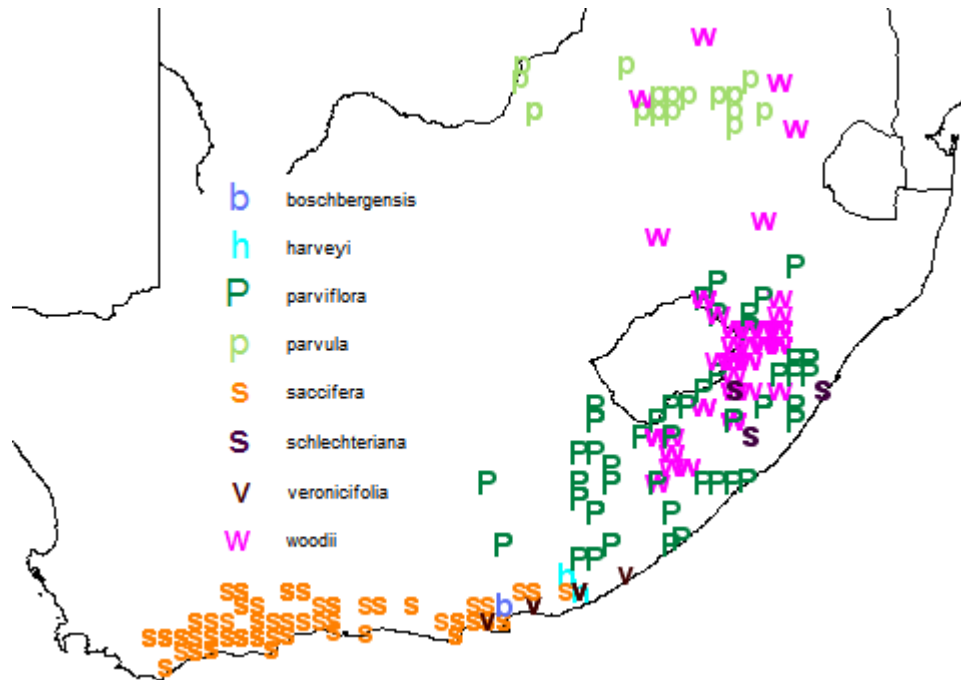


Fig. 4.29 The distribution of the relatively glabrescent species of subsect. *Tomentosae*.

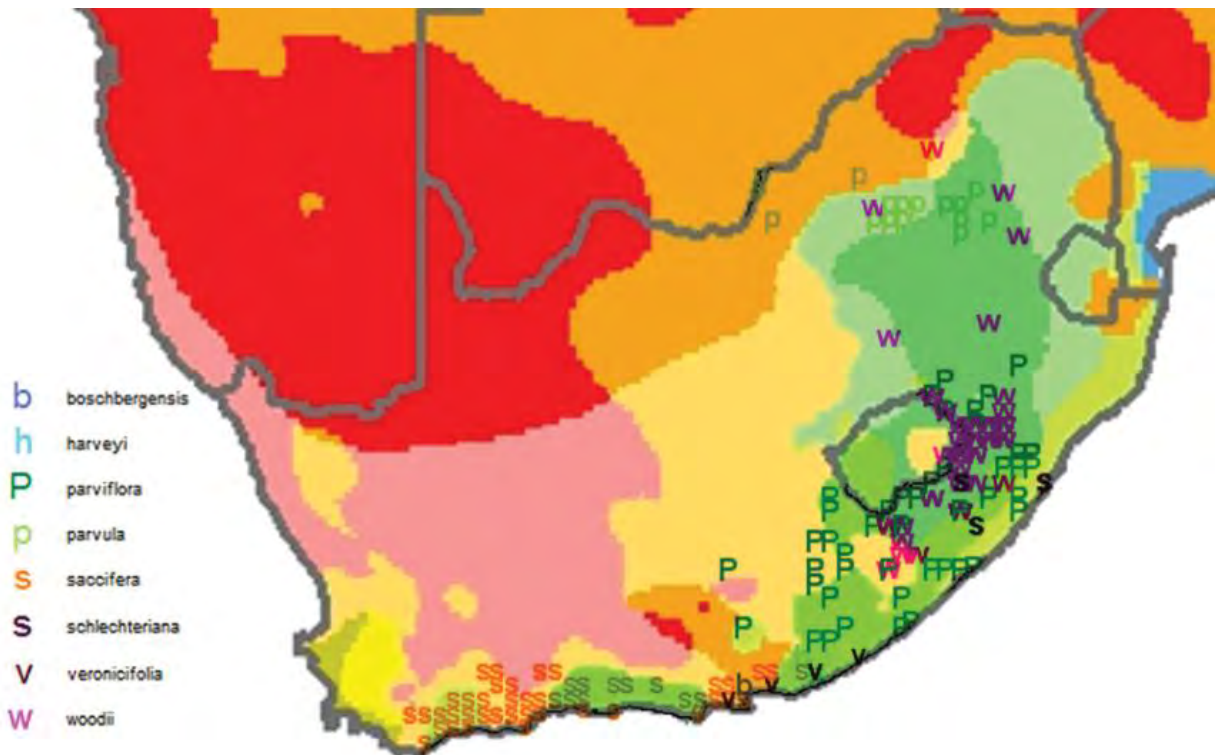


Fig. 4.30 Localities from Fig. 4.29 superimposed onto the Köppen-Geiger climate map.

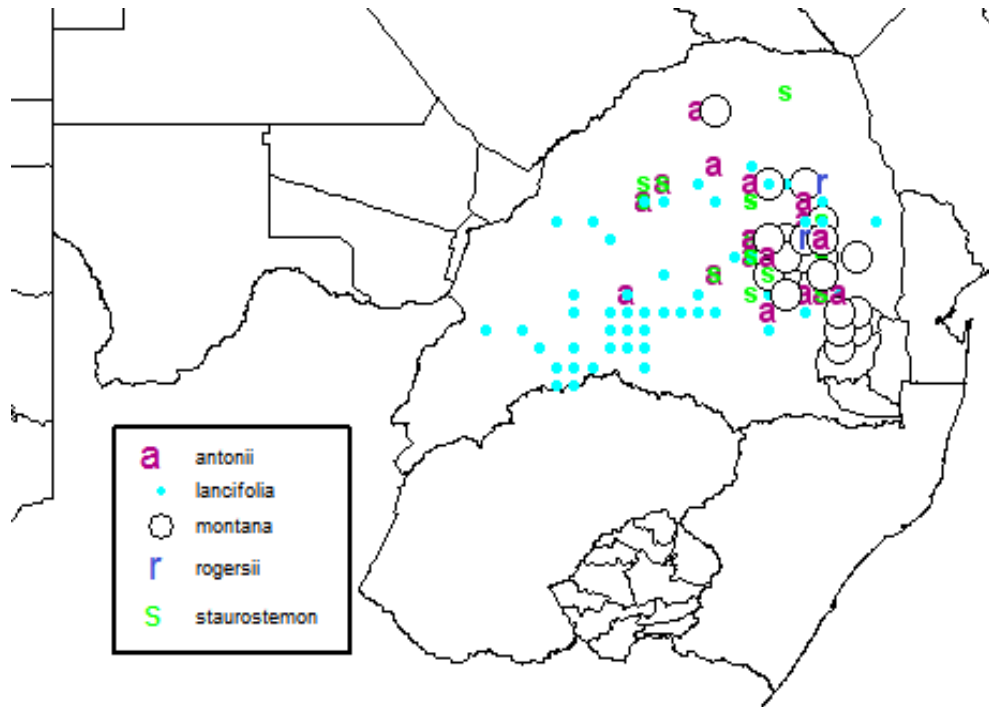


Fig. 4.31 The “Lancifoliae” within subject. *Tomentosae*.

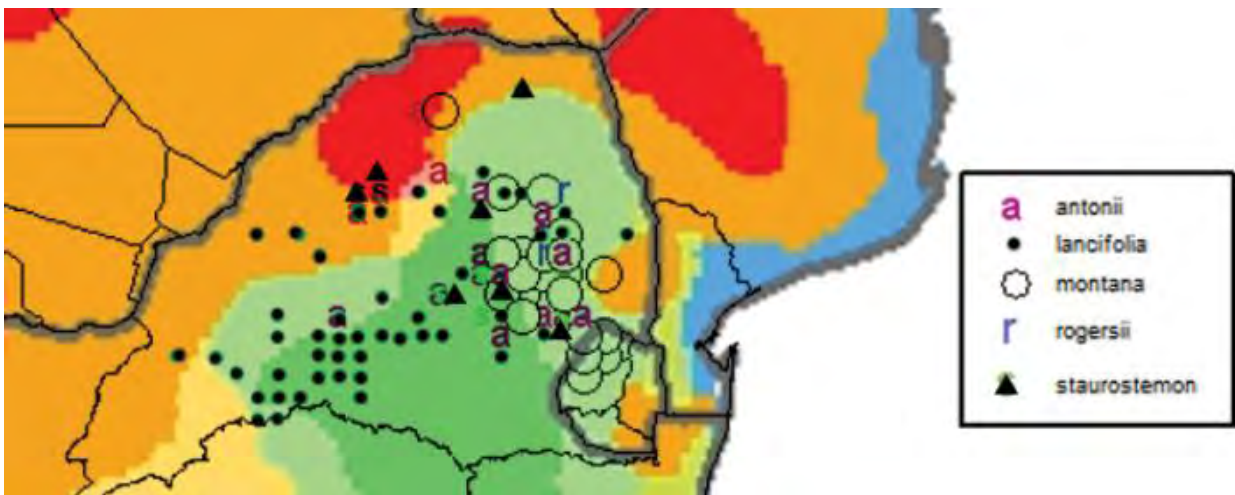


Fig. 4.32 The “Lancifoliae” in subject. *Tomentosae* superimposed onto the Köppen-Geiger climate map.



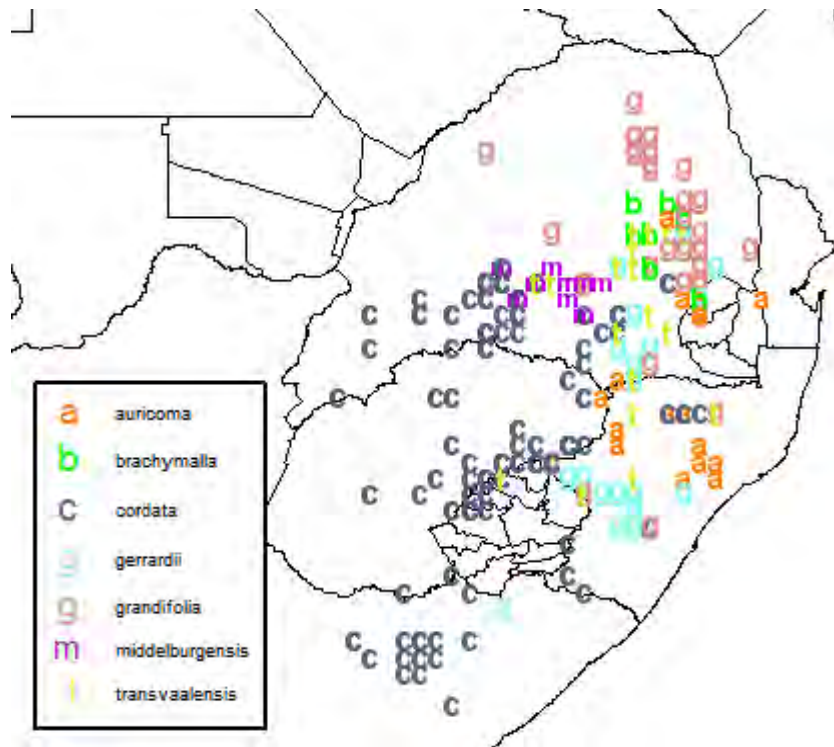


Fig. 4.33 The “Grandifoliae” within the subject. *Tomentosae*.

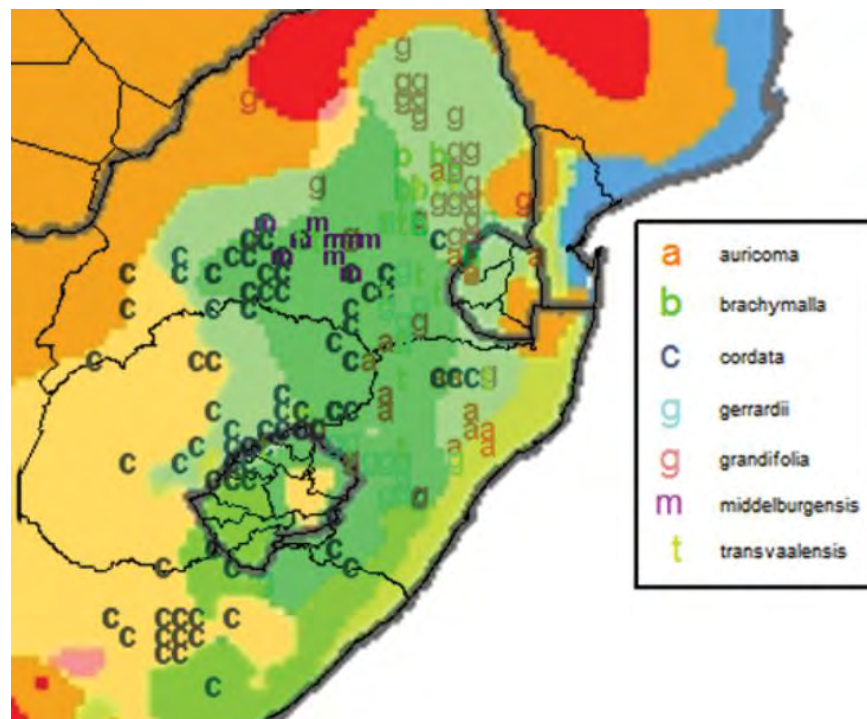
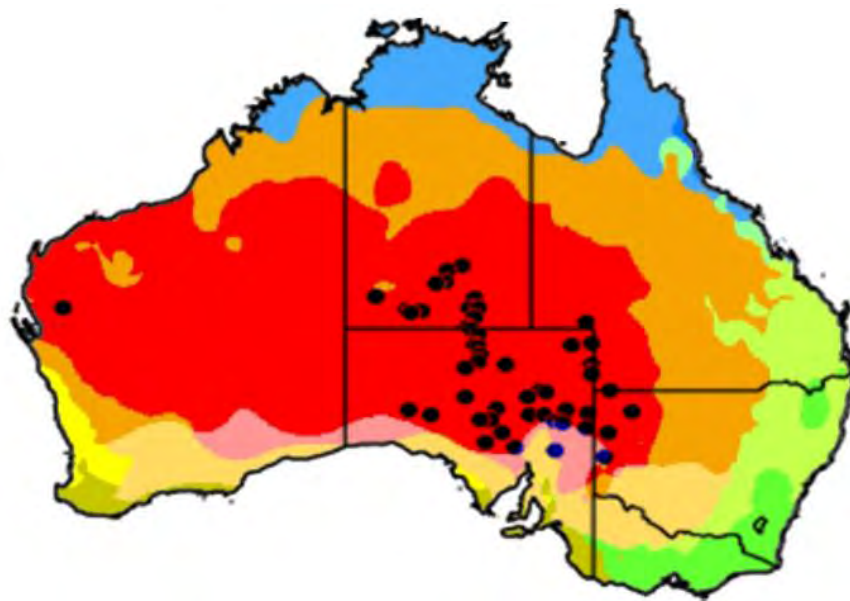


Fig. 4.34 The “Grandifoliae” superimposed onto the Köppen-Geiger climate map.

The centre of diversity for the subsect. *Tomentosae* is from the Drakensberg south-east towards the coast. To the north are the outliers *H. parvula* and *H. woodii*. Only *H. saccifera* escapes the summer rainfall constraint, and grows along the coast and extends as far as the western portions of the winter-rainfall Klein Karoo. *Hermannia saccifera* has a distribution that overlaps five climatic types, and thus is more closely associated with the coast than to any particular climate type (Fig. 4.30). *Hermannia woodii* is mainly associated with a subtropical highland climate (Fig. 4.30). The “Lanceifoliae” (Fig. 4.31, above) all have silver-hairy leaves that are lanceolate in shape. The “Grandifoliae” (Fig. 4.33, above), as the name suggests, all have large leaves that are typically green in colour. They tend to occupy the more mesic portions of the summer rainfall area. The greatest concentration of these species is in the subtropical highland climate Fig. 4.34. ADC values for this climate type are 77% for *H. gerrardii*, and 100% of all *H. middelburgensis* records. All species of “Grandifoliae” and “Lanceifoliae” form a compact group, and there are no particular outliers. The implication of this compactness is that either the climatic envelope is narrow, or the species have a high habitat specificity.



**Fig. 4.35** Distribution map of *Hermannia biniflora* in Australia superimposed on the Köppen-Geiger map.

*Hermannia biniflora* is confined to Australia, and belongs to the subg. *Mahernia*. Fig. 4.30 shows that it is confined almost entirely to the hot arid desert (BWh) climate type.



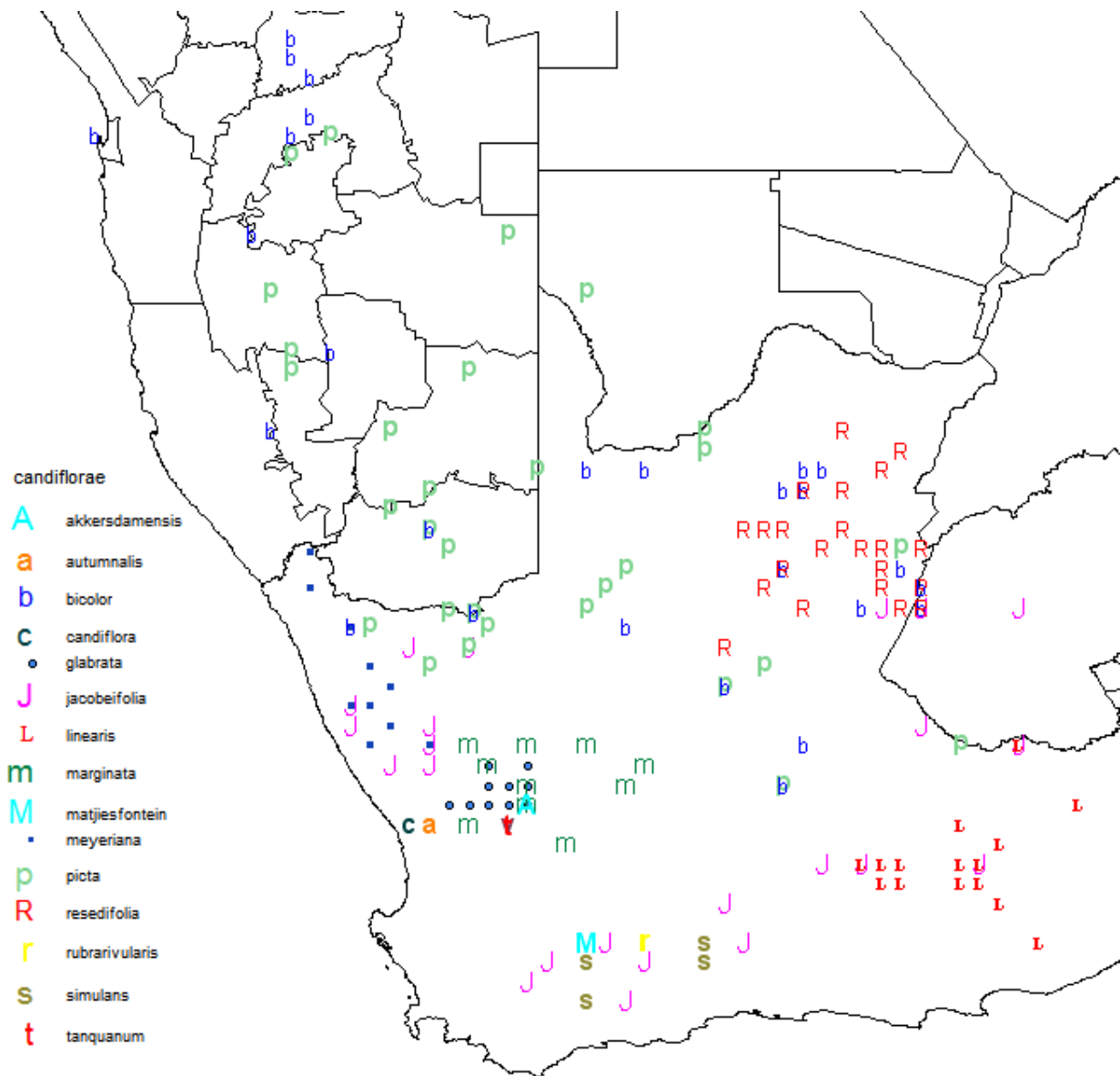


Fig. 4.36 Distribution of the species of the informal group Candiflorae with red and white petals.

#### 4.3.5.4 “Candiflorae”

The “Candiflorae” (Fig. 4.36, above) have about 23 species of which 15 species are plotted. The group is characterised by having lacerated to pinnatifidly dissected leaves with red or red and white striped flowers. It is an arid clade occurring primarily in karroid regions such as Namaqualand, the Klein Karoo, the Groot Karoo and Namibia. There is a distinct distributional patterning in which species tend to be confined to certain areas, and to co-occur with other

species confined to that approximate area. As *H. jacobefolia* transcends geographical boundaries including Namaqualand, the Klein Karoo and the Groot Karoo, as well as several climatic boundaries, it is likely to be a species complex. *Hermannia simulans*, *H. picta*, and *H. bicolor* are other ill-defined species complexes with similar patterns of lack of cohesiveness. Three centres of diversity stand out: the Namaqualand; Klein Karoo; and Kimberley regions, with 9, 5 and 4 species respectively. The most widespread species are *H. picta* and *H. bicolor* that both extend from Central Namibia to the Groot Karoo.

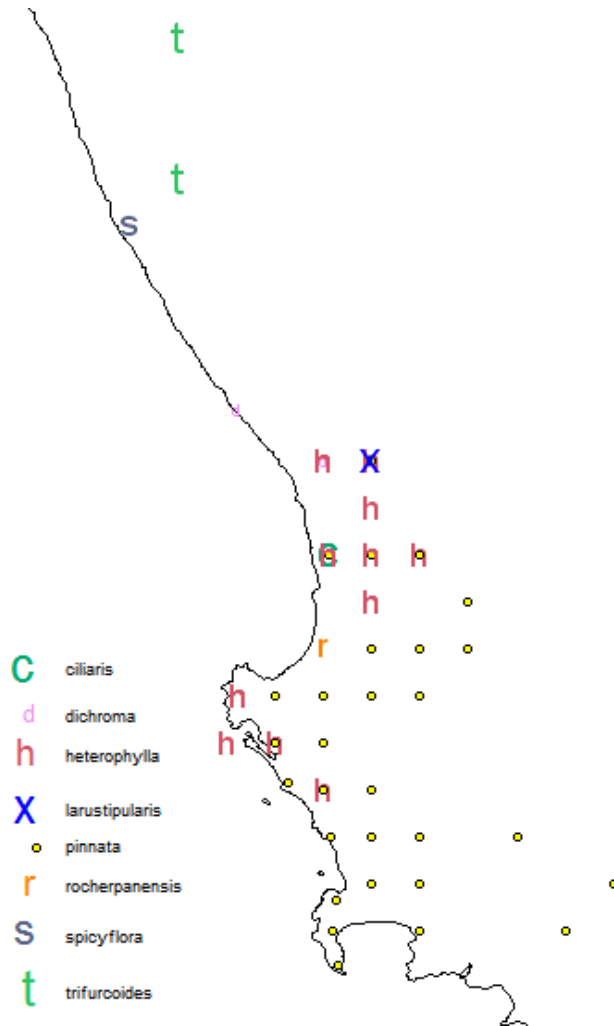


Fig. 4.37 The “Heterophyllae” of sect. *Mahernia*

The “Heterophyllae” (Fig. 4.37, above) forms a recognisable group due to the nearly glabrous narrow leaves, generally with flowers based on a mauve pigment. Most species are restricted to the sandy West Coast and shale lowlands; with *H. pinnata* extending south-eastwards in the lowlands. *Hermannia odoratissima* (prev. *H. spicyflora*) and *H. trifurcoides* have a disjunct distribution in Namaqualand.

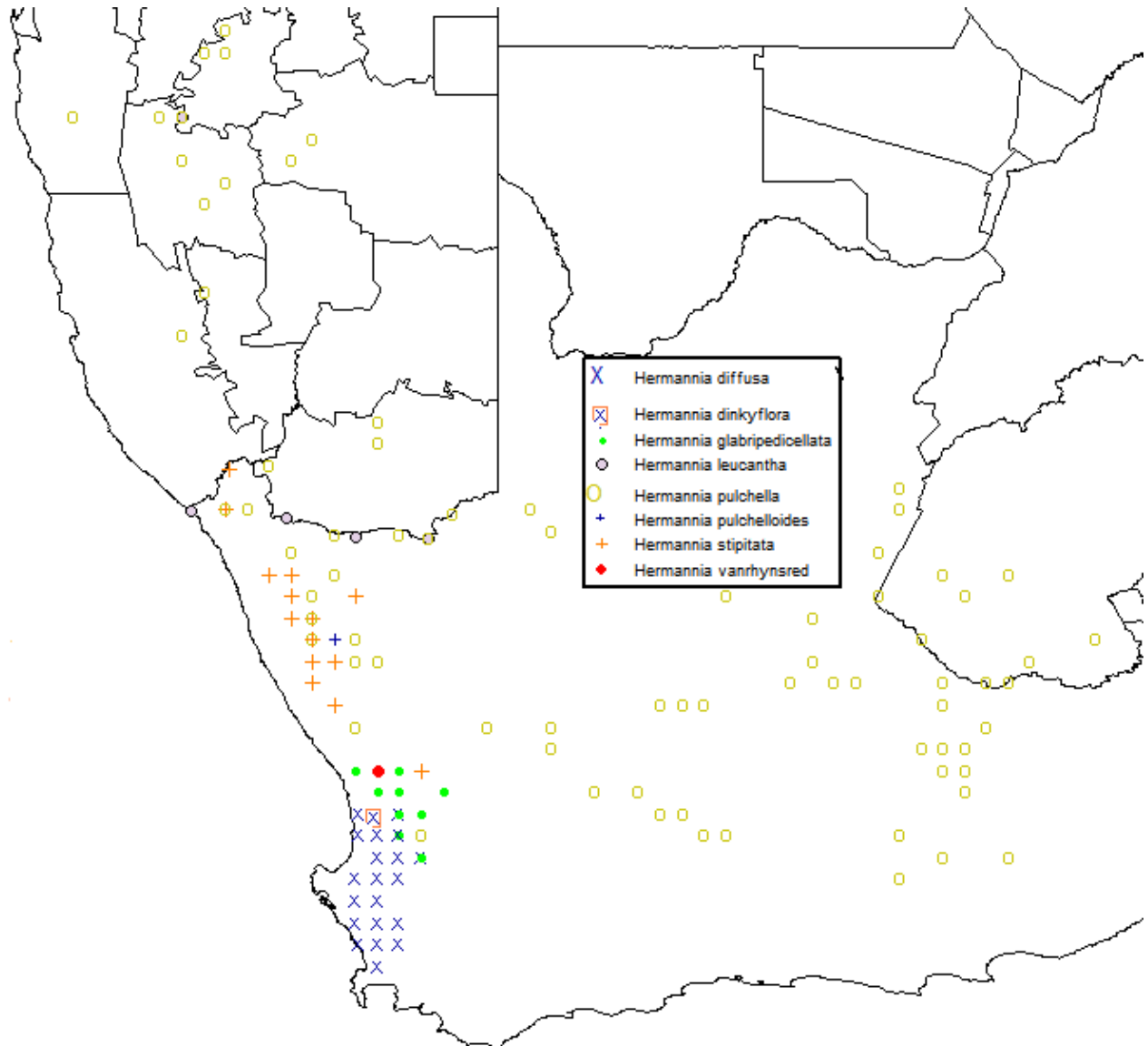
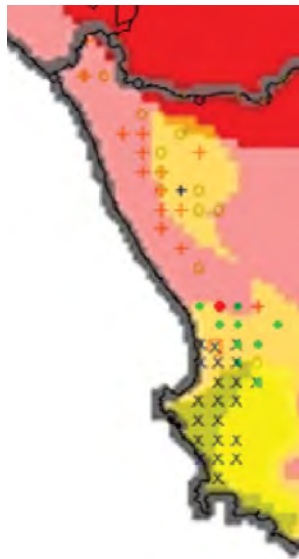


Fig. 4.38 The informal group “Pulchellae”

The “Pulchellae” (Fig. 4.38, above) typically have slender leaves, but unlike the “Heterophyllae”, these tend to be covered in glandular hairs, and petals based on yellow or orange pigments. *H. pulchella* is the only widespread species, occupying only the arid zones from the eastern edge of the distribution of the remainder of the “Pulchellae” throughout the great karoo. *Hermannia pulchelloides* is certainly a sister species, and is only known from the eastern rim of the *klipkoppies* hills in Namaqualand. *Hermannia leucantha* is also very closely related, and differs primarily in having white-pink not yellow flowers. It only occurs along the Orange river. The remaining species occupy the area immediately north of Cape Town as far north as Van Rhyndorp.



**Fig. 4.39** The informal group “Pulchellae” overlaid on the Köppen-Geiger climate map.

Overlaying the distribution map on the Köppen-Geiger climate map (not shown) reveals that while most of the species are found to the west of the BWk boundary line; only *H. pulchella* lies to the east of that line. *Hermannia pulchella* is associated strongly with desert climates (BWh and BWk) and to a lesser extent the cold semi-arid climate (BSk) with an ADC to these regions of 61/63 = 96.8%. A cropped section of this map (Fig. 4.39) shows that *H. diffusa* is largely associated with the Csb or BSk climate type (DE = 17/19 = 89.5%); *H. glabripedicellata* is concentrated around the BSk climate type (DE = 7/9 = 78%) and *H. stipitata* is associated with the coastal BWk climate type (DE=10/15 = 66.7%) with the remainder in the BSk climate type. This group thus generally occupies a distinctly arid climate. *H. dinkyflora* is one of the few species from this group from the more mesic mountainous uplands around Citrusdal.

### 4.3.6 The tropical African species of “Marehnia”

The distribution of all tropical African species is presented in Fig. 4.40. It can be seen that these species are closely associated with a hot desert (BWh) and a hot semi-arid climate (BSh). These two climate types account for 73.9% of all the tropical African species with humid sub-tropical, and humid savanna being the next most important vegetation types. It can be seen in Fig. 4.40 that *H. tigrensis* closely follows the band of hot semi-arid climate that crosses tropical Africa.

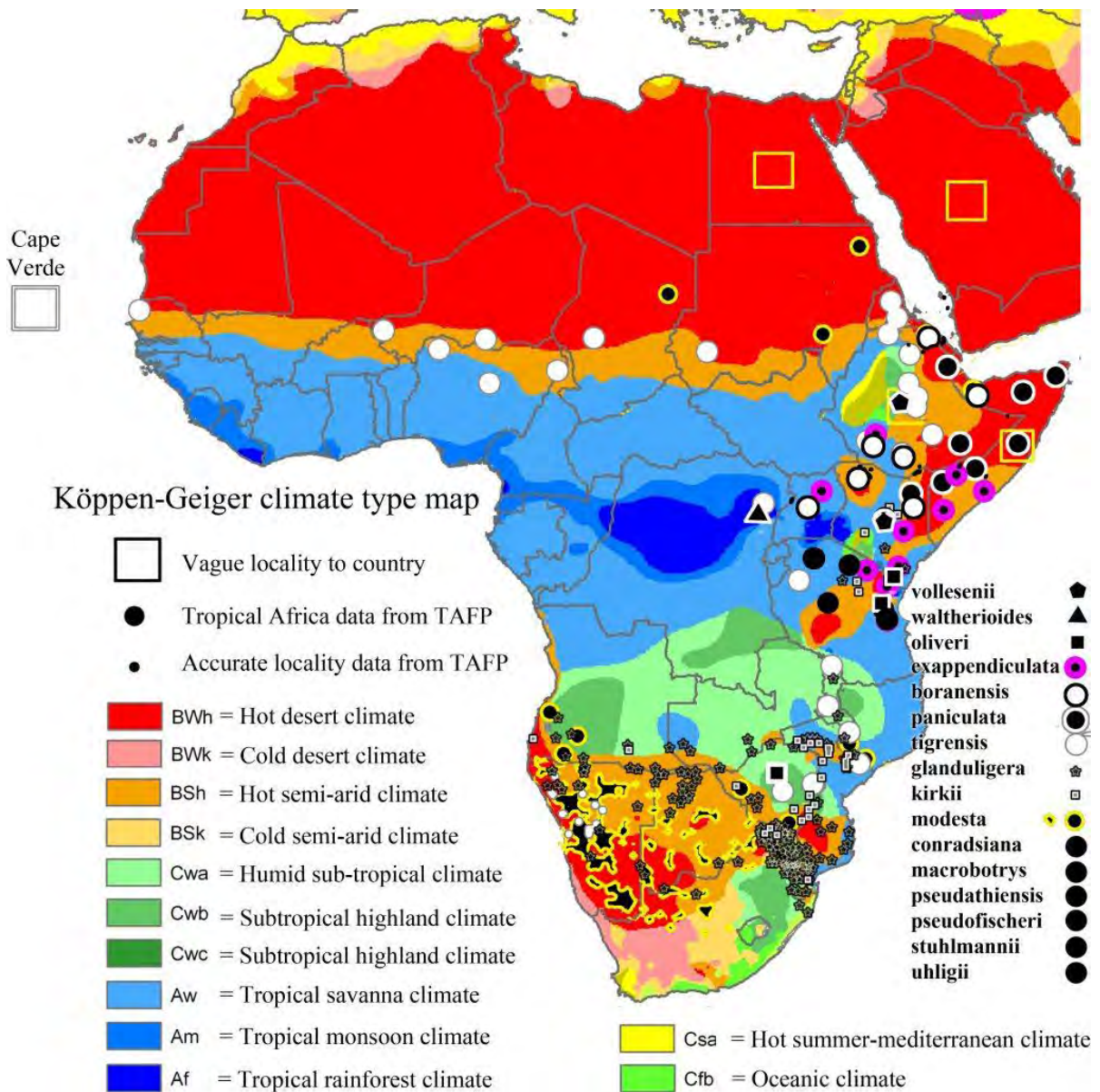


Fig. 4.40 The distribution of all tropical African species overlaid on the Köppen-Geiger climate map.

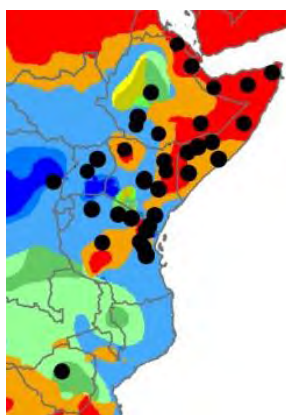


Fig. 4.41 The distribution of just the section “Marehnia” on the Köppen-Geiger climate map.

Table 4.2 Frequency of species occurrences within vegetation types derived from Fig. 4.40 and only for “Marehnia” from Fig. 4.41. Key to vegetation codes is in Error! Reference source not found., with “other” comprising Af, Cwc, BSk and BWk. Species with a „\*” are from the subsect. *Acicarpus*, not “Marehnia”.

Species	Vegetation Types						Total
	Arid		Temperate	Tropical		Other	
	BWh	BSh	AW	Cwa	Cwb		
* <i>H. glanduligera</i>	22	55	10	40	8	1	136
* <i>H. kirkii</i>	7	10	10	5	3		35
* <i>H. modesta</i>	99	79	2	22	3	15	220
* <i>H. tigrensis</i>	17	12	4	5	4	7	49
<i>H. boranensis</i>	4	1	2				7
<i>H. exappendiculata</i>	1	4	5				10
<i>H. paniculata</i>	8						8
<i>H. conradsiana</i>			1				1
<i>H. macrobotrys</i>			1				1
<i>H. oliveri</i>		2			1		3
<i>H. pseudathiensis</i>			1				1
<i>H. pseudofischeri</i>		1	1				2
<i>H. stuhlmannii</i>		1	1				2
<i>H. uhligii</i>					1		1
<i>H. volkensis</i>					1		1
<i>H. vollesenii</i>			1		1		2
<i>H. waltherioides</i>			1			1	2
Total Tropical Afr.	158	165	40	72	22	24	481
% of Total	32.8	34.3	8.3	15.0	4.6	5.0	100
Total Marehnia	13	9	14	0	4	1	41
% of Total Marehnia	31.7	22.0	34.1	0.0	9.8	2.4	100



If one excludes the first four species in Table 4.2, the tropical African members of the subject. *Acicarpus*, a different pattern emerges, as depicted in Fig. 4.41 **Error! Reference source not found.** About half (53.7%) of the records fall into the hot desert and hot semi-arid climates with the other half predominantly occupying a tropical savanna climate (34.1%) and to a lesser proportion the subtropical highland climate (9.8%). From this overall picture of the tropical African species, it would appear that a significant proportion are found in hot desert and hot semi-arid climates.

–*Marehnia*’ can be split into two groups, species that occur in more mesic areas (Fig. 4.42a) and those that are largely confined to more arid areas (Fig. 4.42b).

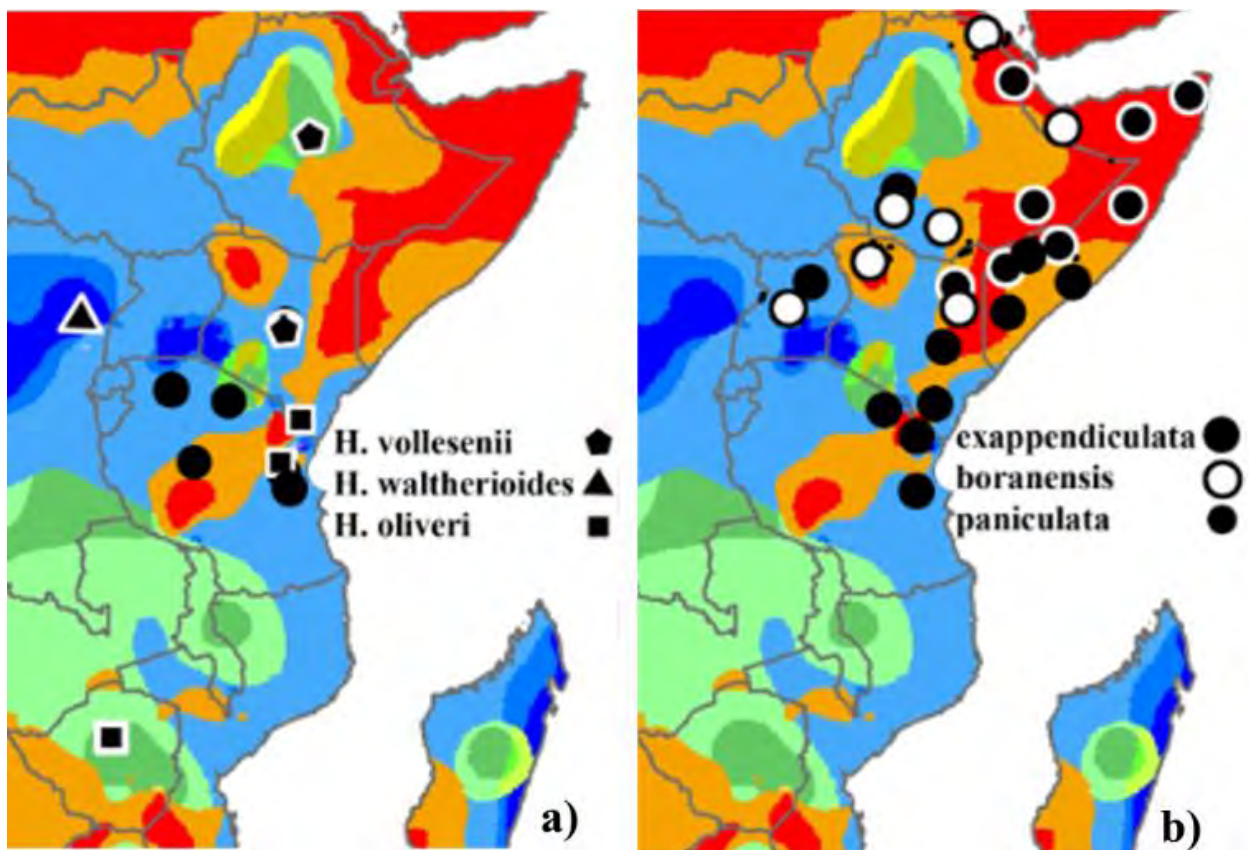


Fig. 4.42 The distribution of species of “*Marehnia*”. Fig. 4.42a shows the distribution of the species associated with a more mesic climate, distinguishing the outliers (*H. vollesenii*, *H. waltherioides* and *H. oliveri*) from *H. conradsiana*; *H. macrobotrys*; *H. pseudathiensis*; *H. pseudofischeri*; *H. stuhlmannii*; *H. uhligii*; and *H. volkensii*. Fig. 4.42b shows the distribution of the more arid species, with *H. paniculata* having a white border around the dots; *H. boranensis* with a black border around a white circle; and *H. exappendiculata* a solid black circle.

In Table 4.2, it can be seen that of those species from the arid areas, 72% are from hot desert and hot semi-arid climates, and the remaining 28% are from tropical savanna. None of the species from the more mesic areas are from the hot desert, whereas for arid-zone species – 27% are from the hot semi-arid climate, 47% are from the tropical savanna, and 27% are from the subtropical highland climate. There are ten species that occupy more mesic areas, and three that occupy the arid areas.

The combined climate and distribution maps demonstrate that within “*Marehnia*” there are species that tend to occupy either more arid or more mesic conditions. A phylogeny of this clade would both help to determine the relationship between these species, and also help to understand the history of the group and whether they have more mesic or more arid origins. This will help to determine how the ancestor of “*Marehnia*” reached tropical Africa from Southern Africa.

## 4.4 Discussion

### 4.4.1 Summary of findings

In this chapter, species are placed within phylogenetically and morphologically informed groups. Strong distributional clustering is demonstrated within clades thus defined. This is suggestive of groups that have limited dispersability and genetic adaptability. The distributional clustering may be seen as indirect support for the taxonomic framework.

### 4.4.2 Distribution patterns

The subg. *Mahernia* is almost entirely confined to Southern Africa with a single dispersal event having given rise to a single species in Australia. The subg. *Hermannia*, in contrast, has several species well-represented north of Southern Africa, with diversification having taken place in Tropical East Africa and America. Distribution gaps in the Northern Cape and Western Namibia are apparent for subg. *Mahernia* (Fig. 4.6a), while a prominent gap is apparent in Pondoland and Lesotho for subg. *Hermannia* (Fig. 4.6b). Interestingly, subg. *Hermannia* is well represented in the Northern Cape and Western Namibia, while subg. *Mahernia* is well represented in Pondoland and Lesotho; thus the gaps cannot be explained by undersampling in the respective regions.



Exploring patterns at sectional and subsectional level it is found that the bulk of sect. *Hermannia* occurs in South Africa west of Swaziland and up to southern Namibia, and does not extend much beyond Windhoek. The subsect. *Mahernia* has an almost identical general pattern, differing only in being better represented north and east of Swaziland. The overall distributions of these two groups are even more contracted towards the Cape, if one excludes the outlying two species of subg. *Hermannia* highlighted in Fig. 4.3, and the outlying five species of subg. *Mahernia* highlighted in Fig. 4.5. Both groups also have a marked absence along the East Coast of South Africa and are confined to South Africa and southern Namibia. The similarity in the distribution of these groups may be explained by their possible Cape origins (or at least affinities), and thus a general intolerance of strong summer rainfall humid climates. The subsect. *Tomentosae* and subsect. *Acicarpus* on the other hand are both absent from the Cape and are largely restricted to summer rainfall regions. These two clades thus exhibit a distribution complementary to that exhibited by sect. *Hermannia* and subsect. *Mahernia*. This feature of complementarity is a general one for the genus *Hermannia*, taking into account also the tropical clade “*Marehnia*”. Thus while the genus as a whole covers most of sub-Saharan Africa, individual clades are restricted in their distributions. This points to the possibility of separate centres of diversity for the different clades, a theme to be taken up further in Chapter 6. The geographic specificity within a species or clade, yet widespread occurrence of the genus as a whole, makes *Hermannia* a good choice of genus for long term climate change studies, a theme to be taken up again in Chapter 7.

#### 4.4.3 Climatic associations

Overlaying the distribution of clades with the updated Köppen-Geiger climate map reveals a number of associations between their distributions and prevailing climatic conditions. The sect. *Pinnatifidae* (subg. *Mahernia*) and subsect. *Mahernia* tend to occur within the south-western portion of Southern Africa, occupying desert, semi-arid and Mediterranean climates. The sect. *Tomentosae*, on the other hand, occupies the north-eastern portion of Southern Africa and is associated with tropical and subtropical climates. In subg. *Hermannia*, sect. *Hermannia* occupies the semi-arid and Mediterranean climate types whereas subsect. *Acicarpus* occupies the hot

desert and hot semi-arid climate types. “*Marehnia*” occupies mostly the hot desert and hot semi-arid climates, and to a lesser extent the tropical savanna climate type. In the subsect. *Tomentosae* the majority of species occupy subtropical and oceanic climates. Some degree of caution is necessary when interpreting these results. Firstly, current climatic conditions cannot accurately portray conditions prevailing when speciation occurred. Secondly, collection localities were assigned discretely to climate types, whereas in reality the border region of two climate types is a continuous gradient. Furthermore, the updated Köppen-Geiger map is coarse. Despite these caveats, the climatic associations exhibited by various clades supports an hypothesis that speciation within *Hermannia* is correlated with climate. This hypothesis is further investigated in Chapter 7. It is worth noting that the updated Köppen-Geiger map, based on 1436 precipitation and 331 temperature stations, has proven to be an adequate representation of climate for phytosociological studies when compared to global climate models (Peel, Finlayson et al. 2007).

#### 4.4.4 Divisions within the cold desert climatic region (BWk)

The central to northern and western Cape encompass the cold desert climatic region (BWk), as depicted in light pink in Fig. 4.24. *H. trifurca* (subsect. *Acicarpus*) and *H. stipitata* (“*Pulchellae*” of subg. *Mahernia*) are confined to a coastal strip of the BWk, while *H. spinosa* is confined to a complementary inland subregion of the BWk, as depicted in Fig. 4.38. A boundary line between these two subregions - the BWk coastal and BWk inland – is included in Fig. 4.24; this division is not made in the Köppen-Geiger climate map. Overlaying the rainfall proportionality map provided by SARVA (not shown) it can be seen that the coastal BWk falls wholly within the winter-rainfall area, whereas the inland BWk is predominantly late-summer rainfall, and rapidly grades from winter in the west, to late summer rainfall in the east (Schultz 2008). These rainfall differences, together with the segregated distributions of particular species mentioned above, are suggestive of a possible refinement to the Köppen-Geiger map. This proposed refinement is further supported by the phytochoria results presented in Chapter 7.

Although the collection localities were assigned discretely to one or two climatic types, there is no natural border, and the climate would continuously grade in space and time from one classification to the next. Within a gradient, local climate conditions not taken into account by

the model would on various scales from micro niche habitats to larger mountain scale effects would allow for habitats to be suitable or unsuitable for a particular species relative to the larger scale climate.

Furthermore limitations of dispersal of propagules would limit the ability of species to reach suitable habitats. Identifying sister species with large distributions and contrasting them with highly endemic species could be used as a means to identify species with either differing dispersal modes, or novel innovations allowing a species to occupy more climatic regions than the more restricted sister species.

#### **4.4.5 Individual species with distributions atypical for their clade**

Several examples have been found of species whose distribution does not fit with that of the majority their clade. The core of subsect. *Acicarpus* is confined mainly to Namibia, consisting of hot desert (BWh) and hot semi-arid (BSh) regions. However, the three species *H. trifurca*, *H. spinosa* and *H. linearifolia* of subsect. *Acicarpus* occur elsewhere: the cold desert (BWk) and Mediterranean (Csa and Csb) climates for *H. trifurca*, the cold desert (BWk) for *H. spinosa*, and the cold semi-arid climate (BSk) for *H. linearifolia*.

The fact that clades at sectional or lower levels tend to associate with a well-defined climatic region or set of regions is indicative of phylogenetic conservatism. This may be explained by characters that limit the potential range of a species to a restricted variety of climate types. The exceptional species within clades may have undergone mutations affecting these characters, endowing them with less ability to survive in the climatic type of their clade, but a newly acquired ability to thrive in a neighbouring climatic region. In particular, this mechanism is in strong contrast to the null hypothesis which implies uniform distribution of all the species of a clade across the entire distribution of the clade, and provides a basis for climatic association. This mechanism also suggests that it is climatic specialisation, not limited dispersability, that plays a larger role in restricting the distribution range of species of *Hermannia*.

#### 4.4.6 Summary of key findings

There are at least four geographically and climatically distinct clades within the genus *Hermannia*, each with a different centre of diversity, typically with outliers considerably removed from the centre of diversity. Species within clades tend to favour similar climates, indicating a mechanism whereby phylogenetically determined characters impose fitness for a constrained variation of climatic conditions. Distributional outliers may indicate important adaptations to a considerably different climate. The distributional constraints of *Hermannia* species are thus apparently influenced by climate rather than dispersability. This makes the genus a potentially useful group for studies of biogeography and climate change. This provides motivation for the cluster and climate analyses of Ch. 7.

## 5. Character reconstruction and evolution

### 5.1 Introduction

The Bayesian analysis of the ITS region presented in Ch. 3 represents the best current estimate of relationships within *Hermannia*. The phylogeny contains representation of a broad range of morphological, ecological and distributional differences which are the product of speciation. These patterns of speciation can be examined through the investigation of character changes and their relative distributions on a phylogenetic tree (Barracough and Nee 2001). The reconstruction of ancestral character state has attained a central role in modern evolutionary biology (Cunningham, Omland et al. 1998), and is the focus of this chapter.

A number of clades have been identified through the use of molecular phylogenetics within Ch. 3. Morphological support for these groups will be evaluated, both with the aim of establishing characters important for their delimitation, and to understand factors influencing their speciation.

Characters for reconstruction were examined that could be readily obtained by visual means or from literature, including the comprehensive pollen dataset from Coetzee and van der Schijff (1979). Pollen morphology has been considered one of the most important characters in the delimitation of genera and species within the Rubiaceae (Naiki and Nagamasu 2003) with the number of colpi particularly useful in their study of *Damnacanthus* (Rubiaceae). Colpi are grooves or apertures on the surface of pollen, and the number of colpi are considered diagnostic in the identification of pollen (Allaby 2004). Colpi frequently vary within a genus, and occasionally within a species. In the Bruniaceae pollen characters such as colpus number have been used to reclassify species of *Brunia* into *Berzelia* (Hall 1986).

A further aim of this chapter is to provide further evidence for the ancestral areas and possible directions of dispersal from or to these areas. Geographic and climatic outliers were identified in Ch. 4, and highlighted as possibly interesting taxa from a historical perspective. A number of these taxa are examined further in this chapter using state reconstruction. A study of a number of

Cape clades as defined by Galley and Linder (2005), shows both immigrations from, and emigrations into the fynbos region for arid groups (Bellstedt, van Zyl et al. 2008; Schrire, Lavin et al. 2009). The highest mountains within South Africa, the Drakensberg mountains, have been shown to provide an important refugial link for Cape taxa. The derived ancestral states will also be examined to determine whether this mechanism may be applicable regarding the Drakensberg *Hermannia* species.

**The Key Questions are thus:**

- a) What can be said about patterns of inheritance of morphological characters in *Hermannia*?
- b) Are there any synapomorphies that can be used to circumscribe clades within *Hermannia*?
- c) What are the patterns of dispersal and colonisation that can be inferred by reconstruction?
- d) What can reconstruction reveal about ancestral habitats and biomes used by *Hermannia*?
- e) Did an annual life-form arise once, or multiple times independently?

**5.2 Methods**

The Bayesian molecular phylogeny derived in Chapter 3 (Maddison and Maddison 2009) was pruned to a single accession per species, resulting in 134 species covering all the major clades. Within each recognised clade, species names are assigned a particular colour to facilitate clade recognition. A new Mesquite matrix of 14 selected characters was initiated, with characters specified as `_unordered'` to reduce *a priori* assumptions of homology. Characters were chosen for their potential taxonomic, ecological or evolutionary utility (Table 5.1). Quantitative characters (rainfall) were split into equal size classes of 100mm each. Pollen diameter was quantized using a method unstated by the authors of the pollen paper (Coetzee and van der Schijff 1979).

**Table 5.1 Characters used in character reconstruction and the number of states**

Character	Number of states	Character	Number of states
Flowers per axil	3	Leaf dissection	4
Horn length	4	Flower colour	9
Capsule shape	3	Vegetation biomes	8
Fruit rotation	2	Rainfall	10
Pollen diameter	6	Distribution	9
Pollen colpi	2	Geology	9
Life history	3		

Character states for flower colour, flowers per axil, capsule shape, capsule-horn length, fruit rotation, life history, and leaf-dissection, were obtained mostly from photographs of the species, as well as from herbarium sheets and taxonomic literature (Harvey and Sonder 1860; Verdoorn 1980). Geology was derived from photographs, herbarium sheets and taxonomic literature. The geographic region was obtained by plotting the molecular accessions on a map of South Africa. The biome reconstruction is represented by the molecular exemplar, and its locality associated with the biome as presented in Rutherford et al. (2006). Pollen diameter and number of colpi were extracted from Coetzee and van der Schijff (1979). Mean annual precipitation reconstruction utilized the locality of the molecular exemplar to place it within a vegetation type *sensu* Mucina et al. (2006). The Mean Annual Precipitation (MAP) for the particular vegetation type was extracted from the climate graphs that are presented in Mucina et al. (2006). The rainfall reconstruction utilized a 100mm class size. For species beyond South Africa, precipitation values were extracted from the average precipitation of the climatic envelope for the species, derived from the Worldclim dataset (See Section 7.2.4).

Ambiguous codings included both possibilities, and uncertain states were coded with a ?. Parsimony reconstruction was utilized in all cases. The outcome of each state represents a majority-rules consensus.

In Mesquite, the phylogenetic trees were rooted on *Hibiscus* as it is a representative within the Malvaceae of the Malvoideae, a distantly related subfamily of the Byttnerioideae. The resulting trees were then ladderized to the right, and orientated vertically. The legend was coloured appropriately and the resulting tree exported as a PDF for subsequent viewing. It is important to note that on the figures of reconstructions, ***only accessions with a block between the terminal tip and the name have been coded***, and where a block is absent, the colour of the branch is a parsimony reconstruction.

### 5.3 Results

The figures (Fig 5.1-Fig 5.13) present reconstructions of the ancestral states for each of the characters. The ancestral states are represented by colouring or shading branches of the phylogenetic tree, thus providing an immediate and accessible visual representation of

reconstruction of states. In cases where the ancestral state is ambiguous, the relevant branch is given split colouring/shading to indicate this.

***Important note: species names that are mentioned in this chapter, but that are not in the phylogeny, are indicated with square brackets eg. [H. lacera].***

### **5.3.1 Flowers per axil**

A single flower per axil distinguishes subsect. *Acicarpus* from other clades within subg. *Hermannia* with the exception of *H. cristata*. The floral configuration is obscured in the sect. *Hermannia* as a number of species have complex cymes, panicles or racemes, frequently with between one and three flowers per axil (Verdoorn 1980). This configuration is usually not apparent on photographs, and is not elucidated in Verdoorn (1980). *H. woodii* is the only species within subg. *Mahernia* that frequently has three flowers. The ancestral condition for the genus unambiguously resolves to being two flowers per axil.



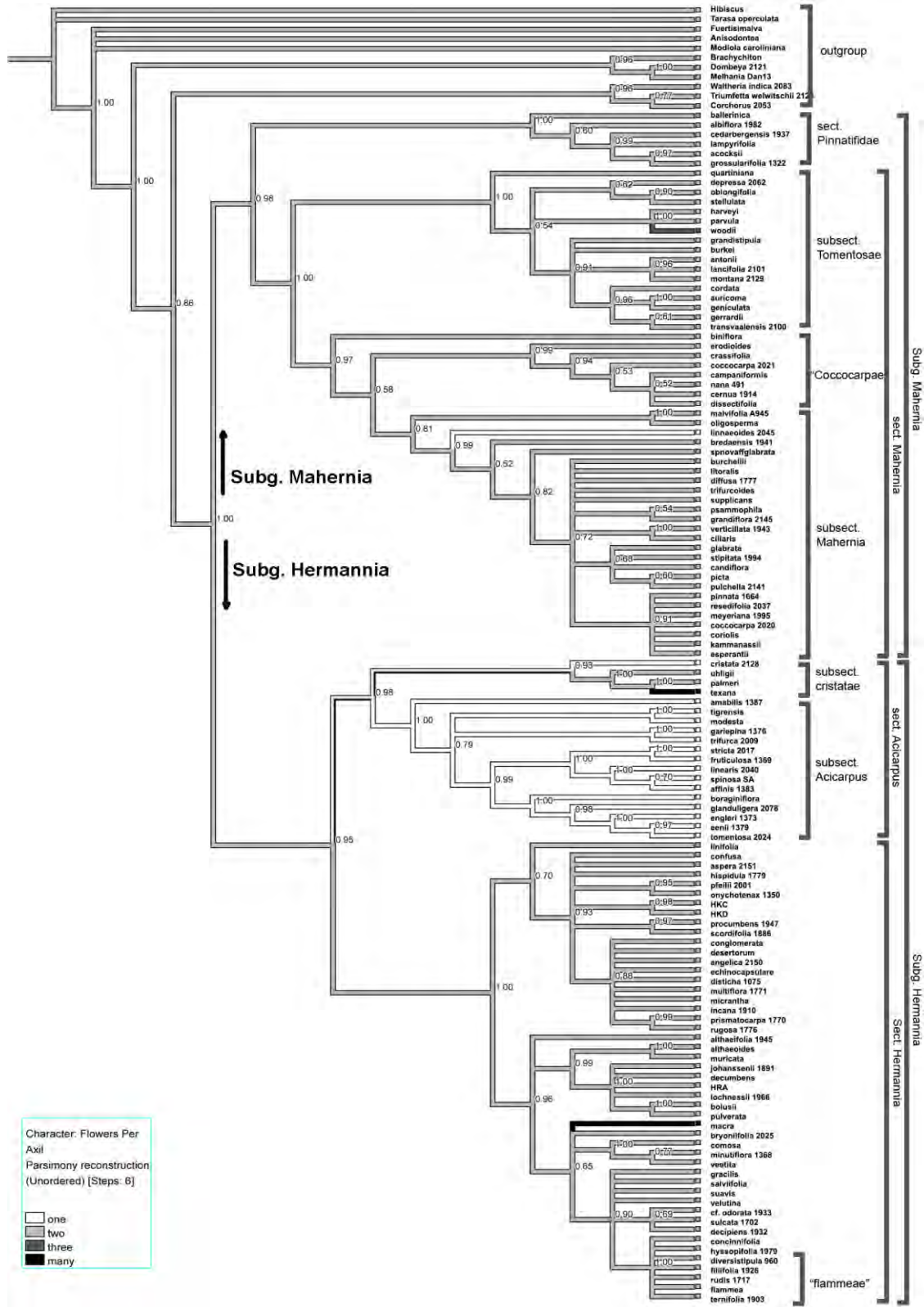


Fig. 5.1 Reconstruction of number of flowers per axil.

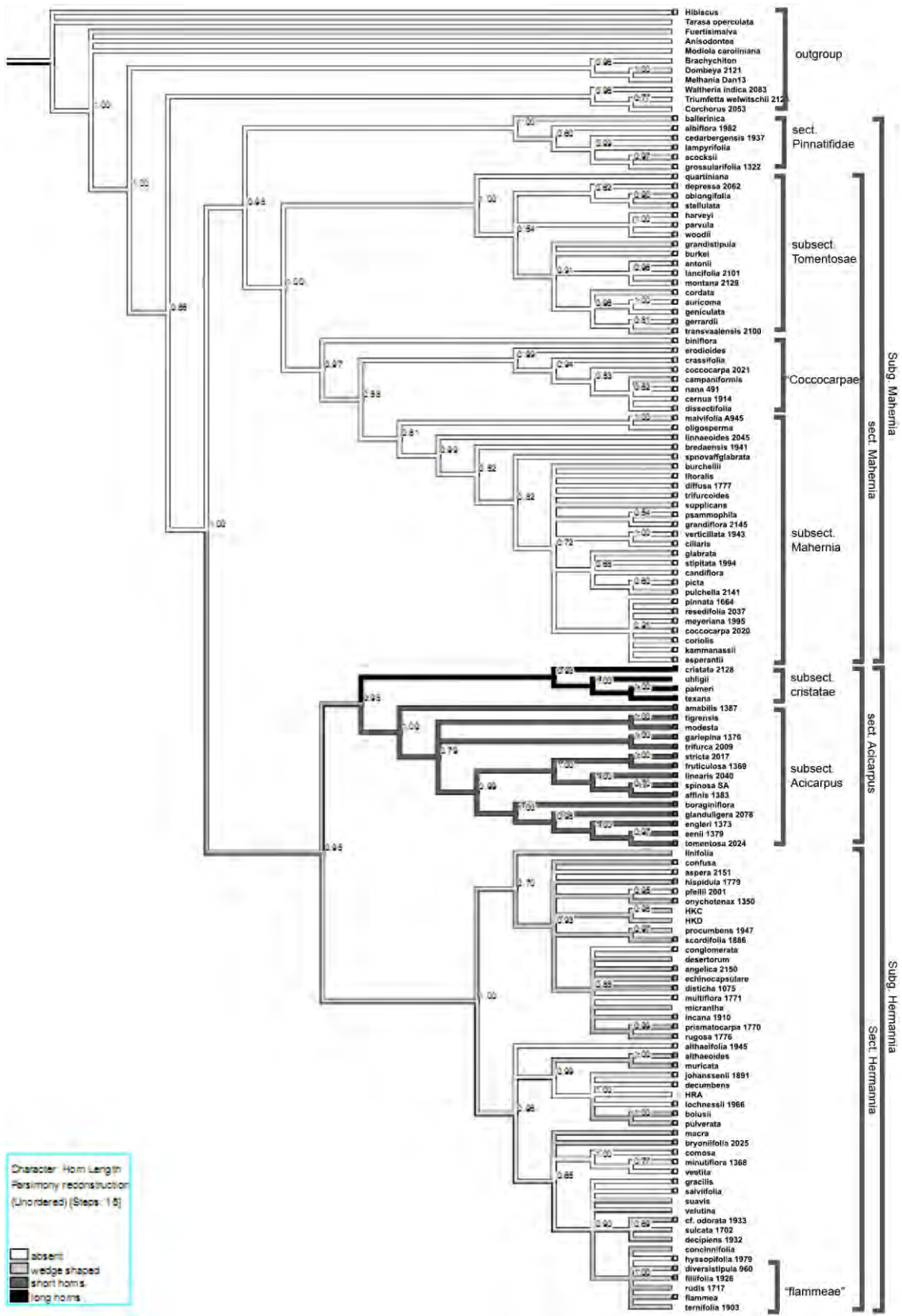


Fig. 5.2 Reconstruction of horn length.

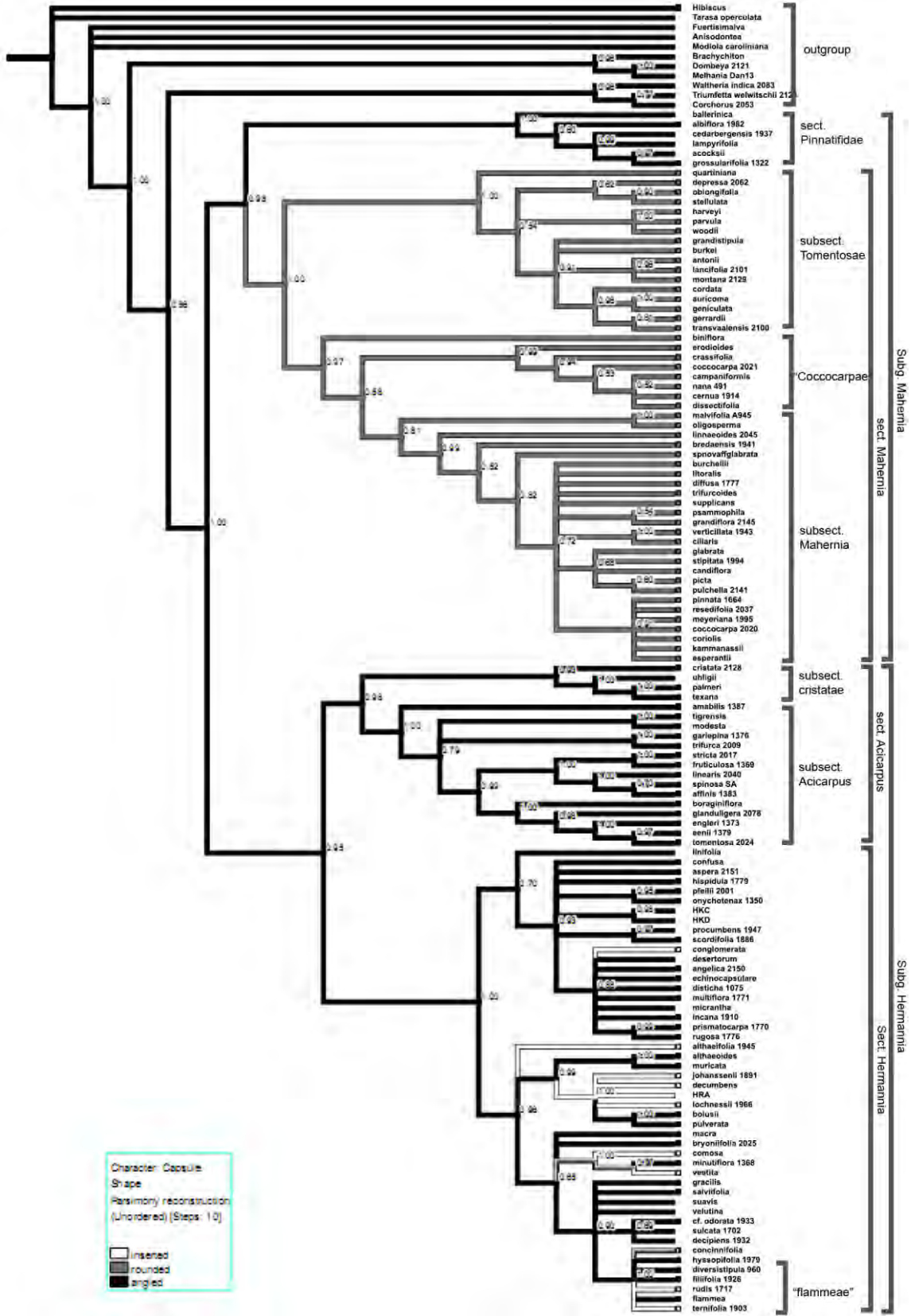


Fig. 5.3 Reconstruction of capsule shape

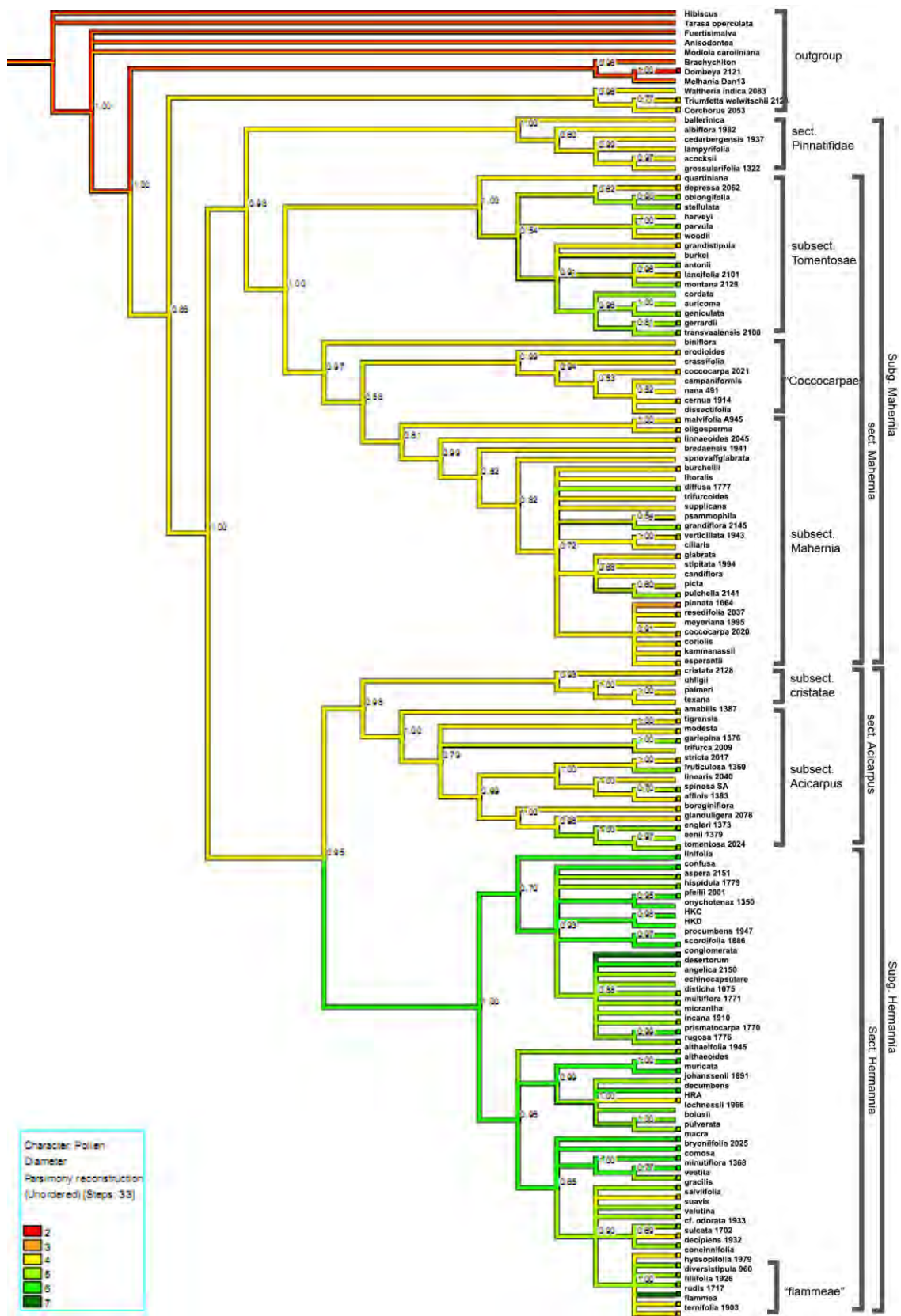


Fig. 5.4 Reconstruction of pollen diameter



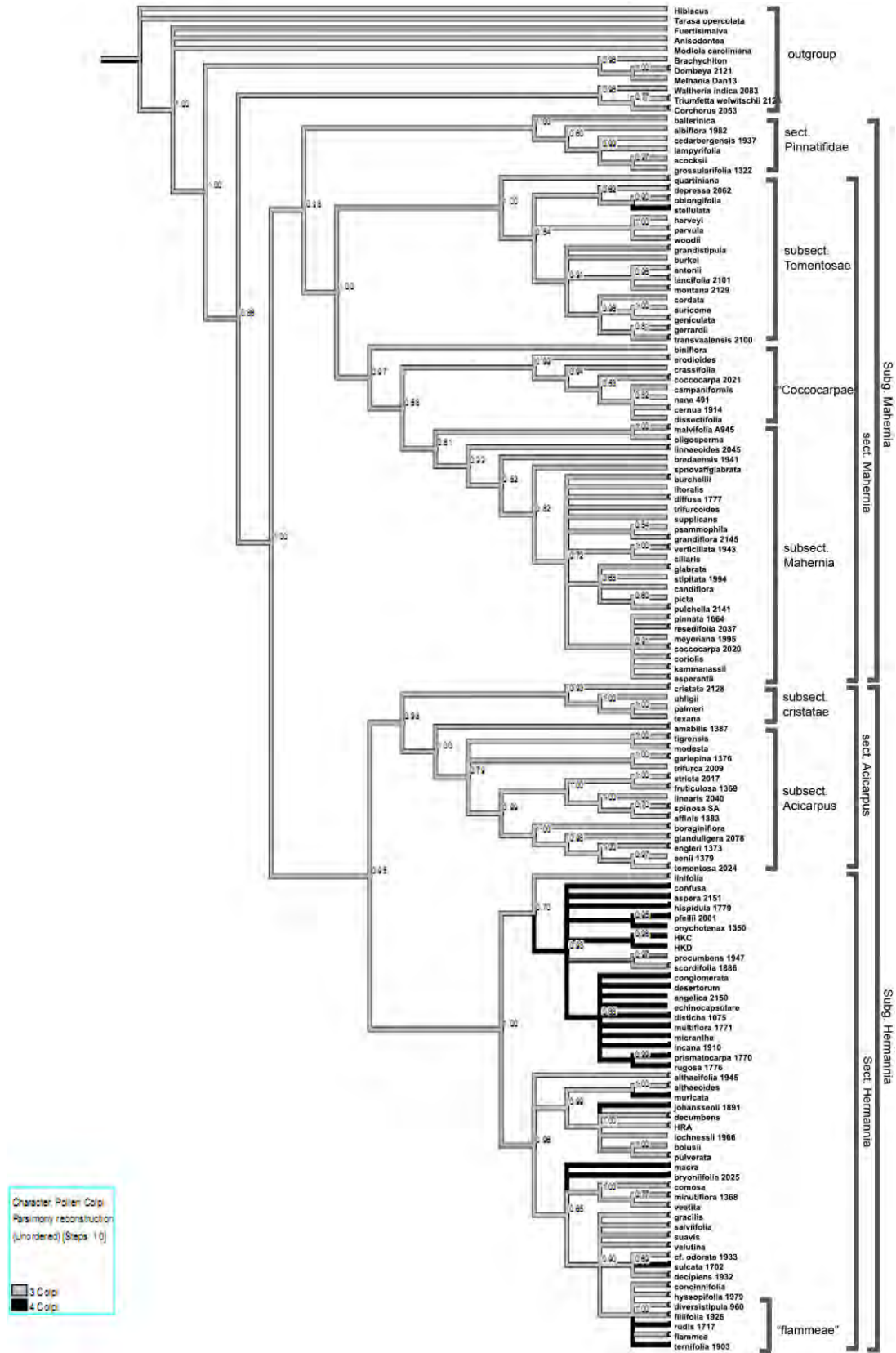


Fig. 5.5 Reconstruction of pollen colpus number

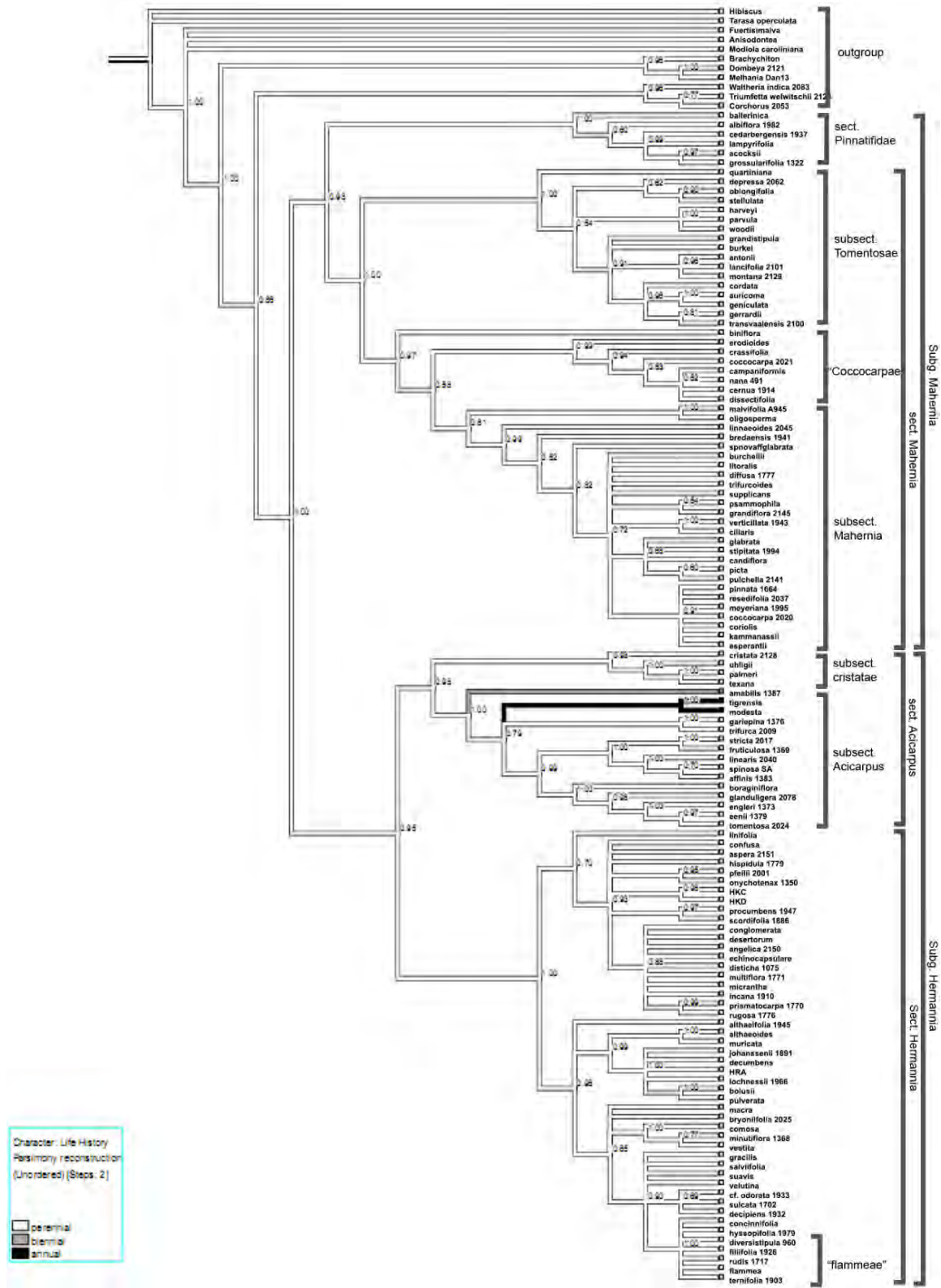


Fig. 5.6 Reconstruction of life history

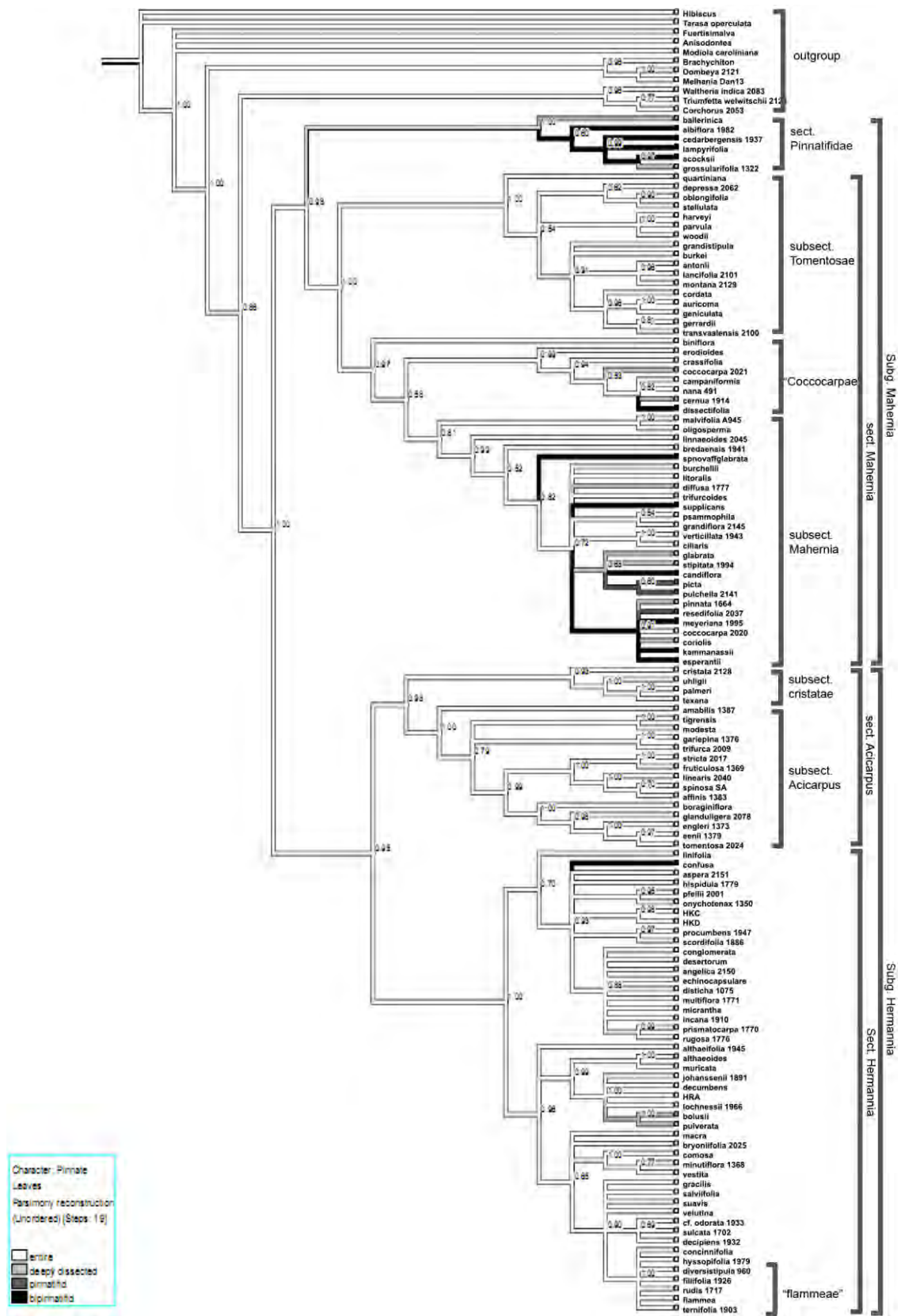


Fig. 5.7 Reconstruction of leaf dissection

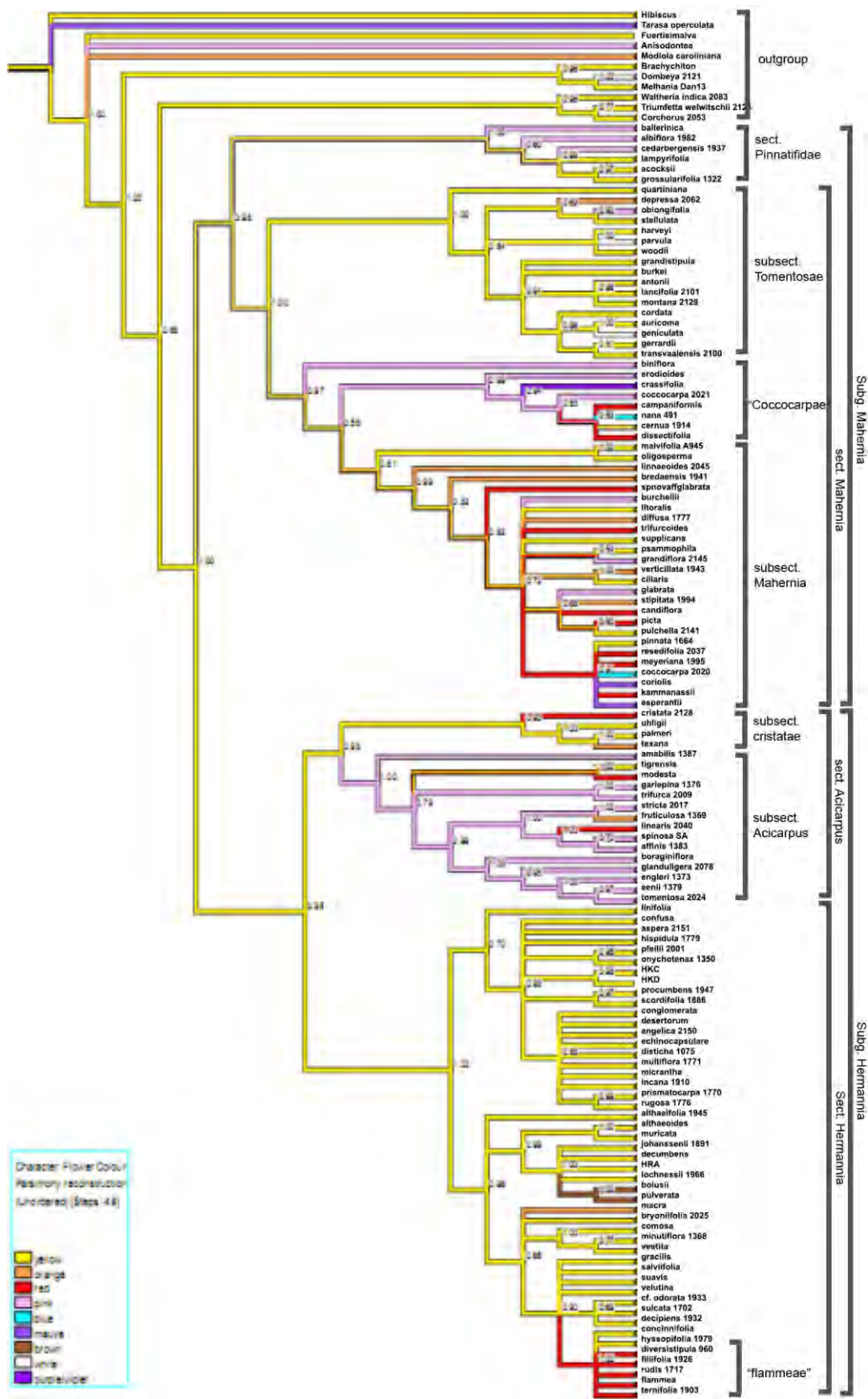


Fig. 5.8 Reconstruction of flower colour



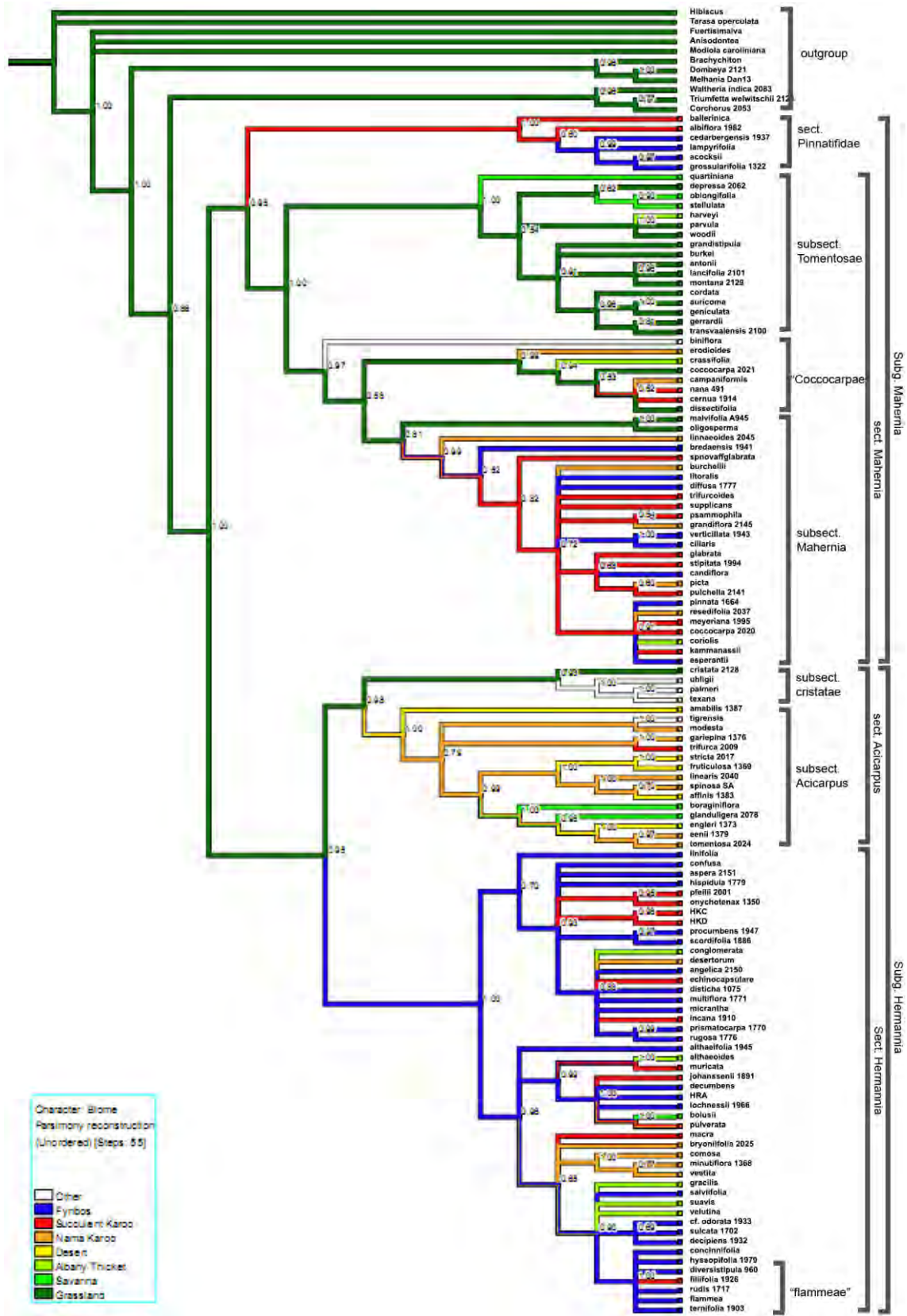


Fig. 5.9 Reconstruction of biomes

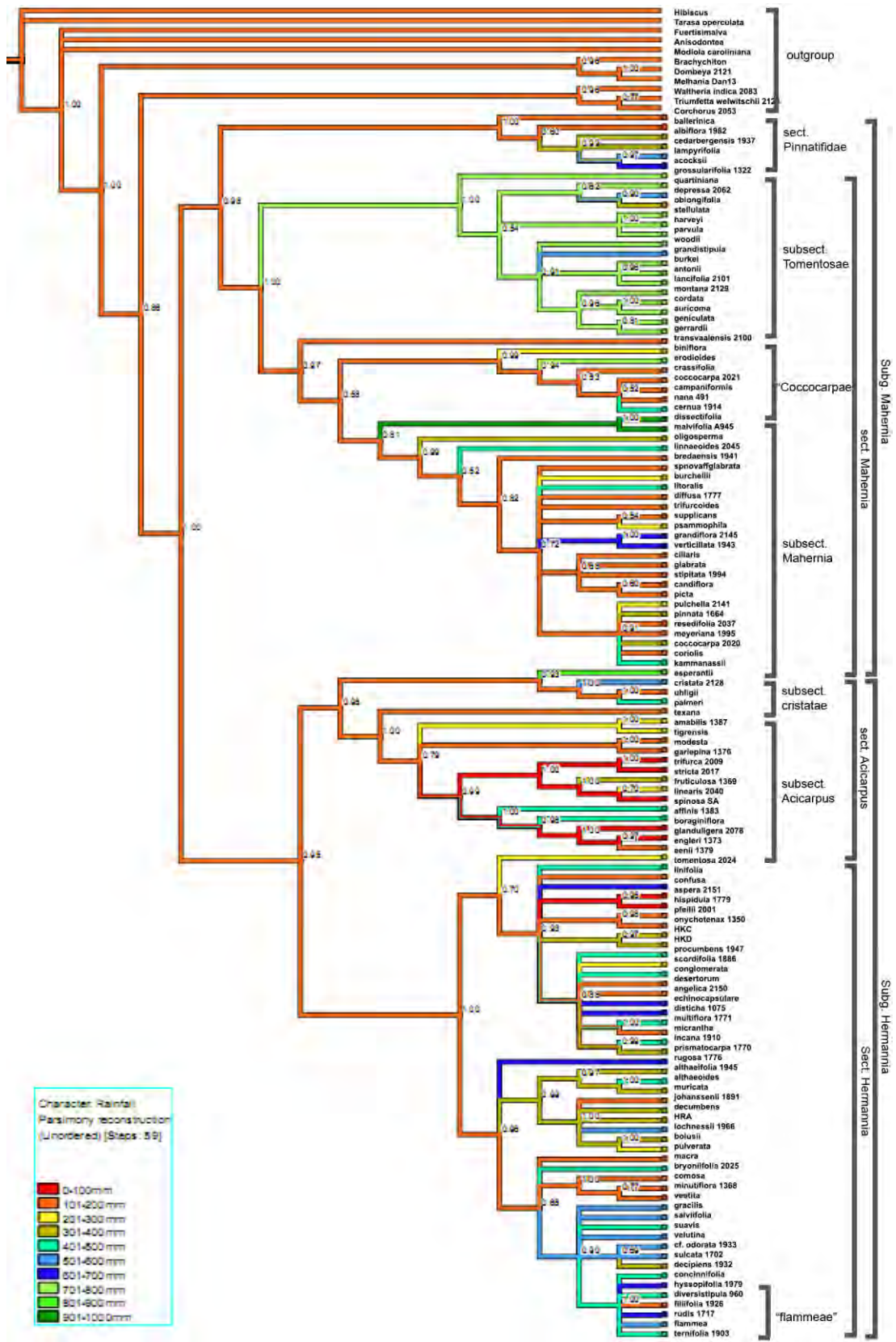


Fig. 5.10 Reconstruction of rainfall

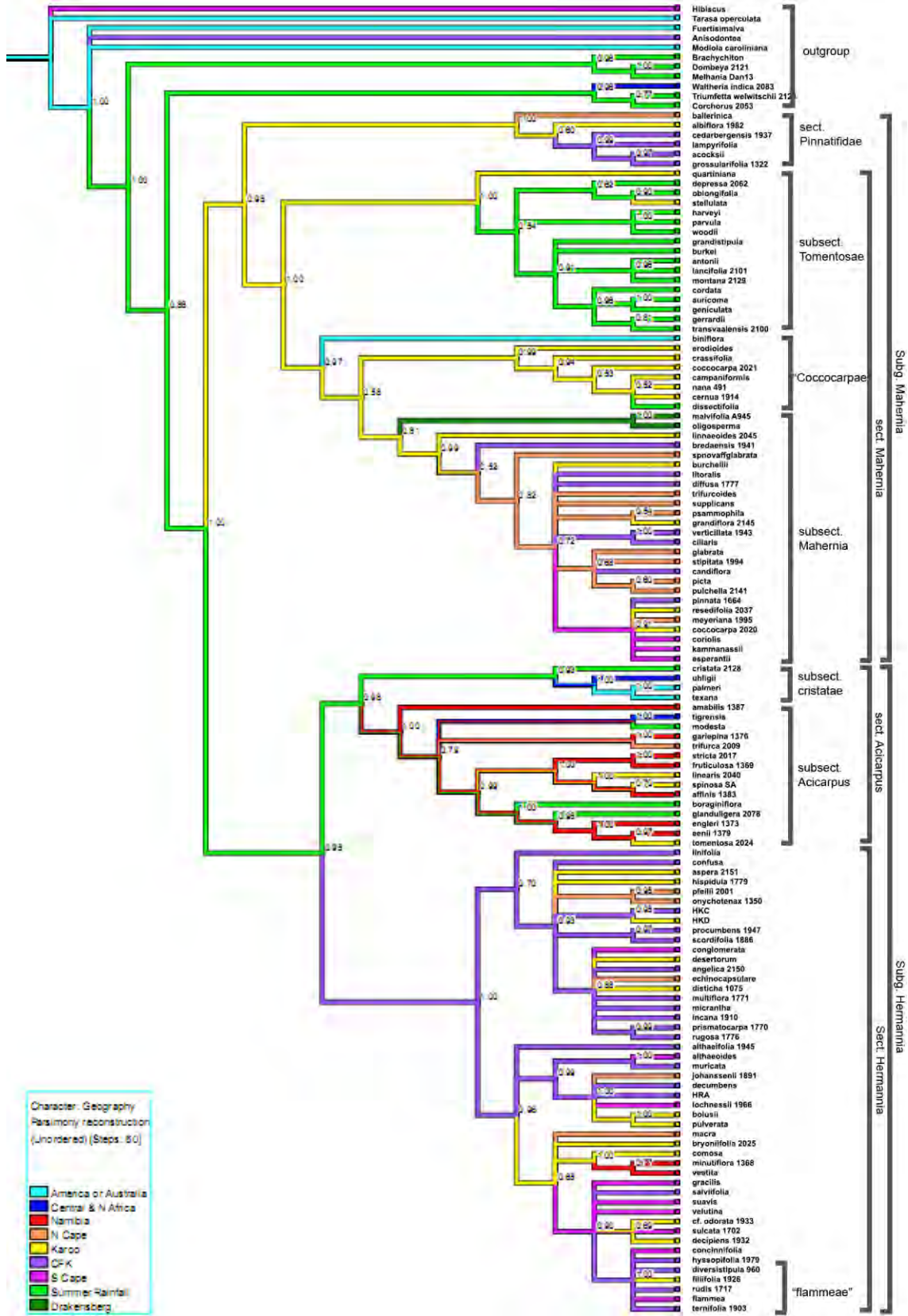


Fig. 5.11 Reconstruction of geography.



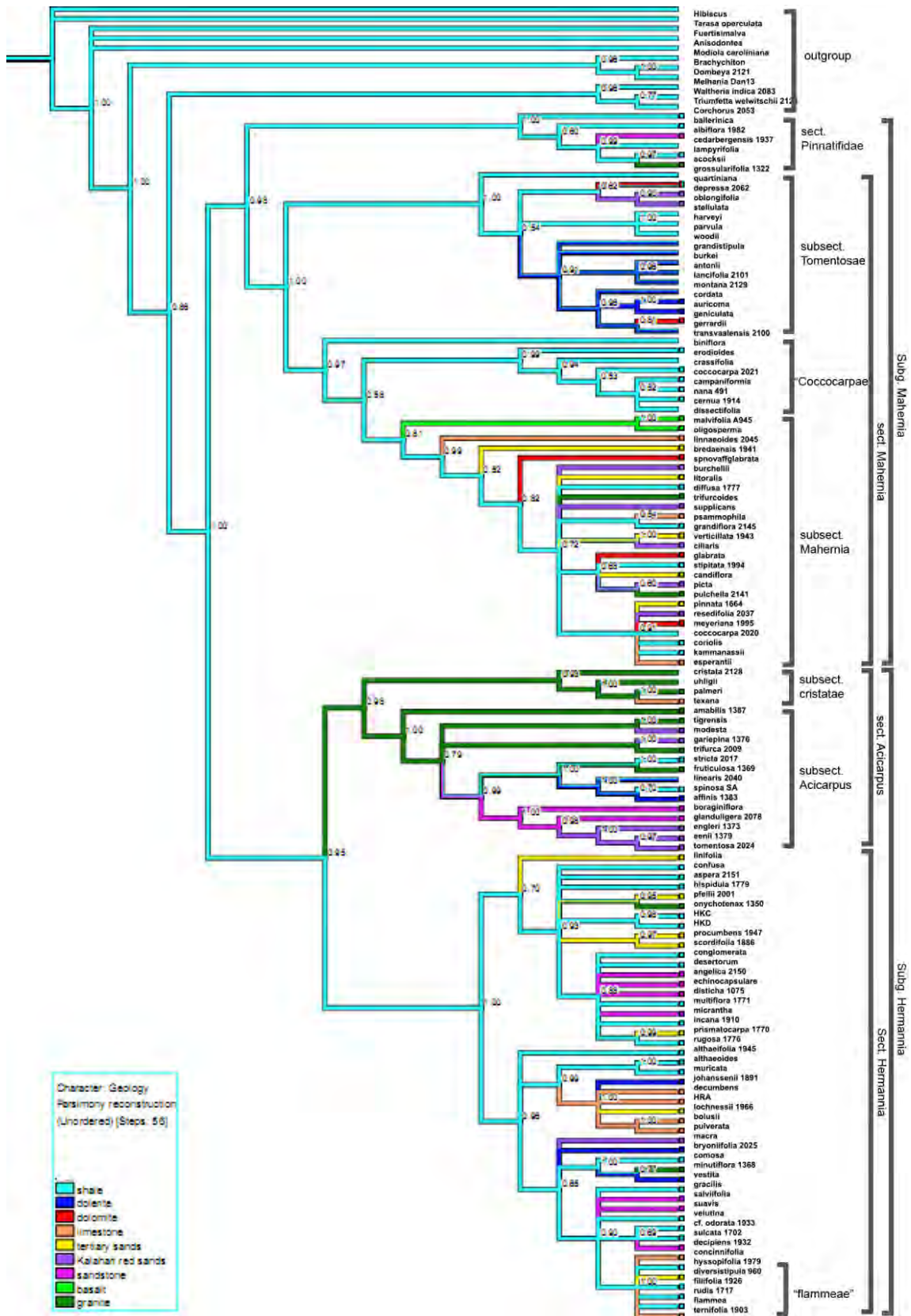


Fig. 5.12 Reconstruction of geology

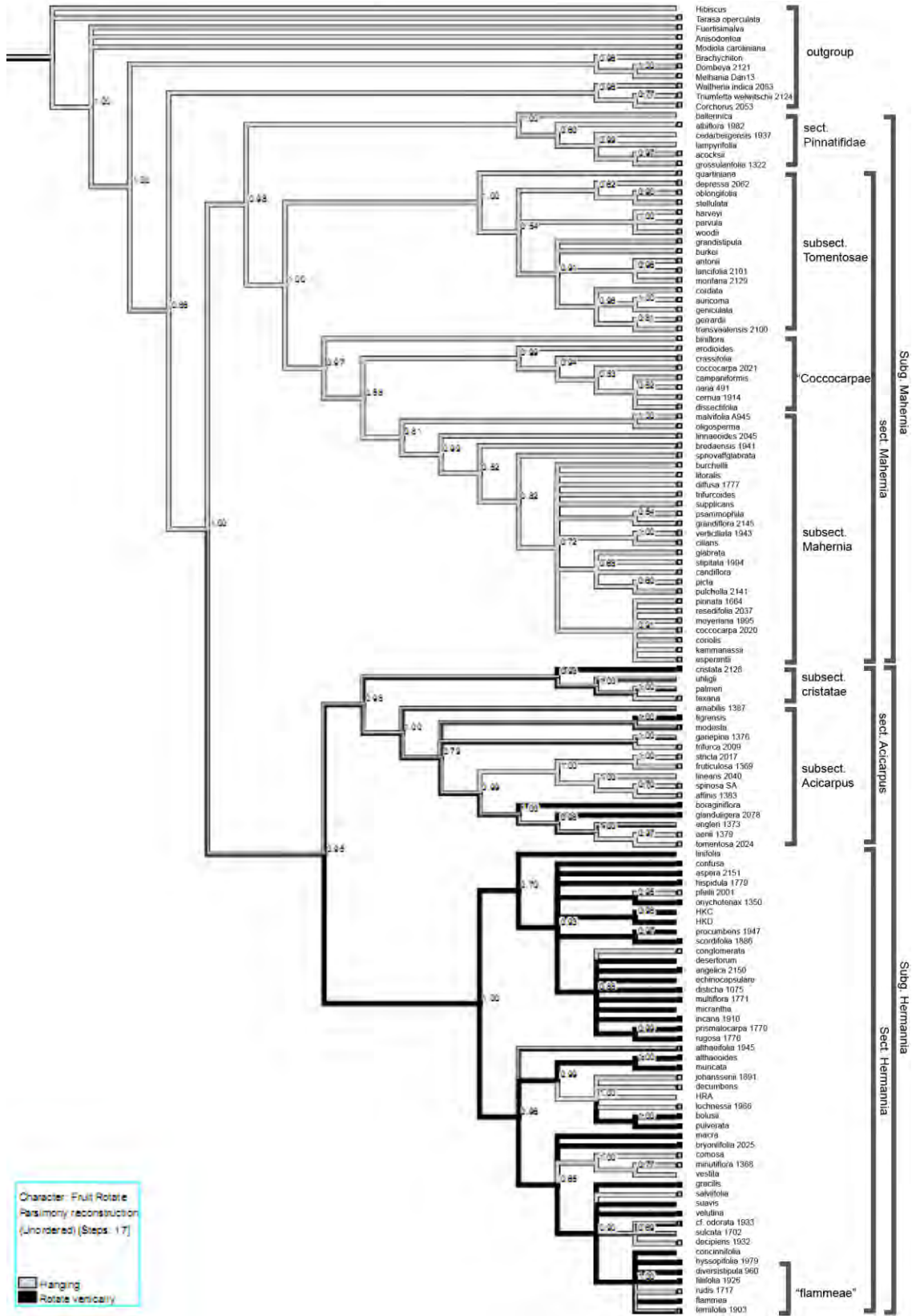


Fig. 5.13 Reconstruction of fruit rotation

### 5.3.2 Horn length

Horns are here defined as apical protuberances of the capsule beyond the generalized shape. Horns are present only in subg. *Hermannia*, and not in subg. *Mahernia* (Fig. 5.2). However, in some species of subg. *Hermannia* these horns are much reduced to absent. In sect. *Hermannia*, horns, if present, are never more than wedge shaped apical protuberances that are here considered a reduced form of horn. All species of subsect. *Acicarpus* have short horns. The subsect. *Cristatae*, with the exception of “*Marehnia*” not only has longer horns, but also filamentous processes that arise along the septum of the capsule. It is important to note that *H. uhligii* from sect. *Marehnia* is not coded here. This species appears to have either angled apices (similar to wedge shaped horns) (c.f. [*H. pseudofischeri*]), or rounded (c.f. [*H. vollesenii*]). An examination of descriptions of “*Marehnia*” species in *Monographieen Afrikanischer Pflanzen* (Engler and Schumann 1900) indicates that most species are without appendages/horns with the exception of [*H. exappendiculata*], which has “gested wings - Kapselkanten geflügelt; capsula subcylindrico-pentagona cristato-alata subtomentosa”. In addition, his work suggests that within “*Marehnia*”, some species have rounded capsules, and others somewhat angled – thus they can be considered to not possess horns.

The ancestral state of the genus *Hermannia* and subg. *Mahernia* is unambiguously resolved as being without horns. The ancestral state of the subg. *Hermannia* is ambiguously resolved as being partially absent, wedge shaped, and short horns. Sect. *Acicarpus* is ambiguously resolved as being partially long horns and partially short horns. Section *Hermannia* unambiguously resolves as being without horns.

### 5.3.3 Capsule shape

Capsule shape is predominantly rounded within the subg. *Mahernia*, and mostly angled within subg. *Hermannia* (Fig. 5.3). Several notable exceptions to this trend exist. The clade sect. *Pinnatifidae* has odd round inflated capsules which are somewhat angled. This may represent a somewhat intermediate position. Within subg. *Hermannia*, “*Marehnia*” as defined by Engler (1900), possesses species with round and angled fruit. The inserted state indicates those species

where the capsule is hidden by the calyx or petals. As such, they represent unknown states that due to being embedded within a wholly angled clade may be assumed to be angled.

Due to coding sect. *Pinnatifidae* as angled, parsimony reconstruction places the overall ancestral state for the genus as angled. The sect. *Mahernia* is unambiguously resolved as having rounded fruit.

#### 5.3.4 Pollen diameter

The reconstruction of equatorial pollen diameter is given in Fig. 5.4. The measurement is uncertain due to insufficient methods given in the source of the pollen data. However, it can be understood that a value of two is narrow, four or five is medium sized, and seven is broad. Regarding the outgroup, the narrowest pollen diameter is possessed by *Dombeya*, though this is phylogenetically distant compared with members of the Grewioideae: *Waltheria*, *Triumfetta* and *Corchorus*. These genera have been found to have the same diameter as most of subg. *Mahernia* and subsect. *Acicarpus*. Subg. *Mahernia* has moderately sized pollen, with the exception of species of the subsect. *Tomentosae* that frequently have slightly broader pollen. *H. pinnata* has the narrowest pollen within the genus. Sect. *Acicarpus* comprises mostly medium sized pollen with some species having slightly larger pollen. Sect. *Hermannia* is comprised almost entirely of species with medium-diameter to broad pollen, of which c. 20% of species have medium sized pollen.

The ancestral state for the genus is resolved as being pollen with a medium-sized equatorial diameter of four. The subgenera *Mahernia* and *Hermannia* also have an ancestral state of four. The subsect. *Tomentosae* tends to have slightly broader pollen than the rest of the subgenus. The sect. *Hermannia* unambiguously resolves as having a relatively broad diameter of 6. The sect. *Acicarpus* has relatively narrow pollen of 4 relative to the remainder of subg. *Hermannia*.

#### 5.3.5 Pollen colpi

The pollen of species that have been examined have been found to be tricolpate with the exception of 19 species which are tetracolpate (Fig. 5.5). These tetracolpate species are all within sect. *Hermannia*, with the single exception of *H. stellulata* in subsect. *Tomentosae*, and appear to

arise a number of times, being found within several informal groups. The ancestral state is unambiguously resolved as tricolpate.

### 5.3.6 Life history

Life history is perennial in all cases except for five species within subsect. *Acicarpus*, series *Modesta*, comprising *H. modesta*, *H. kirkii*, *H. testacea*, *H. tigrensis*, and *H. stuhlmannii* (Fig. 5.6). These are represented by two species in the phylogeny. In this same clade, a species recently discovered in coastal Angola that has similar orange flowers, is perennial and multistemmed. The species *H. amabilis*, which is sister to this clade of annuals, is curious in appearing annual in its growth form, but grows to >120cm tall. It may be a deciduous perennial that produces new shoots that give it an annual appearance.

The life history is unambiguously resolved for the genus and all significant clades as perennial, and thus an annual life-form is a derived feature. As all the annual species appear to be morphologically closer related, it is suggested that an annual life-form has arisen once within *Hermannia*. The annual species are interesting in having a very wide distribution within Africa given the small number of species, and occupying a basal position within subsect. *Acicarpus*.

### 5.3.7 Leaf dissection

Although multiple terms exist for dissection of leaves of *Hermannia* such as pinnatifid, bipinnatifid, tripinnatifid, and pedate, leaf dissection of non-entire leaves has been simplified for this reconstruction to any leaf that is significantly lobed beyond deeply dissected, being deemed pinnatifid or bipinnatifid. The majority of all species and clades within *Hermannia* have entire or sub-entire leaves (Fig. 5.7). An exception to this numerous members of the “Lacerae” clade and closely related species that comprise dissected leaves. Within this clade, there are two distinct forms of dissection: the deeply lobed to lacerate leaves of [*H. lacera*, *H. scabri caulis*], *H. sperata* and *H. coriolis*; and the pinnatifid and bipinnatifid leaves of the remaining dissected species. There are a number of species within this clade that have entire leaves. However many of these may represent derived forms of a dissected leaf, such as *H. grandiflora* with a lobed margin, and *H. psammophila* that has occasional protrusions on an otherwise linear leaf. The dissection in *H. dissectifolia* is an apomorphic character, the leaf being entirely out of character



with the rest of the Coccocarpaceae. The sect. *Pinnatifidae* comprise four species with well-dissected leaves: [*H. sisymbriifolia*], *cedarbergensis*, *H. albiflora* and [*H. lanterna*] all have bipinnatifid leaves. *H. grossularifolia*, [*H. virginalis*] and *H. ballerunica* rather have deeply lobed leaves. Within sect. *Hermannia*, all species have entire leaves excepting *H. confuse*, with bipinnatifid leaves (an apomorphic feature), and sister species *H. bolusii* and *H. pulverata* which have deeply dissected leaves.

The ancestral state is unambiguously resolved as entire leaves at both generic and subgeneric level and at all major lower levels except for the sect. *Pinnatifidae* which has a shared state of entire and bipinnatifid.

### 5.3.8 Flower colour

Yellow flowers are unambiguously resolved as the ancestral state for the genus (Fig. 5.8). They are present in every clade except subsect. *Acicarpus*. Yellow flowers frequently change to orange or reddish flowers as they age. However, it appears that several species have independently adapted from yellow to red or orange flowers. *Hermannia bolusii* and *H. pulverata* have brown flowers. This is a tertiary colour that is derived from yellow pigments. The analysis resolves that they are derived from an ancestor that had brown flowers. The subsect. *Cristatae* is complex in having species with yellow (*H. pauciflora*), red (*H. cristata*), orange (*H. texana*) and blue-grey [*H. merxmulleri*] flowers. Species of ‘Marehnia’ comprises mainly yellow flowers with the exception of [*H. paniculata*] (burgundy) and [*H. exappendiculata*] that have an infusion of orange to red. The subsect. *Mahernia* is also complex, having species with flower colours including red, yellow, orange, purple, blue and brown.

Reconstructions resolve the ancestral state of subg. *Hermannia*, sect. *Hermannia*, sect. *Acicarpus* and subsect. *Cristatae* as yellow while the ancestral state of subsect. *Acicarpus* is resolved as pink. The subg. *Mahernia*, sect. *Mahernia* and sect. *Pinnatifidae* are ambiguously yellow/pink, subsect. *Tomentosae* resolves as yellow, the group ‘Coccocarpaceae’ resolves as pink and subsect. *Mahernia* is ambiguously yellow and orange.

### 5.3.9 Biome reconstruction

The ancestral habitat (Fig. 5.9) is resolved as grassland. Grassland species are found in several sections of *Hermannia*, and include *H. cristata* within the subg. *Hermannia*, most of the subsect. *Tomentosae*, and the Drakensberg species within subg. *Mahernia*. Within subg. *Mahernia*, the sect. *Pinnatifidae* is resolved as Succulent Karoo, the Coccocarpaceae and subsect. *Mahernia* as grassland, and the subsect. *Mahernia* excluding the Drakensberg species resolve as a combination of Succulent Karoo, Nama Karoo and fynbos. The subg. *Hermannia* and the subsect. *Cristatae* are unambiguously resolved as grassland. Subsect. *Acicarpus* resolves as desert. Sect. *Hermannia* is unambiguously resolved as the fynbos biome.

### 5.3.10 Rainfall

The ancestral habitat for *Hermannia* is found to be arid, with a MAP (mean annual precipitation) of 101–200mm (Fig. 5.10). This includes both *H. biniflora* from Australia, and *H. palmeri* from USA. All clades within subg. *Mahernia* are resolved as 100–200mm MAP except for the subsect. *Tomentosae* that has a high rainfall of 700–800mm. Subgenus *Hermannia*, sect. *Acicarpus* and sect. *Hermannia* all resolve as 100–200mm MAP. Throughout the genus, and specifically in most clades, there is a wide range of rainfall patterns. Exceptional clades are subsect. *Tomentosa* and the “Flammeae” group which are uniform in rainfall for most species in the respective clade.

### 5.3.11 Geographic reconstruction

“Summer rainfall” refers to the summer rainfall region of South Africa, which is unambiguously resolved as the ancestral state for the genus *Hermannia* (Fig. 5.11). The subg. *Mahernia* has a number of elements residing in the Succulent, Nama and Central Karoo and is resolved as having Karoo origins. The “Coccocarpaceae” is resolved as a Karoo clade with the summer rainfall *H. dissectifolia* a derived species in this group. Section *Acicarpus* and the subsect. *Cristatae* are resolved as the summer rainfall region of South Africa. The subsect. *Acicarpus* is resolved as partially Namibian in origin, with some minor contributions from the summer rainfall parts of South Africa and tropical Africa. Section *Hermannia* is unambiguously

resolved as the Cape Floral Kingdom (CFK), although a minor clade containing mainly species from the South Coast has its origins located in the Karoo.

### 5.3.12 Geological reconstruction

Shale is unambiguously resolved as the ancestral soil type for the genus *Hermannia*, subg. *Hermannia*, subg. *Mahernia* and sect. *Hermannia* (Fig. 5.12). Additionally, all clades within subg. *Mahernia* are retrieved as shale. Section *Acicarpus*, including the subsect. *Cristatae* and subsect. *Acicarpus* is resolved as occurring ancestrally on granite. These results are well supported by shale being a common substrate for species in the phylogeny.

### 5.3.13 Fruit rotation

Fruit rotation is the movement of flowers from a hanging position to a vertical position subsequent to fertilization. It is entirely absent from the subg. *Mahernia*, and only arises within the subg. *Hermannia*, in which the ancestral state is determined to having fruit rotating. The ancestral state of subsect. *Acicarpus* is ambiguously resolved, whereas in sect. *Hermannia* it is resolved as having fruit rotating. The genus *Hermannia* is resolved as having fruits that do not rotate.

## 5.4 Discussion

In the introduction, we raised the following questions:

- a) What can be said about patterns of inheritance of morphological characters in *Hermannia*?
- b) Are there any synapomorphies that can be used to circumscribe clades within *Hermannia*?
- c) What are the patterns of dispersal and colonisation that can be inferred by reconstruction?
- d) What can reconstruction reveal about ancestral habitats and biomes used by *Hermannia*?
- e) Did an annual life-form arise once, or multiple times independently?

In order to adequately address the issue of patterns of inheritance, we discuss characters individually. In doing so, we also relate the additional information provided by the reconstructions to taxonomic questions. The issue of patterns of dispersal and colonisation is addressed under “Geographic reconstruction”, while the question of how an annual life form

arose is dealt with under “Life history”. The remaining questions, relating to synapomorphies and to ancestral habitats and biomes, are discussed separately.

#### 5.4.1 Flowers per axil

The ancestral state for number of flowers per axil is two, with notable exceptions being the sect. *Acicarpus*, having one flower per axil, and several other isolated species.

Two competing theories have been proposed which relate to the formation of inflorescences in *Hermannia*. Whitlock et al. (2001) found that the monophyletic Byttnerioideae is mostly associated with perfect, actinomorphic pentamerous flowers. The stamens are in fives and opposite the petals. Bayer and Kubitzki (2003) mention the “bicolor unit” (named after *Theobroma bicolor*) as the basic inflorescence structure for the core Malvales that ties together Sterculiaceae, Tiliaceae, Bombacaceae and Malvaceae. The bicolor unit is determinate and bears three bracts, one of which is invariably sterile, whereas the others subtend lateral cymes or single flowers. ... Bicolor units are variously arranged to form complete inflorescences. In many taxa they are terminal on modules that comprise two (or fewer) prophylls. These modules may be arranged in elongated anthocladia or condensed sympodia, which in turn may constitute components of higher order inflorescence structures” (Bayer 1999).

Within the tribe Hermanniae, Whitlock et. al. (2001) states that paired flowers are typically subtended by four bracts”. For *Hermannia* this appears too simplistic a statement, with Bayer and Kubitzki’s (2003) bicolor unit appearing more appropriate, and having more power to explain more complex inflorescences. Evidence of vestigial bracts is visible in *H. affinis* (see Fig. 2.10), lending credence to a single flower being a reduction from a paired cyme.

There are only a few species within subg. *Mahernia* exclusively with a single flower per inflorescence, although a number of species show paired cymes with occasional reductions to a single flower within a plant. Typically on a plant, the pedicel and peduncles of inflorescences with single flowers are longer than the respective organs within a paired inflorescence. *H. linnaeoides* has only a single flower per inflorescence, and is also the lowest growing species

within the genus, appearing to survive grazing by hugging the ground between limestone pebbles. Due to the hanging attitude of all unfertilized flowers within *Hermannia*, the aperture of *H. linnaeoides* is barely one centimetre from the ground. If the above pattern of paired flowers being shorter than single flowers is a developmental constraint, having paired cymes would mean that neither flower is significantly off the ground, and the lower flower would be mostly inaccessible to flying pollinators. *H. linnaeoides* is a diminutive species in many respects, and having a single flower may have been strongly selected in the production of sufficiently long peduncles to effect pollination. It occurs in extremely depauperate limestone gravel, and thus may have alternatively or additionally been an optimization towards placing minimal resources into flowering. *H. depressa* is another ground hugging species which typically has two flowers, but frequently a solitary flower. Thus a single flower likely is a common and easy accomplished reduction or abortion from a paired to a single flower. A new species, *H. rocherpanensis* that is presumably closely related to *H. heterophylla* also appears to have solitary flowers, though the sample size is merely three flowers.

Within subg. *Mahernia*, three-flowered inflorescences have only been encountered in *H. woodii*. It corresponds closely to Bayer and Kubitzki's (1999) diagram B of the "bicolor unit", with the central flower belonging to the ordinarily sterile primary prophyll, and the two side flowers arising from the remaining secondary prophylls. In this configuration, two equal sized lower flowers with equal length pedicels are subtended by a single long-pedicelled flower that terminates the cyme. *H. woodii* is a scrambling grassland species with flowers borne towards the ends of new stems where they reach the grass canopy. This presumably allows for more flowers to be displayed per node, which would be advantageous given the limited capacity of the plant to compete with C4 grasses in growth rate.

The overwhelming consensus of the literature on the East African group "Marehnia" shows that most, if not all species have many flowers in terminal inflorescences. *H. uhligii* has from five to fifteen flowers in axillary panicles, while *H. exappendiculata* and *H. oliveri* have more than 40 flowers in terminal or lateral panicles (Agnew 1974). Thulin (1989) reveals that *H. boranensis* and *H. paniculata* have few to many flowers, with a drawing of the latter showing many flowers. Cheek and Dorr (2007) describe *H. waltherioides* as having a terminal thyrse up

to 12cm long, with partial-inflorescences up to 4.5cm long bearing (1-)2-5(-7) flowers. Other species with more than three flowers per axil include *H. texana*, *H. holosericea*, and *H. paucifolia*. These all appear to come from quite distinct groups (at least informal groups), and as such likely represent independent evolution of multiple flowers. The inflorescences are unlikely even to be homologous, with different kinds of inflorescences in many of the above species.

In sect. *Hermannia*, inflorescences are variously termed “~~in~~determinate cymes”, “~~p~~aniculate cymes”, “~~e~~ymes in terminal heads”, “~~p~~seudoracemes”, “~~s~~ub-racemose” or “~~r~~acemose-paniculate”(Verdoorn 1980). Of 49 verbal descriptions of flowers per inflorescence extracted from Verdoorn (1980) and Harvey (1860) for the sect. *Hermannia*, only one species was coded from both sources as “~~t~~wo flowers”. The remaining inflorescences were described as “~~1~~ 2”(43%), “~~f~~ew-flowered” (18%), “~~3~~” (14%), “~~3~~” (14%), “~~s~~everal” (6%) and only *H. holosericea* was coded as “~~2~~” flowers per axil. This indicates the difficulty in assigning a base number to members of sect. *Hermannia*. However, again it seems likely that two is the base number, and that single flowers reflect a reduction of a single flower, and that three or more flowers are the result of a more complex arrangement of bracts, axils and indeterminate growth points [see Bayer (1999)].

Overall, it appears that most of the deviations from two flowers per axil have occurred as isolated and fairly recent events in the evolution of *Hermannia*. In the case of *Acicarpus*, the inferred loss of one flower has been conserved throughout the section, indicating that the change occurred as a single event.

#### 5.4.2 Horn length

In subg. *Hermannia* there are two main phenotypes: the short/long horns of sect. *Acicarpus* and the absent/wedge-shaped horns of sect. *Hermannia*. In sect. *Acicarpus*, the species of subsect. *Cristatae* (with the exception of “~~M~~arehnia”) have long horns while almost all those of subsect. *Acicarpus* have short horns. The latter subsection includes all of the annual species, some of which extend to Somalia, and several species that extend well into South Africa. The utility of horns for protection or epizoochorous dispersal are possibilities that may warrant further investigation.

A character state not included in the reconstruction is fringed processes, which in some way resemble long horns. The fringed processes are found in three American species (*H. palmeri*, *H. pauciflora* and *H. texana*) and two African species (*H. merxmulleri* and *H. cristata*). Importantly, these five species all belong to subsect. *Cristatae*, a clade containing all of the long horned species, suggesting that the fringed processes could be homologues of long horns. This would support the hypothesis, proposed in Chapter 3, that the American species originated in Southern Africa. Verdoorn (1980) noted horned capsules as one of the potentially diagnostic features distinguishing sections within subg. *Hermannia*, but ultimately discarded this as a key taxonomic character. However, she conceded that features such as this could be used to separate species into “small subdivisions”. Interestingly, Verdoorn mentions in her revision descriptions of two American species that bear a resemblance to *H. cristata* due to their fringed capsules. Although the placement of *H. uhligii* within the subsect. *Cristatae* is well supported, it may be that “*Marehnia*” is sister to the cristate-horned species within the subsect. *Cristatae*. The collection of further species of “*Marehnia*”, and the inclusion of the American species without fringed processes would greatly help to understand the relationships within this subsect. *Cristatae*, especially regarding the role of fringed processes in the taxonomy of this subsection.

The ancestral state for subg. *Mahernia* is reconstructed as an absence of horns. This suggests horns are an acquired attribute which occurred once at the split between subgenera *Hermannia* and *Mahernia*, with subg. *Hermannia* then splitting into the long/short horn forms in sect. *Acicarpus* and the wedge forms in sect. *Hermannia*, the former being a stable transition while the latter being unstable. This would account for the appearance of wedge horned forms interspersed with hornless forms in sect. *Hermannia*, with transitions between the two forms occurring multiple times.

### 5.4.3 Capsule shape

Capsule shape has never been proposed as a character for distinguishing sections within *Hermannia*. The entire subg. *Hermannia* has angled capsules (possibly with the exception of

some species of *Mahernia*). The shape of the capsule is concealed in the case of those species with the “inserted” capsules, and it is inferred from the other species that they are also of an angled nature. Although the capsule shape is presumably not conducive to wind-dispersal, the species which are likely wind dispersed within sect. *Hermannia* (eg. *H. comosa*, *H. vestita*) bypass this genetic constraint by wholly enclosing the capsule in an inflated, parchment-like calyx.

Reconstruction shows that the subg. *Mahernia* is represented by rounded capsules with the exception of the sect. *Pinnatifidae*, which has features in common both with the angled capsules of subg. *Hermannia*, and the spherical capsules of *Mahernia*. Within sect. *Pinnatifidae*, *H. grossularifolia* has a capsule with a substantially larger volume than any other species (pers. obs.), and resembles a bulging football with pinched vertical seams at the septa. This is inverse to the angular capsules of subg. *Hermannia* which are widest at the angled septa. *Hermannia grossularifolia* is representative of the general form of the sect. *Pinnatifidae*. It would be interesting to study whether this structure is suited for wind dispersal, as not only are the capsules suited for secondary dispersal along the ground, but in contrast to most species of *Hermannia*, the capsules of *H. grossularifolia* readily fall to the ground once ripe. If one characterises the capsules of subg. *Hermannia* more specifically as ‘angled and broadest at the septa’, this distinguishes subg. *Hermannia* from all of the subg. *Mahernia* clade which is distinguished by having its capsule rounded and narrowest at the septa.

Overall, the ancestral state is reconstructed as angled, with a single transition to rounded in the case of subg. *Mahernia*, with sect. *Pinnatifidae* possessing a further transition to a distinct shape in which the septa are pinched. The subg. *Hermannia* has uniformly angled capsules. Additionally, a number of species in sect. *Hermannia* have an inserted or hidden capsule – this trait appearing to be acquired and lost in the case of *H. comosa*, *H. minutiflora* and *H. vestita*, indicating a reversible transition.



#### 5.4.4 Pollen diameter

Pollen diameter segregates at the subgenus level, with subg. *Mahernia* generally having a diameter of 4, which is also its reconstructed ancestral state, and subg. *Hermannia* generally having a pollen diameter of 5-6. However, at level of section, few patterns emerge and it is not possible to ascertain whether variation in this character is attributable to gradual genetic drift or whether it is driven by some ecological or environmental factors. A further possibility is that pollen diameter is allometrically scaled according to flower size, which would account for the slightly larger pollen diameter of 5 in subsect. *Tomentosae* of subg. *Mahernia*. However there seems to be little relationship between flower and pollen size in sect. *Hermannia*, thus discounting allometric scaling as a general phenomenon for pollen in the genus.

#### 5.4.5 Pollen colpi

Most species of *Hermannia* have three pollen colpi, which also resolves as the ancestral state. Of the species with four pollen colpi, all but one are found within sect. *Hermannia*. Interestingly, the form with 4 colpi has arisen several times within this section but only once in the remainder of the genus. It therefore seems to be a labile character, with a complex history within sect. *Hermannia*.

#### 5.4.6 Life history

*Hermannia* is found to be an almost exclusively perennial genus, the few exceptions being annual species in the ser. *Modestae* (subsect. *Acicarpus*), which contains around 7 annual species (including *H. atrosanguinea*, *H. filipes*, *H. tigrensis*, *H. holubii*, *H. kirkii*, *H. modesta*, *H. atrosanguinea* and *H. testacea*) in addition to one perennial (*H. capoeira*) from Angola and an intermediate species with annual-like features (*H. amabilis*) from Namibia. The ser. *Modestae* has several of the most widely spread species of *Hermannia* in Africa, and is therefore suggested as being a life form conferring versatility in range of viable habitats. In particular, *H. modesta* is distributed from South Africa to Botswana, Namibia and Angola, and from Somalia to Egypt and Sudan in the north. *H. tigrensis* occurs in Cape Verde and also covers the width of Africa from Senegal to Ethiopia, and extends southwards to Zimbabwe (CJB Database, 2013). Although the annual habit is found in only three recognised species, the variation within these annual species

(flower colour, leaf shape, indumentum) is substantial. Verdoorn (1980) writes that “from the long list of synonyms and the several varieties and subvarieties described, it is obvious that attempts to circumscribe discrete taxa in this [*H. modesta*] complex have failed.” Further molecular work to refine the phylogeny would be especially interesting in better understanding this complex, and may lead to the designation of new species.

In order to understand the origins and distribution of the annual species, it is informative to consider *H. amabilis*, sister to the clade containing the annual species, whose life history is noteworthy as it resembles an annual in having herbaceous green stems, “*caule viridi a medio ramosa*” (Engler 1919), but also resembles a perennial, growing to over a metre in height. Furthermore, its capsules more closely resemble that of *H. modesta* than perennial members of sect. *Acicarpus*. *Hermannia amabilis* is confined to northern Namibia and southern Angola, where it overlaps in distribution with “the missing link”, *H. merxmulleri*, which shares similar capsule appendages with some of the American taxa. Due to the basal position of *H. amabilis* within subsect. *Acicarpus*, and with Namibia as the centre of diversity of sect. *Acicarpus*, as described in Chapter 6, it is suggested that the annuals originated in Namibia, and spread outwards from there. It is proposed that their widespread distributions may be attributable to their early origins in sect. *Acicarpus*, their adaptation to aridity as annuals, and the possibility that the filamentous processes of these species (discussed regarding horn length), may endow them with long-distance dispersal through endozoochory.

#### 5.4.7 Leaf dissection

The ancestral state for *Hermannia* is entire leaves. It appears that complex leaf structures evolved independently several times, most of these occurring in sect. *Pinnatifidae* and subsect. *Mahernia*. The reconstruction also implies that these transitions are reversible – as seen for instance in the complex patterns of dissection and reconstitution of leaf form in subsect. *Mahernia*, and we propose that these transitions are adaptations to environmental factors such as aridity and grazing, as we know outline.

A number of physiological and biomechanical advantages have been found for dissected leaves that are reviewed by Givnish (1987). An advantage in arid environments, is that a reduction in leaf surface area leads to reduced water loss. In the sect. *Pinnatifidae* this appears to be the case, with the two most mesic species, *H. ballerunica* and *H. grossularifolia* having lobed leaves, and the remaining arid species having bipinnatifid leaves. *H. ballerunica*, despite occurring in a region with 100–200mm of MAP, is nonetheless only found in shaded valleys beneath trees. On account of entire leaves being the ancestral state, and morphology making a case for there being two separate lineages (yellow and white/pink flowered), it is likely that the arid species of sect. *Pinnatifidae* represent at least two independent changes to pinnatifidness.

An unusual instance of bipinnatifid leaves is found in *H. dissectifolia*, a species which experiences amongst the highest rainfall in the subg. *Mahernia* (apart from the subsect. *Tomentosae*, in which no dissected species occur). It is unlikely therefore that water-stress is contributing to its dissectedness in this case, but one may suggest that this is an adaptation to grazing. This is a species that occurs in grassland, unlike the more arid environments in which the majority of the other *Hermannia* species of this clade occur. Dissection is possibly explained by the lower feeding efficiency of dissected leaves relative to the more palatable grass (Brown and Lawton 1999).

#### 5.4.8 Flower colour

The ancestral flower colour for *Hermannia* is resolved as yellow. Section *Hermannia* has mostly yellow flowers, many of which turn orange with age. Red flowers dominate the informal group “Flammeae” (sect. *Hermannia*) and appear to have arisen independently in at least four other instances in clades across the genus. As red flowers in other families are often associated with bird pollination, and birds have been observed to visit some woody red-flowered species of *Hermannia* such as woody *H. filifolia* and *H. joubertiana* (pers. comm. Jan Vlok), it may be that these independent transitions to red flower can be partly accounted for by bird-pollinator driven adaptation.

Bird pollination may occur for some of the more woody red-flowered species (eg. *H. filifolia*, *H. joubertiana*) (pers. comm. Jan Vlok) though no potential pollinators have been encountered

for the remaining lower-growing species. A single yellow species from Namaqualand, *H. amoena*, has been photographed with malachite sunbirds consuming the nectar (Fig. 5.14, below). It is likely therefore that the very similar *H. disermifolia* and *H. eruca* from the same area may also attract birds. An upright woody species with similar flowers from further south in the Klein Karoo, *H. incana* is also a candidate for bird pollination, although only insect visitors have been witnessed thus far. The potential for bird-pollination in *Hermannia* appears only to occur in the more arid regions. This appears counter-intuitive, as this is where nectar resources are more scarce (Cronk and Ojeda 2008), as water and consequently nutrients are relatively difficult to generate. However, the water scarcity means nectar is consequently more highly coveted by avian pollinators here, than in the more mesic fynbos areas where *Protea* and *Erica* species already provide generous quantities of nectar. However, it may be that these arid-dwelling *Hermannia* species flower when it is too cold for insects to operate (Cronk and Ojeda 2008).



**Fig. 5.14** A malachite sunbird probing *H. amoena* in Namaqualand. Photo courtesy Dennis Hanson.

Most species in sect. *Hermannia* are uniform in having yellow flowers. In contrast, flower shape, size and tube width are variable – for instance, *H. bryoniifolia* has urn-shaped flowers while *H. johansseni* has narrow-throated flowers. Both of these species have been found to attract a broad spectrum of insect visitors (pers. obs.). This raises the question of what pollination syndromes are found in sect. *Hermannia* and the related question of what role (if any) the yellow colour plays in pollination of the species in this section. It would also be of interest to contrast the pollinator syndrome of this section with that of subsect. *Mahernia* in which a wide variety of flower colours is found.

The brown flowers of *H. bolusii* and frequently *H. pulverata* are unique in the genus, the colour almost certainly having being derived from yellow pigmentation. This suggestion is reinforced by the flowers of *H. pulverata* varying from cream to yellowish to brown. They are very closely related species; indeed, Verdoorn (1980) made *H. bolusii* and *H. pulverata* conspecific. Besides the flower colour, these species are clearly anomalous within the subgenus in having oddly-shaped lobed to pinnatisect leaves, a grey covering of scale-like stellate hairs, and an unusual growth form. Brown flowers are rare in non-wind pollinated flowers, of which *H. bolusii* and *H. pulverata* are presumably examples. In other families, instances of brown flowers with known pollination syndromes have proven to be interesting, with flies found to pollinate most species of *Stapelia* (Bruyns 2000) and rodents found to pollinate certain species in the Proteaceae (Rourke and Wiens 1977), (Rebelo and Breytenbach 1987). Due to the scarcity of brown flowers in nature, together with the unique morphological features of *H. bolusii* and *H. pulverata*, it may be suggested that the shift to brown coloured flowers may relate to a pollinator shift.

The species within sect. *Pinnatifidae* are mostly yellow flowered, with three white species (*H. sisymbriifolia*, *H. cedarbergensis* and [*H. virginalis*]), and two pink-flowered species (*H. ballerunica* and *H. albiflora*). Pink and white in this clade are considered to be similar pigmentally as two of the three white species have blushes of pink, or change to pink after fertilization. This colour shift from yellow to pink may therefore be the result of a single change to pink in the arid species. Another likely explanation is a single change to pink, and subsequent reversion back to yellow flowers. In this context, *H. ballerunica*, a recently discovered pink

flowered species from the forested ravines of Oorlogskloof, N. Cape, is revealing. This locality is home to a number of endemic and putatively relictual species such as *Clivia mirabilis* (Conrad, Reeves et al. 2003), which makes the basal position of *H. ballerunica* in the clade all the more interesting as additional support for this forest being a refugium.

The subsect. *Tomentosae* comprises mostly yellow flowered species with three non-yellow species in the phylogeny, and a further three species not sequenced. *H. parviflora*, *H. parvula* and *H. crassifolia* are three species that are morphologically similar to each other, and have small cup-shaped white flowers that appear to reflect a single change to white. *Hermannia cedarbergensis*, *H. atrofulminalis*, *H. geniculata*, *H. muirii*, *H. octopussyae* and *H. sisymbriifolia* -found in various clades across the genus - appear to have mostly evolved white flowers independently from each other. It is proposed that future efforts should examine the pollinators of white-flowered *Hermannia* species and their non-white sister species to determine if there is convergence due to a single pollinator type – likely moths.

The subsect. *Mahernia* has the widest variety of colours which may reflect the range of habitats and pollinators exploited by the species within this clade. The range of floral morphology and colour suggests a wide range of specific pollinators. The relative paucity of colours in the sister clade subsect. *Tomentosae* may point to conservatism specifically of yellow-coloured flowers, especially in view of the almost uniformly yellow-coloured flowers of sect. *Hermannia* where a similar phenomenon may occur. It would be interesting to determine whether this conservatism is driven by a locally abundant pollinator that selects for yellow flowers, or genetic constraints.

The subsect. *Cristatae* has several floral colours, high genetic diversity and long periods of separation between species. The petals of *H. cristata* are red, in [*H. merxmulleri*] they are blue-grey, *H. texana* has orange petals, and in the remaining species, including the majority of “*Marehnia*”, they are yellow. Interestingly, *H. texana* is yellow in bud, and then becomes orange (J. Saunders pers. comm.), thus its colour in bud matches the ancestral type.

As observed above, a transition from yellow to any other colours is rare in the reconstruction and this may be genetically constrained or driven by pollination syndromes. The subsect. *Acicarpus* comprises mainly pink flowered species and the ancestral type is resolved as pink. In the reconstruction, transitions to orange, yellow or red are found to have occurred independently in three instances. This suggests that the colour pink, in contrast to yellow, is less constrained, at least in the case of subsect. *Acicarpus*. Once again, it will be of interest to uncover the genetic or environmental factors governing this phenomenon.

Examining several sister species one sees that nascent speciation has taken place with concomitant changes in flower morphology. In the case of *H. nana* and *H. cernua* the former has blue flowers and the latter red. In *H. sisymbriifolia* and *H. cedarbergensis* the flowers differ primarily in length. Both species pairs are close genetically, morphologically and geographically proximal to one another. A diversity of floral shape, size, colour and openness in most of subg. *Mahernia* is suggestive of pollinator-driven speciation.

#### **5.4.9 Biome reconstruction**

Biome reconstruction unambiguously resolves the genus as ancestrally occurring in the grassland biome. Grassland species are absent from sect. *Pinnatifidae* and subsect. *Acicarpus*. Section *Hermannia* has only a single variety [*H. erecta*] that occurs in the grassland in Swaziland. *Hermannia cristata* is heavily affecting the outcome of the overall reconstruction. Artificially changing the state of *H. cristata* from grassland to fynbos leads to both subg. *Mahernia* and the overall reconstruction as ambiguously fynbos/Succulent-Karoo. Changing *H. cristata* to desert biome to reflect the presumably closely related [*H. merxmulleri*] leads to the subsect. *Acicarpus* clade being optimized as a desert group. Section *Hermannia* and the overall reconstruction are then ambiguous between fynbos, Succulent Karoo and desert. In view of these considerations, one sees that *H. cristata* has a profound effect on the reconstruction due to its basal position in subg. *Hermannia*. Including species closely related to it will thus likely have a strong impact on the designation of ancestral biomes. In particular, it cannot at this point be concluded with confidence that the overall reconstruction of the genus is indeed grassland.

Subg. *Mahernia* optimizes as ancestrally grassland, and has a number of basal and relictual elements that support this hypothesis. *H. malvifolia* and *H. oligosperma* are both species confined to the Drakensberg Alpine Region (DAR)(Carbutt and Edwards 2001). The percentage endemism of the region has recently been re-evaluated from a 1987 estimate of 30% (Hilliard and Burt 1987) to a more accurate estimate of 20% endemism (Carbutt and Edwards 2001). Nonetheless it is considered an important area of endemism, one of Southern Africa's eight 'hot-spots' of floral diversity, and an historical refugium for Cape elements (Carbutt and Edwards 2001). This refugium hypothesis is clearly supported by the distinct and basal position of the two Drakensberg taxa relative to the subsect. *Mahernia* to which they belong.

The "Coccocarpaceae" are most parsimoniously considered grassland in origin. However, we consider this as an artefact influenced by two factors. Firstly, the species *H. coccocarpa* is in fact a species complex with representatives also in the Karoo, thus its assignment as grassland is not definitive. Secondly, two species not sampled in the reconstruction - [*H. atrofulminalis*] and [*H. octopusyae*] - are found in the Karoo. Thus the reconstruction of this clade as grassland should be regarded as uncertain and subject to further refinements.

The sect. *Hermannia* occurs mainly within the Cape, which includes the fynbos, Karoo and Albany thicket biomes which are often interspersed. *H. bolusii* and *H. bryoniifolia* occur in the Groot Karoo, representing the north-eastern extent of this clade. *H. pfeilii* extends beyond the Richtersveld on the Namibian border, and thus represents the northernmost extent of the species within the "Euneifoliae". Overall, while sect. *Hermannia* spans several biomes, they are related by proximity and thus the section can be seen to have a cohesive biome profile.

In summary, the biome reconstructions are well-supported in the cases of sect. *Hermannia* (fynbos) and subsect. *Tomentosae* while in other clades, in particular in subg. *Hermannia*, subg. *Mahernia* and the genus as a whole, further work is required before more definitive reconstructions can be obtained.



#### 5.4.10 Rainfall

Rainfall patterns are generally complex across the genus. Nevertheless, an arid karroid rainfall profile of 101-200mm MAP is resolved for the genus, the subgenera and all clades except subsect. *Tomentosae* which resolves as 701-800mm MAP. This correlates with the finding (discussed under “Geography”) that subsect. *Tomentosa* is also geographically isolated from most of the remaining *Hermannia* species. It would thus appear that migration to and from the summer rainfall region of South Africa is rare and perhaps genetically constrained.

The sect. *Pinnatifidae* shows some support for an evolutionary gradient in the phylogeny from arid to mesic regions, with the caveat that *H. ballerunica* (sect. *Pinnatifidae*) only occurs in ravine refugia, a less moisture-stressed environment than the otherwise arid vegetation type would suggest.

The subsect. *Tomentosae* (reconstructing as 701-800mm) comprises summer drought-sensitive species that have evolved from arid species to be able to compete in vegetation that experiences frequent fires, summer rainfall and cool winters. This is borne out by adaptations such as thick lignotubers that facilitate resprouting, and larger leaves. In particular, the fact that no species of subsect. *Tomentosae* has re-colonised the Cape is consistent with the theory that plants occurring in a nutrient-rich environment do not adapt easily to nutrient-poor soil (Goldblatt and Manning 2002).

The subsect. *Mahernia* is primarily an arid clade, with the exception of the Drakensberg species *H. malvifolia* and *H. oligosperma*. Thus the reconstruction indicates that *Hermannia* ancestors were arid-adapted species that radiated to wetter conditions in the cases of subsect. *Tomentosae*, the Drakensberg species (sect. *Mahernia*) and the “Flammeae” group together with its sister species (sect. *Hermannia*).

The subsect. *Acicarpus* clade is undoubtedly arid (101-200mm MAP), with exceptions being explicable in terms of geographic location: *H. tigrensis* and *H. modesta* (201-300mm MAP) are annuals with a distribution reflecting a more tropical and hence mesic environment; *Hermannia boraginiflora* and *H. glanduligera* (400-500mm MAP) represent the summer rainfall extent of

this clade; and *Hermannia spinosa* and *H. linearis* (201-400mm MAP) reach the furthest south of the clade to around Grahamstown.

The various species of sect. *Hermannia* reveal a complex precipitation pattern, testament to the success of the group of diversifying into various habitats. Rainfall drops rapidly from around the Peninsula (over 1000mm per year) to <200mm rainfall 300km to the north, and 200km to the east. This steep environmental gradient, combined with a number of formidable mountain barriers, have provided the theatre for a complex choreography of dispersals into and between disjunct lowland habitats.

An interesting feature of the reconstruction is a rapid transition from one precipitation regime to another observable at some of the nodes. This is found twice in subsect. *Tomentosae* (a shift from 601-700mm to 401-500mm), several instances in subsect. *Mahernia* (including a shift from 101-200mm to 901-1000mm) and in sect. *Hermannia* a transition from 101-200mm to 501-600mm for a node in the vicinity of the “Flammeae”). This contrasts with the gradual gradient from arid to wetter conditions seen in the reconstruction of sect. *Pinnatifidae* and the conservatism seen in subsect. *Tomentosae*.

#### 5.4.11 Geographic reconstruction

The ancestral region of *Hermannia*, as well as that of subg. *Hermannia* and sect. *Acicarpus*, is found to be the summer rainfall region, with subsect. *Acicarpus* having complex origins including Namibia. The reconstruction of subg. *Hermannia* as summer rainfall is surprising, given the rarity of this geographical region amongst the subgenus. It appears that *H. cristata*, occupying a basal role, as well as the outgroups, may play a significant role here. Indeed, artificially replacing *H. cristata* with its sister species [*H. merxmuelleri*] leads to an ambiguous Karoo/Namibia/CFR ancestral region for the genus, with the subsect. *Acicarpus* and the subsect. *Cristatae* then becoming unambiguously Namibian clades. Thus the conclusion that the ancestor of subg. *Hermannia* inhabited the summer rainfall region of South Africa is tenuous, and should be considered as provisional subject to a more extensive molecular-based phylogeny.

The subsect. *Acicarpus* which includes several tropical African species, is ambiguously resolved but given as mostly likely having Namibian origins. In some cases the coding of region for species of subsect. *Acicarpus* was not clear-cut. For instance, *H. boraginiflora* and *H. glanduligera* occur in summer rainfall, arid savanna and Namibia, with *H. glanduligera* found as far north as Kenya. The species *H. modesta*, *H. kirkii* and *H. tigrensis* are some of the most widespread species in Africa, reaching tropical Africa and Namibia.

The subsect. *Cristatae* is unambiguously resolved as summer rainfall. This is unlikely to be the true reconstruction, since there are around 10 central African species of ‘*Marehnia*’ and many more new species to be found that appear to fall into this clade. Given its sister position to subsect. *Acicarpus* and the fact that it contains [*H. merxmulleri*], it is possible that with an extended molecular phylogeny subsect. *Cristatae* may resolve as having Namibian origins.

The sect. *Hermannia* resolves as having origins in the CFR and this is supported by a large proportion of its species inhabiting this region. Indeed, this clade fulfils the criteria of a ‘Cape clade’ sensu Linder and Hardy (2005) in that the majority of species have arisen within the CFR in the last 10 My. The Namibian species in the reconstruction, such as *H. minutiflora* and *H. comosa*, also grow in the Northern Cape and have leaves that are amongst the most tomentose in the genus. This increased indumentum density may represent an adaptation to a more arid environment, allowing better condensation of atmospheric water vapour.

The subgenus *Mahernia* resolves as Karoo, as do all of its clades. The basal position of *H. linnaeoides* within subsect. *Mahernia* may play an important role in determining the origins of the subsection as Karoo, and this may have a knock-on effect on the determination of the origins of the subgenus. Nevertheless, unlike the situation with subg. *Hermannia*, the Karoo region is fairly well represented in subg. *Mahernia*, including a clade (the group ‘*Coccocarpaceae*’) that is

predominantly found in the Karoo. Thus the designation of Karoo for the subgenus is well supported.

The subsect. *Tomentosae*, whose species are found mainly in the summer rainfall region, has *H. quartiniana* (a Karoo species) at a basal position and this apparently plays an important role in determining the origins of the clade as Karoo. It would seem likely that the ancestor of this clade had small leaves like the two Karoo representatives *H. quartiniana* and *H. stellulata*.

The subsect. *Mahernia* is diversified in a number of Cape regions including the Karoo, the Southern Cape, Northern Cape and CFR. This is consistent with this clades diversification with respect to several of the other characters examined.

Overall, the current reconstruction indicates that the origins of *Hermannia* were summer rainfall. This conclusion is uncertain given the pivotal role of the subsect. *Cristatae* in this determination as well as the paucity of summer rainfall species especially in subg. *Hermannia*. One may expect that a fuller analysis making use of future more detailed molecular studies could yield a different origin for the genus, such as a Cape region. If the origin of *Hermannia* were indeed the summer rainfall region, the reconstruction suggests migrations from there to the Cape (sect. *Hermannia* and subsect. *Mahernia*), Namibia (subsect. *Acicarpus*), tropical Africa (the informal group “*Mahernia*”, subsect. *Cristatae*), America and Australia, with the Drakensberg as a refugia. It also indicates an intermediate transition to Karoo, in the case of subg. *Mahernia*, followed by migrations to the Cape (subsect. *Pinnatifidae* and subsect. *Mahernia*), the Drakensberg (*H. malvifolia* and *H. oligosperma*) or a return to the summer rainfall region in the case of subsect. *Tomentosae*.

#### **5.4.12 Geological reconstruction**

Shale is the most ubiquitous substrate and optimizes as the ancestral state for the genus and all major clades except for subsect. *Acicarpus* and the subsect. *Cristatae* which are recovered as granite. The proportions are mapped as follows: shale (36%); Kalahari red sands (13%); tertiary sands (12%); sandstone (10%); limestone (9%); granite (8%); dolerite (6%); dolomite (4%) ; and basalt (2%). The geological diversity on which *Hermannia* is encountered is a reflection both of

its adaptive success, and its widespread nature. It occurs on nutrient-rich soils (shale, limestone, dolomite), nutrient-poor soils (sandstone), alkaline soils (limestone, dolomite) and acid soils (sandstone, tertiary sands) (Quint and Classen-Bockhoff 2006). It has been stated that a change from acid to alkaline soils requires a major shift in physiology, thus soil chemistry is considered an important factor in preventing calcifuge species from inhabiting these alkaline habitats (Quint and Classen-Bockhoff 2008).

The subg. *Hermannia* shows two quite distinct patterns of evolution, with sect. *Hermannia* mostly retaining an adherence to shale substrates, while sect. *Acicarpus* displays a shift to granite, subsect. *Cristatae* and part of subsect. *Acicarpus*, with the remainder of subsect. *Acicarpus* diversifying to other substrates, especially sandstone and sands.

Most Cape clades are predominantly found on nutrient-poor sandstone soils in montane regions, such as the Bruniaceae with only one species on the limestone compared with 77 species on sandstone. The Cape clade of sect. *Hermannia* has seven species (15%) on sandstone, a further seven species (15%) on tertiary sands which may be alkaline or acidic depending on how far leaching has proceeded and six species (12%) on limestone. This reflects an interesting and unusual ability of *Hermannia* to thrive and diversify on nutrient-rich soils in the Cape, unlike many other Cape groups. It should be noted that there is a distinct grouping of species in sect. *Hermannia* found on alkaline soils, with two apparent independent transitions from shale to limestone.

The reconstruction of subg. *Mahernia* shows some groups, namely sect. *Pinnatifidae* and “*Coccocarpae*” which have remained largely or entirely on shale, with subsect. *Tomentosae* and subsect. *Mahernia* showing successive splits from shale to other substrates (in the latter case, this appears as a ‘staircase’ of transitions) always with at least some representatives remaining on shale.

The subsect. *Tomentosae* appears to have diversified from shale origins, but the extent of this is difficult to assess currently as many species were not possible to assign to geological environments, due to technical difficulties.

The sect. *Pinnatifidae* occur predominantly on shale, but have adapted to nutrient-poor sandstone once, giving rise to two very similar species: *H. cedarbergensis* and *H. sisymbriifolia*. Concomitant with edaphic adaptation of these two species is considerable morphological change such as leaves that are amongst the most narrowly bipinnatifid of the clade and plants that are woody and upright, different from most of the clade.

The subg. *Hermannia* is conspicuously absent from the Pondoland sandstone flora (see Chapter 4, Fig. 4.5). The Pondoland Centre of Endemism (Van Wyk and Smith 2001) contains a number of Capensis elements, defined by Mucina (2006) as species of typical Cape clades that occur outside the fynbos including: *Erica*, *Anthospermum*, *Muraltia*, *Raspalia*, *Watsonia*, *Struthiola*, *Leucospermum*, *Roella*, *Agathosma*, *Calopsis*, *Tetraria* and *Leucadendron* (Mucina and Rutherford 2006). There are also a number of disjunct distributions at the species level such as *Cliffortia odorata*, *Loxostylis alata* and *Restio triticeus* (Mucina and Rutherford 2006). As the rainfall is dissimilar to the CFR being mainly summer rainfall, this similarity is geologically driven due to the predominance of sandstone in the area (Mucina and Rutherford 2006).

As evident in the geological reconstruction of subg. *Hermannia*, there are few species of Cape clades that extend into the summer rainfall areas. Three notable species are *H. dissectifolia* that appears to have derived from the Karoo *H. coccocarpa* complex and is now distributed within Gauteng; and *H. saccifera* that extends along the S. Coast as far as the Eastern Cape, with *H. harveyi* being a derived endemic from the Grahamstown area. Additionally, there are relatively few *Hermannia* species that grow on sandstone within the Cape, i.e. *H. disticha*, *H. angelica*, and *H. salviifolia*. There are therefore two conditions imposing adaptive challenges on Cape-derived *Hermannia* species from adapting to the Pondoland region: the summer rainfall regime, and the presence of sandstone.

In summary, the various groups within *Hermannia* appear to have been influenced differently by soil types in regard to their speciation. Within subg. *Hermannia*, the sect. *Hermannia* has undergone some diversification to other soil types yet a significant proportion of species remain on shale; thus soil type has played some role in speciation but not a dominant one. In sect.

*Acicarpus* a more complete transition of soil type has occurred with few species remaining on shale. In subg. *Mahernia* the “*Eococarpae*” have remained entirely on shale, suggesting that soil type has not played a direct role in speciation. Indeed, large floral variation suggests that pollinator-driven speciation may be more relevant for this group. The subsect. *Mahernia* occurs across a wide diversity of substrates. Many species groups like the ‘*Candiflorae*’ occur in similar habitats, but are separated by spatial distance. Thus it would seem that both geology and geographic separation are drivers of speciation in this group. In subsect. *Tomentosae* it is difficult to interpret the role of soil type in its speciation due to paucity of data.

#### **5.4.13 Fruit rotation**

Fruit rotation after fertilization is entirely absent from subg. *Mahernia*; indeed, this is resolved as the ancestral state for genus *Hermannia*. In subg. *Hermannia*, the ancestral state for sect. *Hermannia* is rotating, and this is by far the most common state for species of the section. The sect. *Acicarpus* has a mix of rotating and non-rotating states with too little data at present to discern any particular patterns. The functional significance of rotating fruit has not yet been accounted for in *Hermannia*. In Janzen (1984), a mechanism of endozoochorous dispersal by herbivores was proposed by which an animal may be attracted to edible foliage proximal to the fruit and ingest the fruit in the course of eating the leaves. In *Hermannia*, it could be that the rotation of fruit in some species after fertilization provides exactly such proximity of the fruit to the closest leaves that such a mechanism could take effect. It is thus of interest to test this hypothesis in species displaying fruit rotation. If this were indeed the case, it would further be worthwhile to examine dispersal patterns across the genus with regard to fruit rotation to determine whether dispersal agents have played a role in driving speciation.

#### **5.4.14 Synapomorphies and support for the phylogeny**

As *Hermannia* is a genus that has proven difficult to separate into smaller groups based on morphology, identifying robust distinguishing features is of critical importance. In the reconstructions, several distinct synapomorphies emerge. These can be separated into true synapomorphies; that is, a character state unique to a particular clade, and approximate synapomorphies; that is, a character state that is mostly found in a particular clade with isolated

exceptions outside of the clade. The true synapomorphies found include the long horns exclusively found for all members of subsect. *Cristatae* except those in the informal group “*Marehnia*”, short horns found exclusively in all members of subsect. *Acicarpus*, the rounded capsules found exclusively for all members of sect. *Mahernia* and the annual species found exclusively for a subset of subsect. *Acicarpus*. An approximate synapomorphy includes the single flower per axil for all members of subsect. *Acicarpus*, a character state shared by two species outside the subsection (*H. cristata* in subsect. *Cristatae* and *H. linnaeoides* in subsect. *Mahernia*).

A corollary of the reconstructions is that patterning of character forms according to groups may be seen as indirect support for the integrity of the phylogeny. Thus if a particular group tends to cluster with regard to many characters, this provides indirect support for the close relationship of its member species. At the level of subgenus, we find that all species of subg. *Mahernia* have no horns (subg. *Hermannia* having a complex pattern) and all species of subg. *Mahernia* have hanging fruit (with subg. *Hermannia* having a complex pattern dominated by rotating fruit, while all but one species of subg. *Hermannia* have entire leaves, while subg. *Mahernia* has a complex pattern. Regarding sections and subsections with subg. *Mahernia*, we find that sect. *Pinnatifidae* is characterised by having angled capsules and subsect. *Tomentosae* is characterised by occurring in the summer rainfall area (one other species in subg. *Mahernia* shares this trait). With subg. *Hermannia* we find that subsect. *Cristatae* is unique in being either geographically separated from the rest of the subgenus, or occurring in grassland vegetation which is unique for subg. *Hermannia*; subsect. *Acicarpus* is unique in having short horns; sect. *Hermannia* is separate from subsect. *Acicarpus* and part of subsect. *Cristatae* in having two or more flowers per axil and geographically distinct from the remainder of subsect. *Cristatae*; and the informal group “*Flammeae*” is unique within sect. *Hermannia* in having red flowers. Although the informal group “*Coccocarpaceae*” has no uniquely identifying feature, its species are mostly located in the Karoo, an uncommon location for species of subg. *Mahernia*. The lack of any clear identifying feature for subsect. *Mahernia* may be related to its generally high level of variation across the character set.



Overall, we find several useful synapomorphies for clades in the genus, as well as identifying characters for most of the clades. This can be seen as indirect support for the integrity of the phylogeny.

#### **5.4.15 Variation of character traits and drivers of speciation**

The genus as a whole displays a wide variety of forms with respect to certain characters such as biome, rainfall, geography and geology. This is especially pronounced in subsect. *Mahernia* for which leaf dissection and flower colour also display a wide variety of forms. In the latter case, this phenomenon strongly suggests adaptability across the clade to a number of environmental pressures, perhaps including variation in herbivores, dispersers, pollinators, available nutrients and water availability. More specific drivers of speciation can be suggested for other clades. The split between sect. *Acicarpus* and sect. *Hermannia* may have been influenced by geological adaptation (sect. *Acicarpus* initially moving to granite substrates and then speciating to sands and shale) and pollinator selection (the majority of flowers in sect. *Acicarpus* being pink while those in sect. *Hermannia* being mostly yellow). Within sect. *Hermannia*, the informal group “Flammeae” are distinguished by their red flowers; this could indicate a shift in pollinator syndrome. Within subg. *Mahernia*, subsect. *Tomentosae* are likely to have migrated to the summer rainfall region by adapting to a higher rainfall regime with its concomitant pressure for access to sunlight above the grassland canopy, possibly enabled by their rambling habit and thick rhizomes allowing resprouting after fire .

#### **5.4.16 Conclusion**

The reconstructions carried out in this chapter generally provide strong although indirect support for the integrity of the phylogeny, with most clades having a uniquely identifying state for at least one of the characters. Patterns of inheritance for the characters differ. Simple patterns of inheritance (i.e. little variation within clades) are found for the characters flowers per axil, capsule shape, number of pollen colpi and life history. Complex patterns of inheritance (high variation in most of the clades) is found for the characters biomes, rainfall, geography and geology. Mixed patterns (some clades with simple inheritance and others with complex inheritance) are found for horn length, pollen diameter, leaf dissection, flower colour and fruit

rotation. It is likely that complex patterns of inheritance are related, in some cases, to environmental pressures (such as pollinator syndromes and adaptive changes in flower colour).

Four true synapomorphies have been found – the subsections *Cristatae* and *Acicarpus* containing unique horn lengths, sect. *Mahernia* unique in its species having rounded capsules, and subsect. *Acicarpus* unique in containing the only annual species.

The ancestral biome of the genus has not been successfully identified with a high degree of certainty, due to strong influences of individual species basally attached to the phylogeny, in particular *H. cristata*. It is thus not possible, from the reconstructions alone, to discuss the origins of the genus and its subsequent dispersal. It is suggested that the annual life form originated once only, in Namibia, and spread outwards from there, now occupying a wide range across Africa.

## 6. Diversity patterns of *Hermannia*

### 6.1 Introduction

*Hermannia* is largely a southern African genus, with outlying species extending to the horn of Africa, and disjunct species around south-western North America and western Australia. Several subdivisions of the genus have been proposed in the past {Verdoorn, 1980 #561;Engler, 1900 #1530;Harvey, 1860 #1356}, of which Engler's (1900) sections have been considered to have "natural geographic ranges" (Livingston 1921). These sections were elucidated and refined in Chapter 3, with the phylogeny being used to inform the re-classification of the remaining species into two subgenera, and five major clades. These clades are centred around Namibia (subsect. *Acicarpus*), the Cape Floral Region (CFR) (sect. *Hermannia* and subsect. *Mahernia*) and the summer rainfall region of South Africa (subsect. *Tomentosae*). A further clade, the subsect. *Cristatae*, is distributed in America, the Brandberg area of Namibia, the grasslands of eastern South Africa, and appears to include a species group ("Marehnia") that is centred around eastern Africa. This chapter explores the biogeographic diversity and patterns of this genus, in order to understand how past conditions have created the present distributions. Factors leading to the diversity of the CFR and beyond are discussed, along with an assessment of conservation priorities through an analysis of species hotspots.

#### 6.1.1 Drivers of diversity in the megadiverse Cape Floral Region

All major clades (sections and subsections) of *Hermannia* have representatives within the CFR. The diversity of this region has been the focus of numerous studies (eg. Linder 2003; Burgoyne, van Wyk et al. 2005; Galley and Linder 2006; Cowling, Proches et al. 2009; Verboom, Archibald et al. 2009). A concerted effort has been made over the past few decades to understand the factors that have led to this area being termed "megadiverse" (Thuiller, Midgley et al. 2006), and especially to the unusually high species-to-genus ratio that is characteristic of the CFR (Cowling and Holmes 1992; Cowling, Proches et al. 2009). The radiations of major Cape lineages such as Aizoaceae (Klak, Reeves et al. 2004), Iridaceae (Goldblatt, Savolainen et al. 2002), *Muraltia* (Forest, Nanni et al. 2007), *Indigofera* (Schrire, Lavin et al. 2003) and *Pelargonium* (Bakker, Culham et al. 2000), show multiple periods of radiations since the start of the Oligocene, about 40Ma, with only *Heliophila* radiating exclusively in the Pleistocene

(Mummenhoff, Al-Shebaz et al. 2005). Ecological and landscape scale modes of speciation favoured by many contemporary authors, such as pollinator shifts (Goldblatt and Manning 2006; van der Niet, Johnson et al. 2006), fire-created niches (Bond, Midgley et al. 2003), limited gene-flow (Ihlenfeldt 1994), and a high diversity of topography and soils, inadequately explain the disproportionately high diversity on account of their occurrence in other regions (Cowling, Proches et al. 2009; van der Niet and Johnson 2009). Radiations have also been attributed to key innovations such as wide-band tracheids (Klak, Reeves et al. 2004), round leaves (Klak, Reeves et al. 2004) or underground storage organs (Bakker, Culham et al. 2005; Oberlander, Emshwiller et al. 2009), but these are more features of succulent plants that are associated with arid karroid regions rather than the CFR.

Proponents of a climatic explanation for the high diversity of the CFR have attributed rapid radiation to the prevailing Mediterranean climate in the region (Thoday 1925; Weimarck 1941; Dahlgren 1963; Levyns 1964). Most notably, fire promotes a regular turnover of flora, allowing those species that are fire-adapted to speciate and occupy formerly forested areas (Cowling and Holmes 1992; Bond, Midgley et al. 2003; Bond, Dickinson et al. 2004). The higher concentration of CFR taxa in the south-west compared to the eastern CFR has been considered a result of longer ecological gradients (greater variation in altitude and rainfall) that may promote parapatric speciation (Barraclough 2006) as well as greater edaphic heterogeneity in the south-west (Oliver, Linder et al. 1983). However, Cowling (1992) disputes this, having found an equally large amount of heterogeneity in Humansdorp in the east (Cowling 1984). Furthermore, the greatest change in rainfall seasonality occurs around the Breede River, thus one would expect an abrupt decline in thicket and forest taxa that are generally associated with the tropics. This abrupt transition has not been found, with thicket and forest taxa gradually declining from the east, suggesting factors other than rainfall (Cowling, Rundel et al. 1996). Faced with this evidence, Cowling et al. largely dismiss notions of diversity based solely on contemporary conditions .

A more recent approach to understanding the drivers of local diversity, used various multivariate models to explain local species richness (Thuiller, Midgley et al. 2006). Stepwise regression was used to identify environmental and topographical variables with the greatest

ability to predict diversity within South Africa. A number of simple models were fitted using boosting methods, and the combined predictions used to look at the response using a boosted regression tree (BRT). Topographic heterogeneity was found to be the most important environmental variable explaining South African floral diversity, especially in the savanna, Nama-Karoo and Succulent Karoo. Mean annual precipitation (MAP) was found to be the most important variable in the fynbos and grassland, and second most important in the savanna. Cowling et al. (2009) recently concluded that it is not simply landscape and geomorphic heterogeneity that is important, but the timing of that heterogeneity that was conducive to diversification of South African flora.

A further finding of Thuiller et al. (2006) supports Cowling's (1997) conclusion that areas of high richness are mainly found along and below the Great Escarpment. This is an ancient geomorphological feature that is associated with the splitting of Gondwana, with subsequent back-cutting erosion away from the coast (Cowling, Proches et al. 2009). Above the escarpment is a region of relatively low diversity. Its frost-prone landscape of plains with intermittent hills includes the Nama-Karoo biome. Below the escarpment is a rugged and dissected coastal plain that is relatively warm. Its flora that encompasses the Succulent Karoo and fynbos biomes, is far more diverse.

Goldblatt and Manning (2002) compared the CFR to other Mediterranean regions in the world to look for factors that explain the higher alpha and beta diversity in the CFR. They, like Cowling et al. (2009), discounted most climatic and edaphic factors as being similar to other systems, instead invoking historical factors to explain the extraordinary diversity. They noted that unlike in the northern hemisphere and Chile, pollen cores show a remarkably stable vegetational signature (Meadows and Sugden 1991), suggesting a relatively stable environment since the Pleistocene (Goldblatt and Manning 2002). Linder et al. (1992) attribute the high species number within a limited number of sclerophyllous genera as a signature of the CFR being an edaphic (low-nutrient soils) and climatic (winter-rainfall) 'island' since the onset of contemporary conditions at the end of the Tertiary (Deacon 1983). Thus, the summer-arid conditions prevalent since the Tertiary, in concert with lightning-strikes upon proto-fynbos, may have led to the extinction of many pyrofloric taxa unable to tolerate fire. The fitter sclerophyllous

genera that were pre-adapted to nutrient-poor, summer-arid conditions, are thought to have undergone subsequent explosive speciation (Cowling 1983). Non-CFR taxa have been unable to adapt to the CFR except for marginal or zonal habitats. The barriers to colonization are considered less extreme in the southeast than the southwest, with soils in the former region being less depauperate and summer-drought less harsh. The low number of summer rainfall elements in the CFR may be explained by more pronounced climatic barriers in the past (Cowling and Holmes 1992).

Cowling et al. (2009) provide a synthesis of our current understanding on prior conditions that have been conducive to speciation. Additionally, they describe the putative ancient geomorphic conditions that have been largely neglected in modern botanical literature with the exception of Axelrod and Raven (1978). Evidence suggests that glacial periods were markedly drier and cooler than the interglacial periods (Deacon and Lancaster 1988), leading to karroid elements becoming widespread, whereas fynbos, thicket and forest species were confined to refugia. In the south-west, however, an increased frequency of frontal rains would have rendered the southwestern region wetter leading to the survival and even expansion of fynbos elements. This period of mild conditions conducive to floristic survival, would have been suitable for the generation and maintenance of species, resulting in a high number of habitat specialists and local endemics together with a high floristic turnover and regional richness (Cowling and Holmes 1992). During the late Oligocene to middle Miocene (ca. 25-16Ma), the CFR underwent a return to predominantly warmer and wetter conditions (Zachos, Pagani et al. 2001). At the start and end of the Miocene (23.8-5.3Ma), a hot magmatic plume between 1000km and 3000km under the mantle produced a rise of some 150m altitude in the west, and as much as 600m-900m altitudinal increase in the eastern parts of the African subcontinent. The subsequent period of erosion during the late Miocene was thus responsible for the exposure of large areas of nutrient-rich soils and clays in the lowlands, as well as the widespread development of large areas of coastal calcareous substrata (Cowling, Proches et al. 2009). These nutrient-rich habitats are where the majority of the CFR *Hermannia* species are to be found.

### 6.1.2 Richness and diversity

Richness is a measure of the number of species occurring in a particular region, which does not take into account the relative abundances of each species. It is useful for giving an overall measure of the diversity in a particular region, but cannot be used for comparing the species abundances of two regions with similar total numbers of species. A simple measure of Richness is that of Menhinick's index. This is a useful measure for simple comparisons or where the number of individuals within a sample is not known or is not relevant. Although richness adequately provides a measure of gross differences between areas, diversity measures are more relevant and meaningful for understanding the relevance of compositional heterogeneity when systematic plots are undertaken. As the data we are using is from sporadically collected herbarium specimens rather than systematic plots, the differences between richness and diversity are not as meaningful.

Biological diversity is defined by Magurran (2004) as “the variety and abundance of species in a defined unit of area”. Alpha diversity measures species abundances within a particular area, beta diversity is “a measure of the extent to which the diversity of different spatial units differ” (Magurran 2004), and gamma diversity can be defined as “the diversity of a landscape or other large area” (Magurran 2004), while other definitions have also been used for the latter. Species diversity is an index that incorporates both the number of species in an area, and the relative abundance of each species. It is considered a more refined value than species richness (Magurran 1988) because it differentiates between two regions having the same total number of species but having different relative abundances of the component species. On the other hand, the measures of alpha, beta and gamma diversity are complex and do not directly relate to richness. Regional richness is a measure that takes into account alpha, beta and gamma diversity. It was applied to the CFR in a study of the diversity of the Agulhas Plain (Cowling 1990).

The basic equation used in calculating diversity is the relative abundance of a species, measured by

$$D = (n / N)^2$$

where  $n$  is the total number of collections of a particular species and  $N$  is the total number of collections of all species within the defined area.  $D$  is the diversity value, with values between 0 and 1 where the latter value is the highest diversity that can possibly be attained.

Early studies by Cowling on a limited plot-based dataset showed that alpha diversity was invariant across the CFR. Both beta and gamma turnover were found to be approximately 1.6 times higher in the south-west than the south-east. To account for differences due to longer ecological gradients in the west resulting from greater altitudinal and rainfall ranges, physiologically matched eastern and western sites were subsequently assessed. Cowling (1992) then found the species density to be 1.8 to 3.8 times higher in the west compared with the eastern CFR. Cowling discovered that regional richness is lower in the lowlands than the montane sites, supported by subsequent findings based on Linder's QDS data (Cowling, Holmes et al. 1992). In summary, Cowling (1992) found that regional richness in the south-western CFR is linked to higher turnover (change in species) within and between habitats. This was considered to be due to historical processes driving differing rates of evolution of habitat specialists (beta diversity) as well as affecting other measures such as gamma diversity.

An important statistical instrument for calculating richness is rarefaction. It is especially useful when handling data collected in an uneven way from different regions. If the cumulative number of observed species is plotted against some measure of sampling, the resulting graph is a species accumulation curve (Colwell, Mao et al. 2004). Colwell (2004) explains that rarefaction uses a statistical technique that uses random sampling to produce a smoothed curve that is the expectation of the corresponding accumulation curve. Rarefaction of a sample provides an estimate of expected species richness at  $n$  sample size from a given of a randomized total sample pool. It is an ecological technique used to calculate richness when using samples of differing collection intensity. The purpose is to make direct comparisons within communities based on the number of individuals in the smallest sample (Magurran 1988). It assumes that the number of species found is a result of sampling intensity. Its usefulness is limited when any species is very rare or very common, or when beta diversity is very high. If a single taxon is particularly common or rare, the number of collections will be relative to the extremes of the number of individuals of that species, not to the intensity of sampling. In applying rarefaction it is assumed



that spatial distribution of individuals is random. A further caveat is that only species richness is taken into account, not species abundance (Magurran 1988).

An “estimator of richness” provides us with the apparent richness of an area ( $S$ ), which is determined by the sampling effort. The total number of species in an area,  $S_{max}$ , can be calculated using a number of approaches as implemented in Diva-GIS. The estimate “*Chao*” uses a simple equation that takes into account only singletons (a single available accession for a given species), whereas “*Chao modified*” provides a less biased equation that accounts for doubletons as well. The Michaelis-Menten approach has been found to severely underestimate richness by as much as 67–80% in samples of 100 and 1000 species (Magurran 1988). Keating and Quinn (1998) report similar levels of underestimation for their study of vascular plants in Glacier National Park, Montana. First order jackknives are found to consistently perform better than the other stated methods, with ACE typically performing the best (Magurran 1988).

### **6.1.3 Conservation priorities and complementarity**

One of the ultimate goals of assessing diversity is in the planning and assessment of conservation priorities. Diversity measures provide us with a broad means of understanding the resulting patterns of speciation, diversification and persistence of species in the landscape. An area of high diversity may be due to the immigration of species from surrounding areas, or the endogenous generation of species. This region would likely lose its species under changing climates, unless they were able to persist in refugia. Thus identifying regions of high diversity allows us to uncover possible refugia to future climate change. As species are the handle by which we can understand diversity, regions of high species diversity can generally be considered proxies for general ecosystem diversity. Thus conserving areas of high diversity provides the most effective protection of the products of speciation.

Conservation is a major challenge in the CFR, a region not only extremely diverse, but also with the majority of the area transformed by human activity (Rouget, Richardson et al. 2003). Of the 19 critically endangered vegetation types within South Africa, 13 occur within the CFR. Of these, all are located in the lowlands, with conservation targets determined at between 25 and 32% (mean: 28.1%). However, only 7% to 31% (mean: 17.6%) of area remains, with a mean of

0.6% currently under formal protection (Mucina and Rutherford 2006). The widely used IUCN (International Union for the Conservation of Nature) target recommends that 10% of vegetation types should be under formal conservation, in order to preserve a conservative 75% of species. Diamond and May (1976) calculated that 10% of area conserved would save closer to 50% of the species. Desmet and Cowling (2004) questioned whether saving 50% of the planet's terrestrial species is truly adequate. Due to varying levels of diversity, abundance and distribution of species within the CFR, Desmet and Cowling established that to effectively conserve 75% of the species, the target for local vegetation types should be between 5 and 48%, depending on the region. In view of the large variance in the estimations of projected outcomes of conservation strategies, it is clear that further information obtained from poorly studied taxa on the levels of diversity in different regions should form a critical part in determining these strategies.

As *Hermannia* is such a widespread genus throughout South Africa, finding regions of high diversity may be used to focus conservation efforts for identifying future nature reserves. Analysis of the diversity of *Hermannia* is thus particularly pertinent, as it is located in the lowlands where much of the transformation from natural to cultivated land has taken place.

To establish areas of conservation priority based on *Hermannia* diversity, Rebelo's complementarity approach is adopted. This algorithm iteratively chooses the most diverse area, followed by the next best area that conserves the most dissimilar complement of species from those already selected (Rebelo and Siegfried 1992; Rebelo 1994). In this way, the algorithm provides an ordered sequence of regions in decreasing order of conservation priority, such that available resources can be utilized to conserve these areas from the top down. It should be noted that output of the complementarity algorithm is not always unique, as the choice of next most diverse and distinct region may be between one of several equally eligible options.

#### **6.1.4 Endemism**

Areas of endemism are generally considered the units of biogeography (Hausdorf 2002), with levels of endemism within the CFR being amongst the highest in the world (Goldblatt and Manning 2002). Gentry (1986) defines a local endemic as a species occurring in area of less than 50 000km<sup>2</sup>. All South African local endemics occupy an area of less than 2 000km<sup>2</sup>, with some

occupying less than 5km<sup>2</sup> (Cowling, Holmes et al. 1992). Centres of endemism are delimited by the approximate coincident distribution of taxa confined to that area. The CFR is well-recognised as one such region, with around 9 000 species of which some 69% are endemic. These figures are rivalled by regions such as SW Australia, Madagascar and New Zealand, though the CFR is around three times smaller than the smallest comparable area of endemism. Weimarck's study (1941) was the first to show coherent centres of endemism within the CFR. These five centres have remained largely unchanged, with adjustment provided to include the limestone adapted species of the Bredasdorp-Riversdale centre (Cowling, Holmes et al. 1992), later termed the Agulhas Plains region (AP) (Goldblatt and Manning 2000). In the eastern CFR, an area particularly rich in karroid succulents, the Kaffrarian Transition Zone (Cowling, Holmes et al. 1992), has been recognised and supported as a centre of endemism (Cowling 1983; Hoffman and Cowling 1991; Clark, Barker et al. 2007). Endemism provides a particularly valuable tool for estimating conservation value, as endemic species are typically the most liable to extinction, and thus worthy of conservation. Endemism is generally, although not necessarily, concentrated in areas of high diversity. In order to fully establish conservation strategies, it is thus important to separately measure regions of high endemism. Though this is not done in this chapter, we mention its importance to future work.

### **6.1.5 Aims and questions**

In this chapter, the richness and diversity *Hermannia* and sect. *Hermannia* are studied. The following questions are asked: (1) Where are the regions of highest turnover, diversity and endemism, and what are the possible drivers of this diversity? (2) Is *Hermannia* a 'Cape element'? (This is defined by Carbutt and Edwards (2001) as a taxon whose species are most heavily concentrated in the CFR relative to its distribution elsewhere.)

## **6.2 Methods**

### **6.2.1 Specimens, data and gazetteering**

Herbarium specimens were examined, and the labels and notes compiled from the following herbaria: Bolus (BOL); Compton (NBG); Albany Museum (GRA); North West University

(PUC); and the two Mozambican herbaria within Maputo, the National Institute of Agronomic Research (LMA) and Eduardo Mondlane University (LMU). The Pretoria (PRE) Herbarium records were personally validated for the unrevised subg. *Mahernia* but assumed correct for subg. *Hermannia*, as Verdoorn undertook her revision from the Pretoria Herbarium. The Windhoek Herbarium (WIND) records were obtained digitally, and included simply a species name and QDS. Additional sources of information for the new species include my private field-herbarium of *Hermannia* specimens, which is housed within the Bolus Herbarium. All specimens were either placed within a QDS (Fig. 6.1, below), or were excluded from the analysis. Likewise a significant portion of undetermined species were included in the overall distribution map of species presence, but were otherwise excluded.

The localities were placed using a number of gazetteer resources including the Fuzzy Gazetteer (<http://dma.jrc.it/services/gazetteer/>), The Algoa Gazetteer (Skead 1993), and the NGA Geonet names server (<http://earth-info.nga.mil/gns/html/index.html>).

	X°	15"	30"	45"	X+1°
Y°	AA	AB	BA	BB	
15"	AC	AD	BC	BD	
30"	CA	CB	DA	DB	
45"	CC	CD	DC	DD	
Y+1°					

Fig. 6.1 Scheme denoting the placement of quarter degree grid squares (QDS) within a latitudinal / longitudinal degree.

### 6.2.2 Clades and groups used in analysis

All botanical records were entered into Brahm's 6.04 and grouped according to major clades (*Hermannia*, subg. *Mahernia*, subg. *Hermannia*, ~~–Marehnia~~ and subsect. *Acicarpus*) as identified in Chapter 2. *Mahernia* was split further into two groups: a combined paraphyletic group, Western *Mahernia*, that combines the subsect. *Mahernia* and the sect. *Pinnatifidae*; and the subsect. *Tomentosae* that comprises species mainly from the summer rainfall area of

Southern Africa. Profiling of the groups by using climatic niche modelling (bioclimatic profiles) and climatic envelopes allows for a generic climatic identity for each group. Species outside the 95% confidence limit provided by the two-dimensional plots were marked in both analyses by appearing in red instead of green. As these species did not match the pattern of the group, and could not be categorized into their own group, the following widespread or summer rainfall species from the subsect. *Acicarpus* were excluded from analyses: *H. solaniflora*; *H. tigrensis*; *H. grisea*; *H. tomentosa*; *H. boraginiflora*; *H. modesta*; *H. kirkii*; and *H. micropetala*. A single outlying specimen of *H. glandulosissima* was removed from central Angola due to its significantly different climatic characteristics compared with the other members of the group (see top values of three highest peaks in Fig. 7.18f). The karroid and Cape species, *H. trifurca* and *H. linearifolia* remain within subsect. *Acicarpus*. All groups were exported to DIVA GIS, and analysed separately.

### 6.2.3 Distribution maps

Species were plotted by informal group or major clades, and depicted with various complementary symbols and colours to optimize the visibility of species distributions.

### 6.2.4 Diversity and richness

In order to determine the patterns of diversity and richness within the genus, as well as the contribution to the overall pattern of the major clades, the *point to grid* feature of DIVA-GIS was utilized. There is a very low density of records of “*Marehnia*” within tropical Africa. As diversity measures are based on the scale of QDS, “*Marehnia*” did not have a sufficient density nor diversity of species within a QDS to allow for any meaningful comparisons. Only two of the four American species overlap, and there is only one Australian species. Analysis was therefore confined to southern Africa. All measures implemented in the *point to grid* feature of the software were examined, with the most revealing results discussed in the chapter. In some cases the circular neighbourhood algorithm was utilized that averages out the density for a QDS based on contributions from proximate cells. A value of one was used that only examines adjacent cells. An artefact of this technique is that diversity appears to occur in the sea. As values vary from analysis to analysis, they are not necessarily comparable. As we are interested in comparing diversity, in all richness and diversity maps the upper most class is termed “very rich”, the

second highest class “rich” and the third highest class “moderately rich”. Similarly, the lowest class is termed “poorest” and the second lowest class “poor”.

#### 6.2.4.1 Rarefaction

As noted in Thuiller et al. (2006), PRECIS data varies tremendously in collecting intensity, with entire QDSs in the northern Karoo being devoid of collections, contrasting with a high density of collections alongside major roads. Rarefaction attempts to calculate richness given this differing sampling effort. "Rarefaction generates the expected number of species in a small collection of  $n$  individuals (or  $n$  samples) drawn at random from the large pool of  $N$  samples" (Gotelli and Colwell 2001). In other words, by comparing two regions of differing sample size, the question asked is: “If we know how many species are in the larger sample, how many species would we expect to find given a smaller sample?”. The underlying assumption is that the greater the effort, the more species will be found. Rarefaction takes the proportion of samples from a smaller grid, and compares it to the average expected number from a larger sample size. The method computes variance and standard deviation to provide a measure of significance.

Rarefaction curves are necessary in order to estimate species richness. The computation of rarefaction curves is derived from the formula (Heck, van Belle et al. 1975):

$$fn = E[Xn] = K - \binom{N}{n}^{-1} \sum_{i=1}^K \binom{N - N_i}{n}$$

Where:

$N$  = total number of items

$K$  = total number of groups

$N_i$  = the number of items in group  $i$ . ( $i= 1, \dots, K$ ).

In the case of this analysis,  $N$  are the total number of collections.  $K$  the total number of species, and  $N_i$  the number of collections within a species. This is done for each QDS to come up with a rarefaction value.

### 6.2.4.2 Collecting density

Collecting density was derived from the total number of collections per QDS, and plotted in DIVA-GIS. Although duplicate collections from different herbaria were included in the count, this should not introduce bias favouring any particular region.

### 6.2.4.3 Centres of diversity

Table 6.1 shows the five different diversity indices implemented in DIVA-GIS that were used to produce diversity maps under the point-to-grid feature (Hijmans, Cameron et al. 2005). The value  $S$  in these indices is the equivalent of the value  $K$  used in rarefaction, with  $N$  being equivalent in both instances.

**Table 6.1 Diversity index calculations extracted from the DIVA-GIS 5.2 manual (Hijmans, Guarino et al. 2005).  $S$  is the number of unique classes (species) per cell;  $N$  is the number of observations per cell;  $n_i$  is the number of individuals in the  $i$ -th class; and  $p_i$  is the proportional abundance of the  $i$ -th class =  $n_i / N$ .**

Index	Formula
Margalef	$D_{Mg} = (S - 1) / \ln(N)$
Menhinick	$D_{Mn} = S / \sqrt{N}$
Shannon	$H' = -\sum p_i \ln p_i$
Simpson	$D = \sum (n_i (n_i - 1) / N(N - 1))$
Brillouin	$HB = (\ln N! - \sum \ln n_i!) / N$

Both Margalef and Menhenicks species richness indices are aimed at compensating for sampling bias. They do so by dividing the richness (the number of species recorded,  $S$ ), by the natural log and the square route of the number of individuals in the sample ( $N$ ) respectively. Despite intentions, both measures remain highly influenced by sampling effort. The Brillouin index of species richness is appropriate for circumstances where the randomness of a sample cannot be guaranteed (Magurran 1988). The Shannon index is a more recent and refined form of the Brillouin index. Both estimates of diversity are similar and usually correlated. The Brillouin index is always lower, as it describes a known collection about which there is no uncertainty. On the other hand, the Shannon index estimates the diversity of the sampled in addition to the

unsampled portion of the community, thus introducing a bias. Magurran (1988) cites a number of advocates who prefer the use of Brillouin over Shannon in cases where samples are non-random or collections are made. Magurran (1988) cautions that the Brillouin index can give unexpected results where there is a highly unusual species abundance distribution, or when the number of individuals ( $N$ ) is low. The Simpson index belongs to a different family of species richness than the above measures, being a dominance measure (Magurran 1988). As a diversity measure, it is considered one of the most meaningful and robust measures available. It captures the variance of the species abundance distribution, and is weighted by abundance of the most common species. As noted in the manual (Hijmans, Guarino et al. 2005), the Simpson index is rated with maximum diversity at zero, and minimum diversity at 1. The complement is used for the mapping implementation by taking  $1-D$ . In its complemented form, the value of the measure rises as the assemblage becomes more even.

### **6.2.5 Complementarity**

Rebello's (1994) complementarity algorithm has been implemented by DIVA GIS on the full *Hermannia* dataset. Maximizing the total number of species selected in as few cells as possible requires non-linear optimization. Rebello's iterative procedure calculates an approximate optimal solution. In each iteration, the "value" of each grid cell is calculated, based on the species present in that cell, and in relation to the species in the cells already selected. If there are two or more cells with the same "value", one is selected at random. Hence, this procedure can lead to slightly different results every time it is run.

DIVA GIS provides two complementarity options. With the "equal weight" option, each category (eg. species) has the same weight. With the "rarity" option, the value of a cell is calculated using the "rarity value" for each observation. The rarity value is the number of observations of a category divided by the total number of observations. Both equal and rarity based weighting is assessed, with the number of iterations set to 100.

#### **6.2.5.1 Turnover**

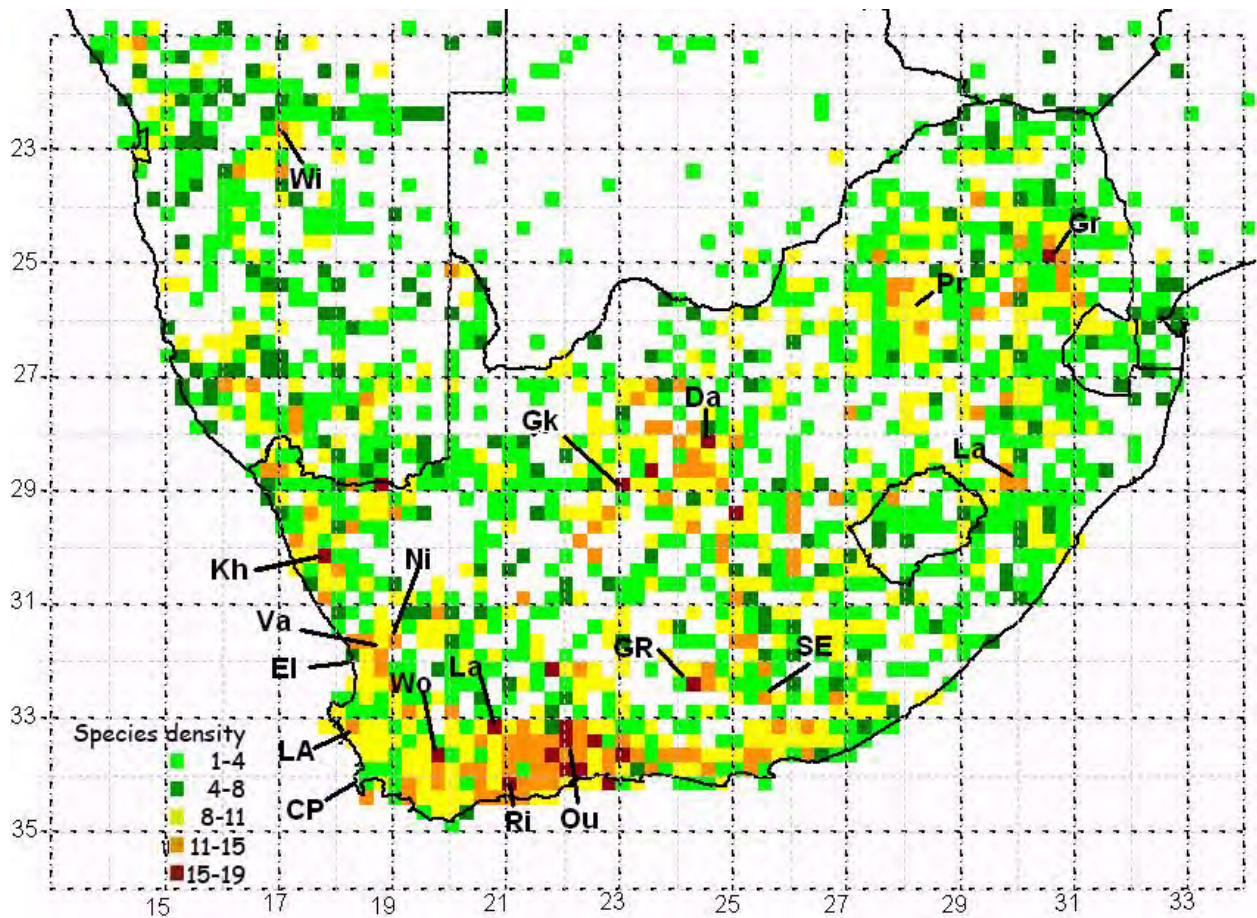
Arita (2002) defines turnover as: "a measure of changes in species composition in spatial or temporal gradients"; otherwise known as beta diversity *sensu* Whittaker (1972). Turnover is an



estimate of how different a number of nearby areas are. The Diva-GIS manual (Hijmans, Guarino et al. 2005) provides a scenario in which there are two areas comprising a number of grid cells but having a similar number of species overall. If one area has different species in all its grid cells, and another has the same species in all its grid cells, Then former area would have a high turnover; the latter area a low turnover.

### 6.3 Results

In the figures depicting results of analyses, a number of regions of biodiversity interest are identified. These are indicated by acronyms in Fig. 6.2. These locations are relevant variously to high richness and high diversity values, as described in detail with regard to results presented later. The actual data in Fig. 6.2 is not discussed here.



**Fig. 6.2** Key to places of importance in Southern Africa that are encountered during this chapter: Cape Peninsula (CP); Danielskuil (Da); Elandsbay (El); Griekwastad (Gk); Graskop (Gr); Graaff-Reinet (GR); Khamieskroon (Kh); Ladysmith (La); Langebaan (LA); Niewoudtville (Ni); Oudtshoorn (Ou); Pretoria (Pr); Riversdale (Ri); Van Rhynsdorp (Va); Windhoek (Wi); and Worcester (Wo). The species density is per QDS.

### 6.3.1 Distribution mapping of major species groups

Fig. 6.3 provides an overview of the distributions and sampling that make up the diversity calculations below. Although not visible in this figure, it should be noted that the members of sect. *Acicarpus* have very little overlap in their distributions, therefore this section was not analysed separately for richness or diversity. The subsection. *Tomentosa* has a distribution largely complementary to that of the remainder of the genus; thus diversity in the summer rainfall region is attributable to this subsection.

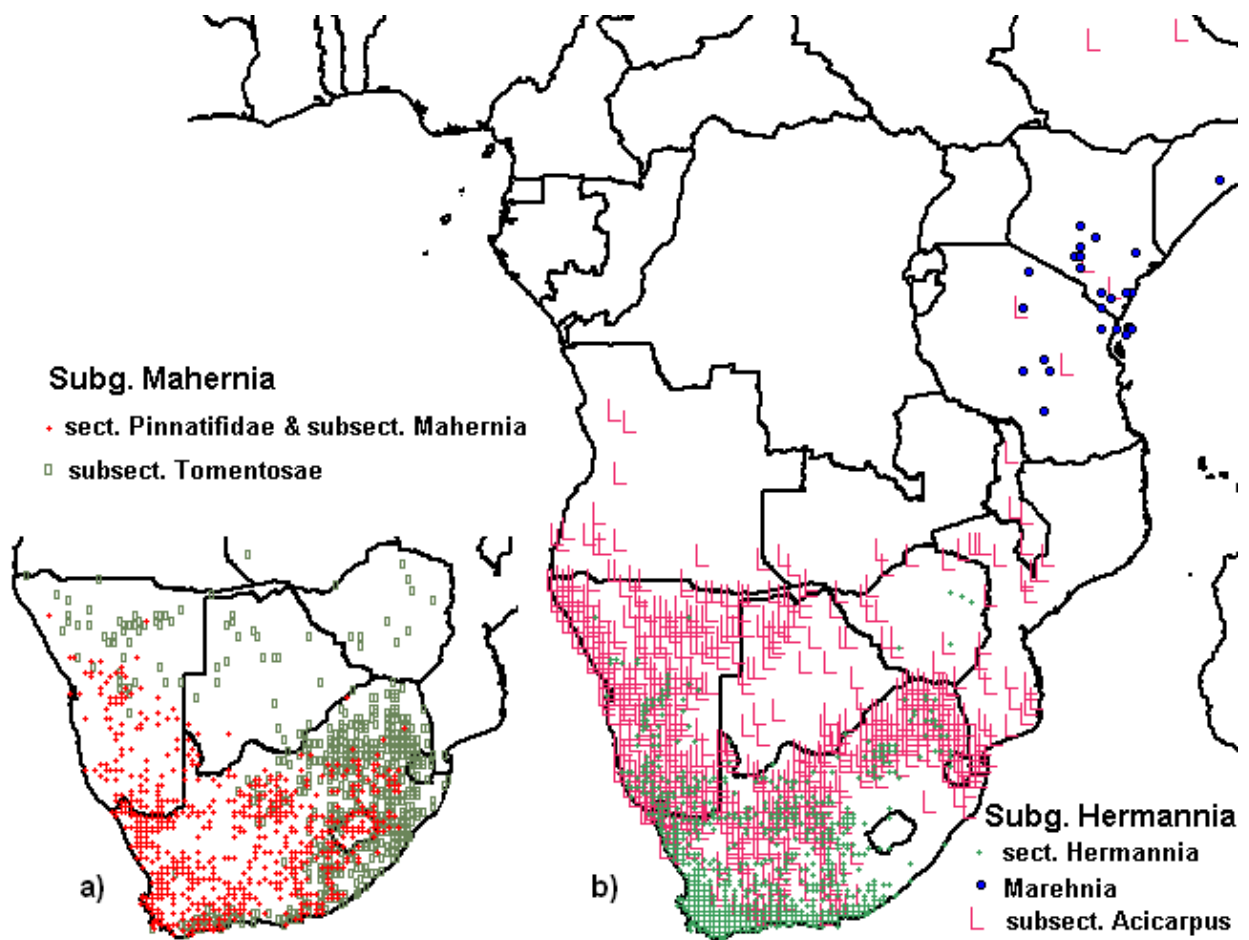


Fig. 6.3 A reproduction of Fig. 4.5, for the sake of accessibility. Distributions of the major sections of *Hermannia*: a) the western group of subg. *Mahernia* with sect. *Pinnatifidae* and subsect. *Mahernia* combined, and distinguished from the summer rainfall subsect. *Tomentosae*; and b) subg. *Hermannia*, with sect. *Hermannia*, “Marehnia”, and subsect. *Acicarpus* separated.

### 6.3.2 Richness

The collecting density is shown in Fig. 6.4a, while the outcome of various analyses of richness are presented in Fig. 6.4b-f. The maximum collecting density of 162 collections per QDS (Fig. 6.4) occurs around the Cape Peninsula and Port Elizabeth. Both regions are considered to have major cities, and have local herbaria. Other areas with high numbers of collections are the West Coast National Park, Springbok, Kimberley, Mossel Bay and Oudtshoorn. The genus *Hermannia* has a richness of 15-19 species per QDS for several cells (Fig. 6.4b). These cells correspond to Cape Town, Clanwilliam in the northern Cedarberg, the Agulhas Plain around Swellendam, and the Klein Karoo around Ladismith and Oudtshoorn. Rich squares (11-15 spp.) occur from Namaqualand through the Cedarberg to the Cape Peninsula, eastwards mostly within one degree of the coast. Specifically, Springbok and Khamieskroon in Namaqualand, Niewoudtville and Van Rhynsdorp in the Northern Cape, Lamberts Bay, Darling / Malmesbury and Piketberg on the West Coast, Clanwilliam and Citrusdal in the Cedarberg, and Cape Town and its surrounds. Eastwards from Cape Town along the coast, Hermanus, de Hoop, Jeffrey's Bay and Port Elizabeth have high values of richness. Inland from Cape Town Riviersonderend and Swellendam are also rich. The karroid areas with high richness are Worcester, Matjiesfontein, and the Grahamstown/Somerset-East region that includes the Sneeuberg. More than two degrees from the coast, only Graaff-Reinet and Pretoria are rich.

#### 6.3.2.1 Estimators of richness

Similar patterns to that of richness were output by the various estimators of richness (Fig. 6.4c-f). Areas beyond these maps did not have high values of estimated richness. The Chao corrected estimate (Fig. 6.4c) showed very high values of richness only in the Khamieskroon region of Namaqualand. Five QDS are found to have high values of richness: along the SW coast, in the limestones of the South Coast, one in the Klein Karoo, and two in the Kimberley area. Chao and Lee's algorithm for estimating richness, ACE (Fig. 6.4d), has three QDS with very rich cells in the Klein Karoo, and one in the Orange Free-State (OFS). The South Coast and Klein Karoo have the highest overall values for an area, with a disproportionate number of QDS at a high level (17-22). Jackknife algorithms (Fig. 6.4e) retrieve the highest values for two cells in

the South Coast and a single cell in the Klein Karoo, with high values found primarily within 100km of the coastal portions of the CFR. The Michaelis-Menten algorithm (Fig. 6.4f) indicates a single hotspot in the Nieuwoudtville area, and three rich areas along the eastern portions of the South Coast.

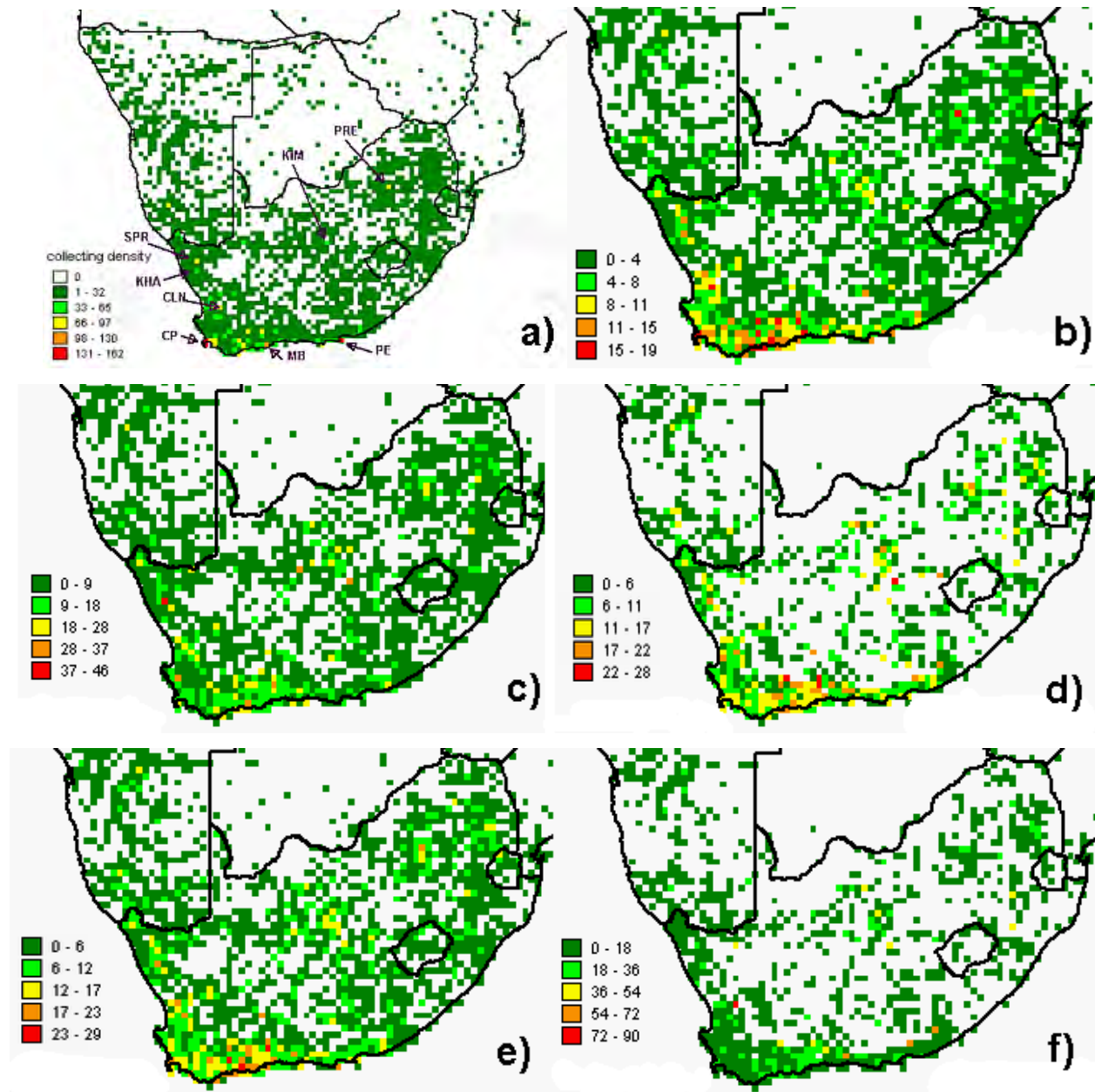


Fig. 6.4a Density of collections of the genus *Hermannia* with the regions of highest density indicated: Clanwilliam (CLN); Cape Peninsula (CP); Khamieskroon (KHA); Mosselbay (MB); Port Elizabeth (PE); Pretoria (PRE); and Springbok (SPR). b) Richness of *Hermannia*. Estimators of richness of *Hermannia*: c) Chao corrected; d) Chao and Lee ACE; e) Jackknife; and f) Michaelis-Menten. In b) to f), white space indicates a richness value of zero, while dark green indicates a positive value.



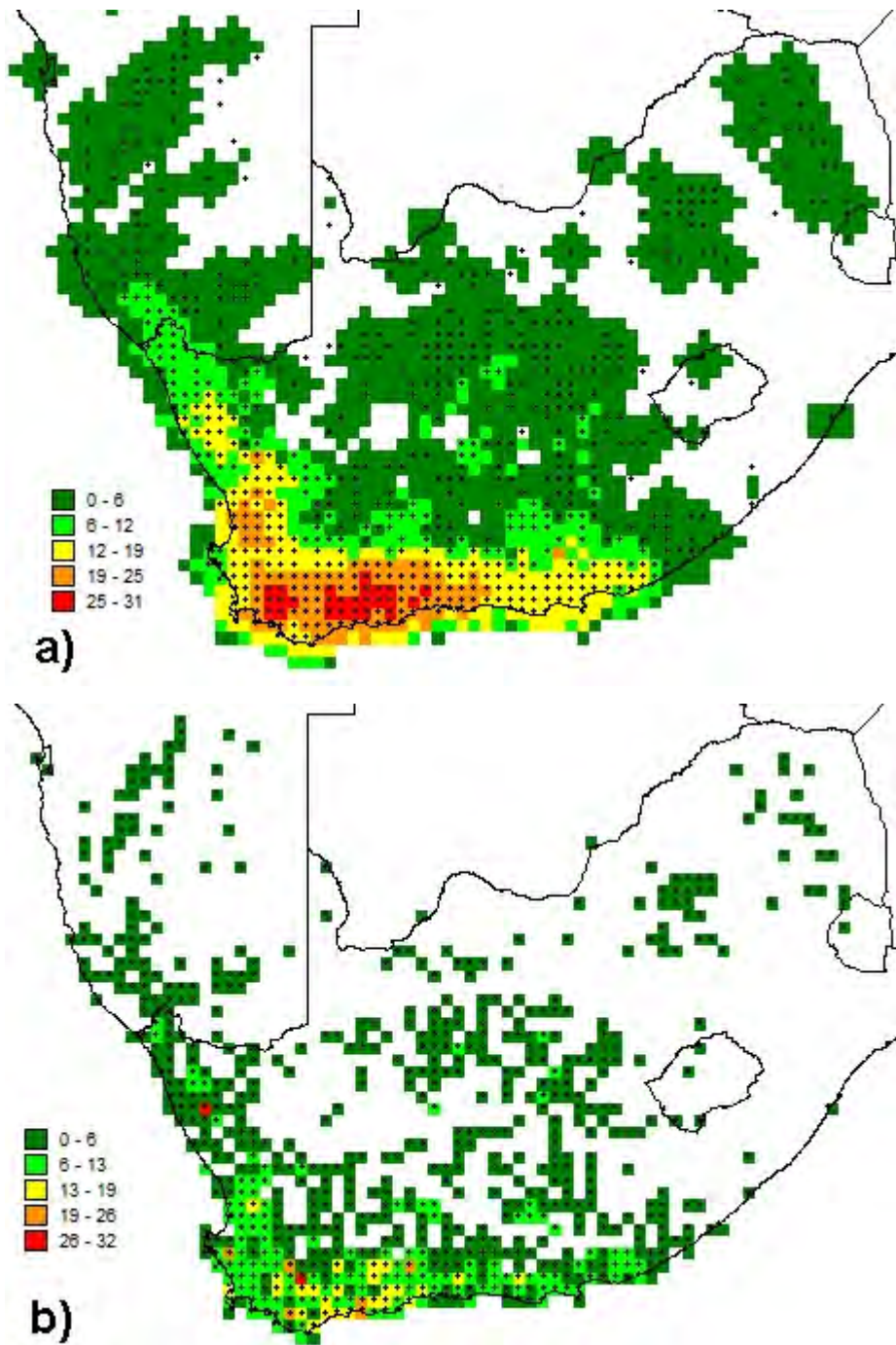


Fig. 6.5 Estimates of richness for the sect. *Hermannia*. a) Chao and Lee S4 algorithm, with circular neighbourhood smoothing applied; b) Chao corrected without smoothing. Dots on this and subsequent maps show the presence of a species record within a QDS, i.e. no dot indicates an absence of any collections for a given group. White space indicates a richness value of zero, while dark green indicates a positive value.

The results of estimating richness for the sect. *Hermannia* are provided in Fig. 6.5a,b. Using circular neighbourhood smoothing accentuates the regions that have generally high diversity (not depicted for the genus). Very rich regions with 36-44 species per QDS occur: from Van Rhynsdorp to Elands Bay on the coast; Worcester; the region of the western Klein Karoo from Montagu to around De Rust which forms the largest region of high diversity; and along the South Coast at De Hoop/Stilbaai. An isolated rich patch (27-35 spp.) occurs near Khamieskroon separated by about 150km from the main core of richness. This core extends from the Matzikamma plateau from Niewoudtville and Calvinia southwards around the mountains to around Ceres. The northern boundary of the core then extends eastwards roughly at the same latitude adjacent to the Witteberg and Swartberg Mountains. It encompasses the entire Klein Karoo extending as far as Joubertina, and the Agulhas Plains to the south of the Klein Karoo. A somewhat disjunct centre of richness occurs around Port Elizabeth, and a single QDS around Pretoria. Moderately rich areas (19-26) occur near the Brandberg in Namibia, the Namaqualand region, Kimberley in the Orange Free State, around Pretoria largely encompassing the Magaliesberg region, and the Lydenburg-Nelspruit mountainous region extending to the north-eastern portions of Swaziland.

### 6.3.2.2 Rarefaction

Rarefaction values are highest in the CFR for both *Hermannia* (Fig. 6.6a) and the sect. *Hermannia* (Fig. 6.6b) with the Southern Cape containing the majority of the highest values. There is considerably more diversity in central South Africa when considering the entire genus (Fig. 6.6a), than diversity within the sect. *Hermannia* (Fig. 6.6b). This implies that the subg. *Mahernia* and in particular the subsect. *Tomentosae* is primarily contributing to high rarefaction values in the summer rainfall areas.

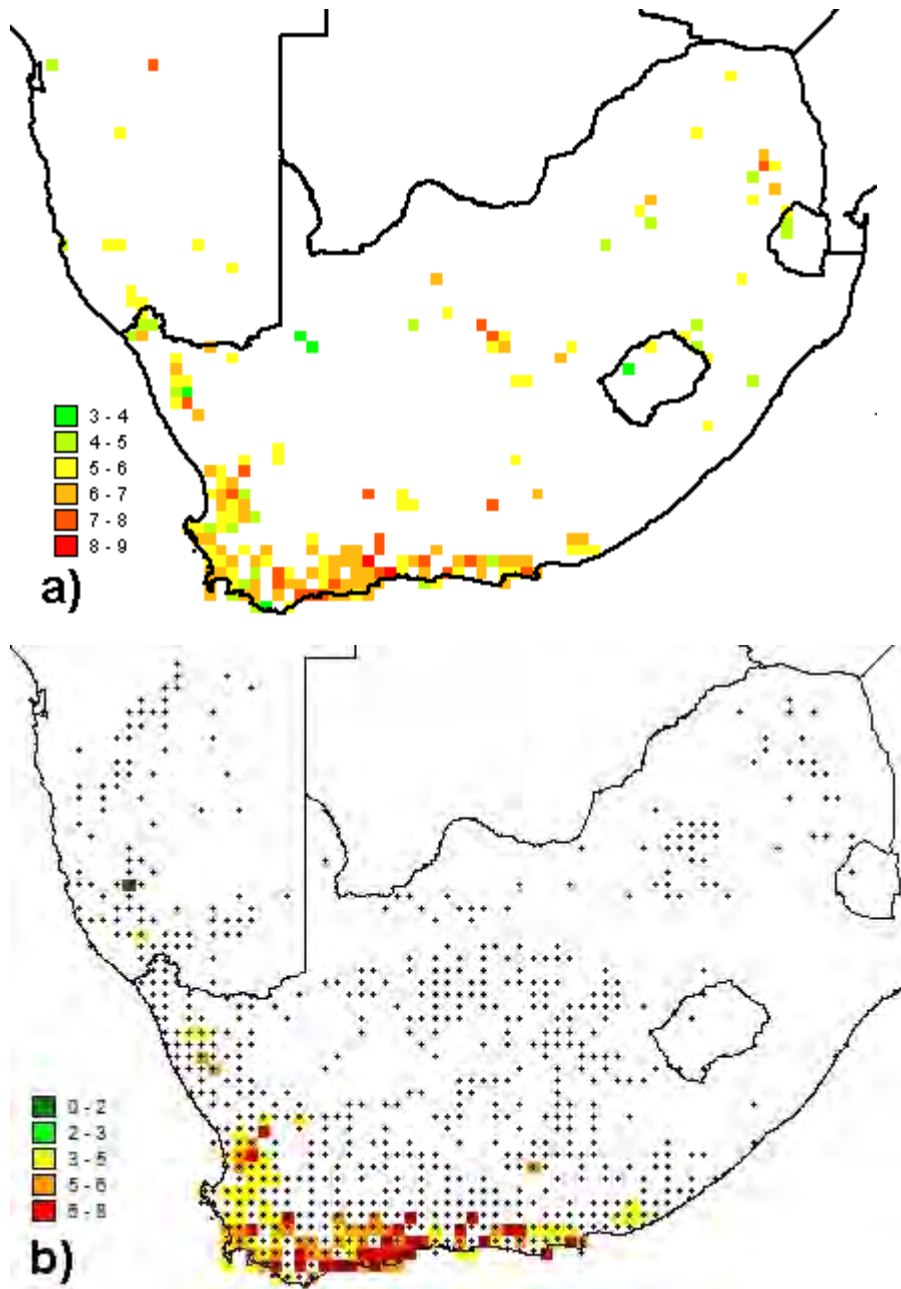


Fig. 6.6 Rarefaction overview for a) *Hermannia*; and b) sect. *Hermannia*. White space indicates a value of zero, while dark green indicates a positive value.



### 6.3.3 Diversity

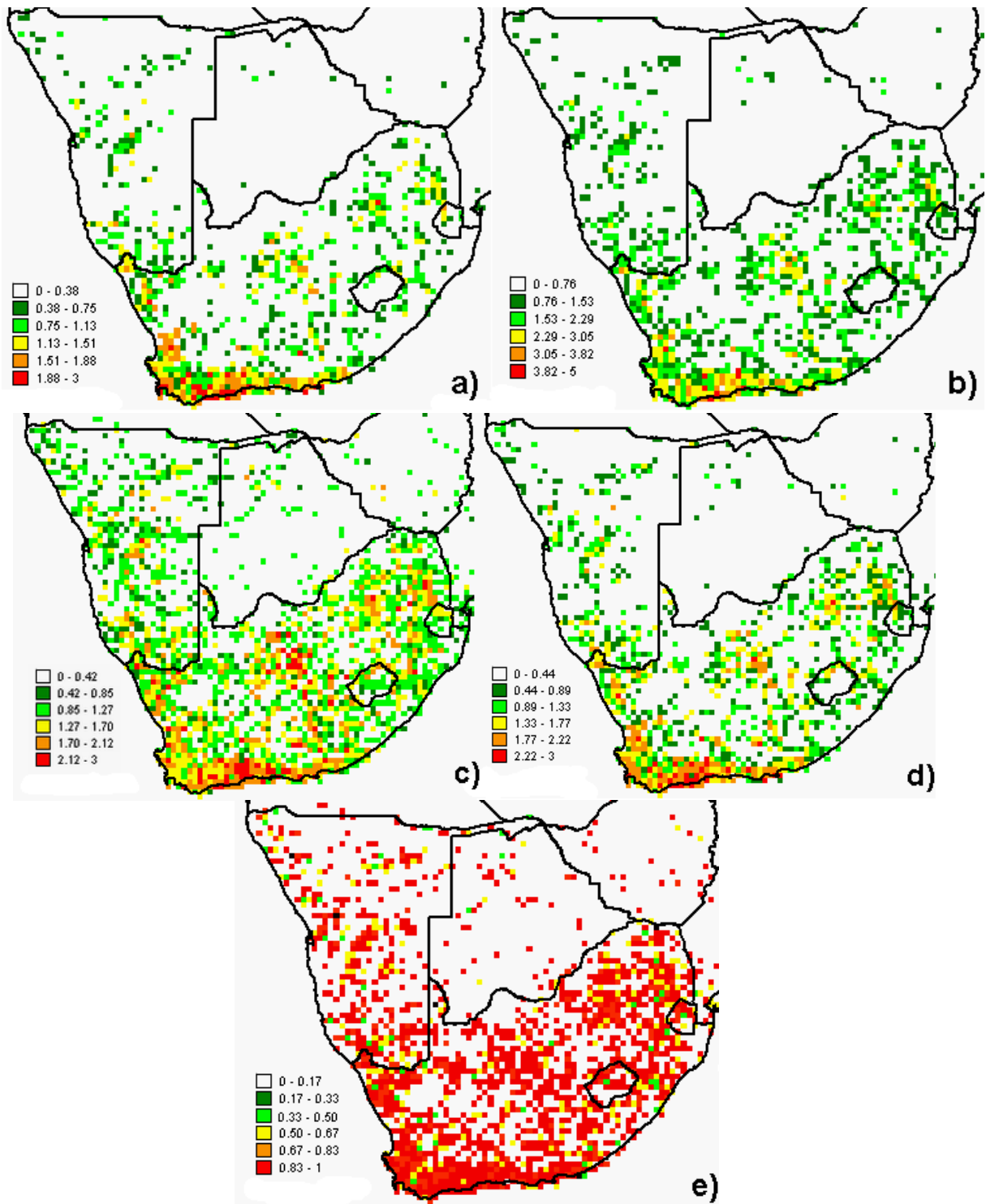


Fig. 6.7 The Diversity of *Hermannia* using the methods of: a) Brillouin; b) Margalef c) Menhenick; d) Shannon; and e) Simpson.

**Table 6.2 Summary table of diversity hotspots: (++) highest index; (+) high index; (0) medium or lower index; (=) denotes equal rank. This is a run-on table, with the CFR and Namaqualand above, and the Summer Rainfall regions below. The total „+“s occurs in the column for the entire table is on the right, and the total „+“s for each region occurs at the bottom of each region“s column. Each region is ranked according to the most „+“s indicating the most diversity measures that retrieve that region as a hotspot.**

	CFR				Namaqualand		
	S. Coast	Cape Peninsula	W. Coast	Oudtshoorn	Khamieskroon	Van Rhynsdorp	Clanwilliam
Brillouin	++	++	+	++	++	+	++
Shannon	++	+	+	++	++	+	++
Margalef	++	0	0	++	+	+	++
Mehnhenick	++	+	++	++	++	++	+
Simpson	++	++	++	++	++	++	++
Total +'s	10	6	6	10	9	7	9
Rank	1=	8=	8=	1=	4=	6=	4=

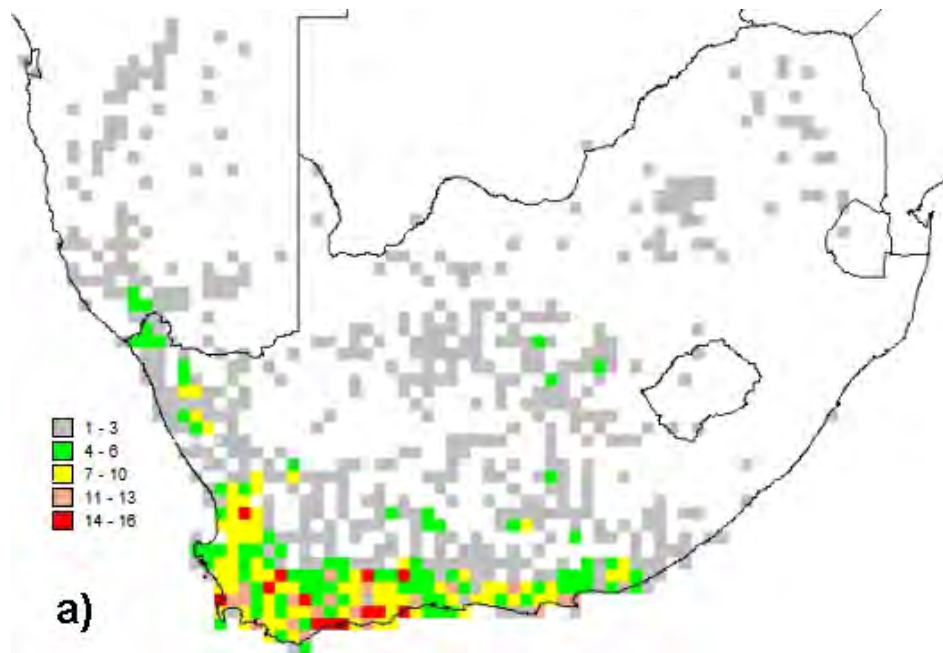
	Summer-rainfall			Total +'s
	Kimberley	Pretoria	Lydenburg	
Brillouin	0	++	+	15
Shannon	+	++	+	15
Margalef	0	++	+	11
Mehnhenick	++	++	++	18
Simpson	++	++	++	20
Total +'s	5	10	7	
Rank	10	1=	6=	

Diversity includes both the number of species per QDS, and a measure of the combined abundance of each species within the area. Table 6.2 provides an coarse aggregate of the diversity values for the different regions of the diversity maps (Fig. 6.7). The Simpson index portrays nearly the entire map as having a uniformly high diversity (Fig. 6.7e). Though the Simpson index map has been included in creating Table 6.2, it is likely that for the data set used, the Simpson index is not an appropriate measure. All areas mentioned refer to a generalized contiguous area of very high diversity. The rank reveals the order of each region from highest diversity (most number of „+“s) to lowest, with an „=“ indicating it is of the same rank as another region. The Oudtshoorn, Pretoria and the South Coast are the most robust hotspots of diversity, appearing strongly in all five analyses (Table 6.2). The final „total“ column for all three regions indicates that Margalef is the most conservative algorithm with only 11 diversity hotspots found,

contrasting with the 20 hotspots identified using Simpson that, with an almost uniformly high diversity across most of the map.

### 6.3.3.1 Diversity of sect. *Hermannia*

The diversity analysis that utilized only species from the section *Hermannia* is shown in Fig. 6.8a-b and Fig. 6.9.



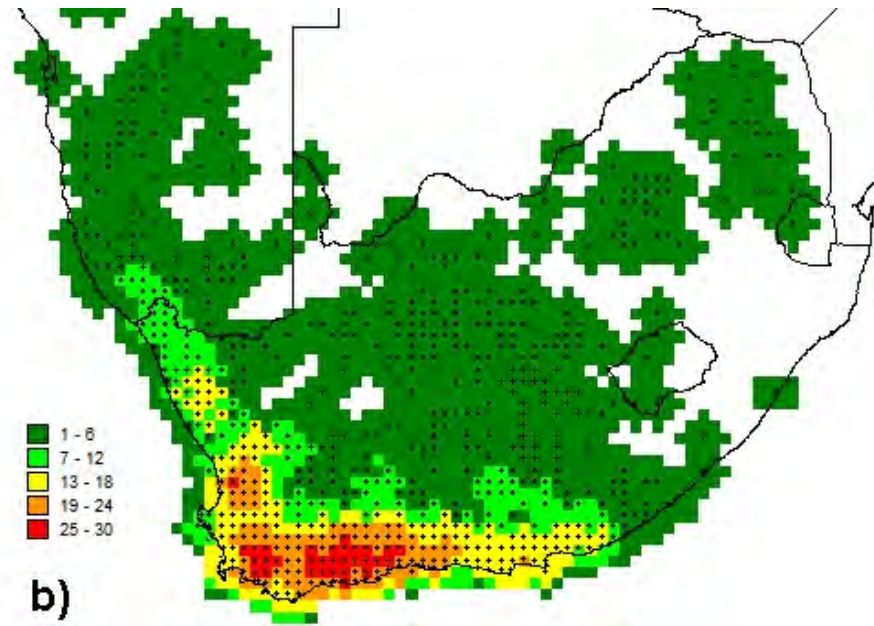


Fig. 6.8 Overall diversity of sect. *Hermannia* using a) simple grid and b) one square circular neighbourhood smoothing. White space indicates a value of zero.

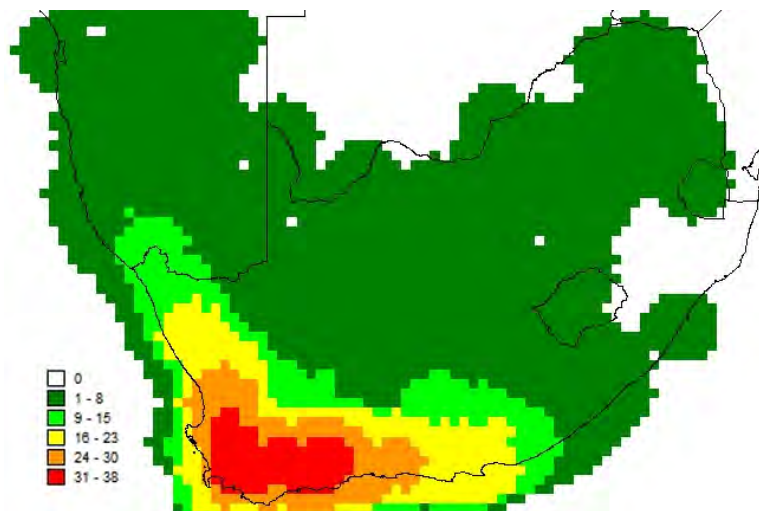
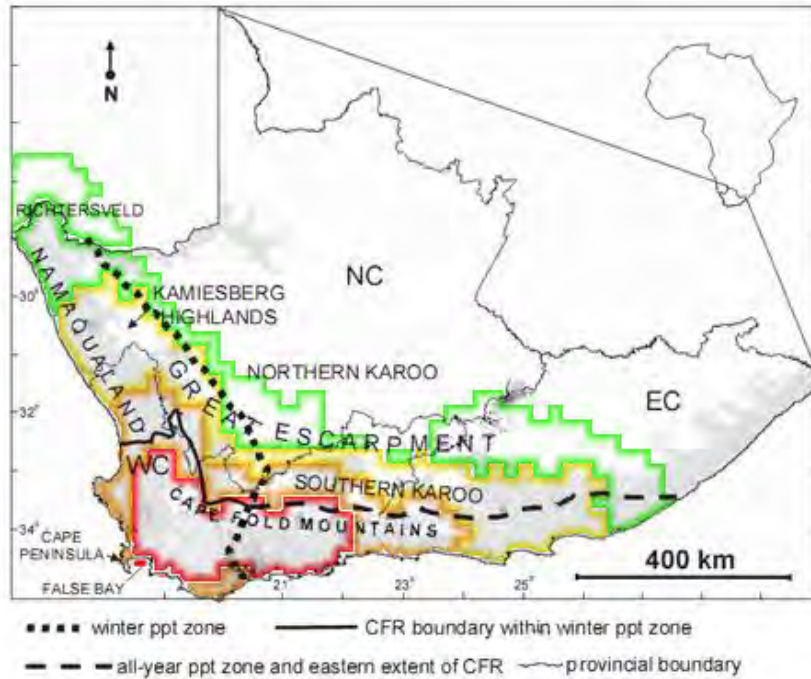


Fig. 6.9 The sect. *Hermannia* overall diversity using a two-square neighbourhood diversity algorithm.



**Fig. 6.10** This map shows the locations of the Cape provinces of South Africa, as well as a number of features important to the distribution of high diversity within *Hermannia* such as the high-elevation escarpment, rainfall seasonality boundaries, and the location of the Cape Fold Mountains. Inland and to the east of the winter precipitation zones (shown within thick solid and broken lines), rainfall occurs predominantly in the summer months. CFR – Cape Floristic Region. WC – Western Cape, NC – Northern Cape, EC – Eastern Cape. The outlines of the major boundaries of significant diversity as shown in Fig. 6.9 are in colour. Reproduced with permission from N. Bergh.

The diversity of sect. *Hermannia* focuses on a winter-rainfall clade with mostly members of the *Cuneifoliae* group that extend to Namibia and the eastern extremities of its distribution. The hotspots of diversity, comprise 13 QDS with 14-16 species per grid cell (Fig. 6.8a, above). These are south of the 33<sup>rd</sup> parallel, with the exception of a single QDS around Van Rhynsdorp. The remaining hotspots are in the Cape Peninsula, Worcester area, Swellendam, De Hoop, Mossel bay and around the Swartberg in the Klein Karoo.

Applying a one square circular neighbourhood algorithm (Fig. 6.8b) generalizes the main areas of diversity. The three regions of highest diversity are a Van Rhynsdorp centre, a SW centre that is centred around Worcester, and a large region that includes much of the Klein Karoo and the western South Coast. The region corresponding to >7 species per QDS closely matches

the CFR region experiencing winter-rainfall and all year-rainfall as shown in

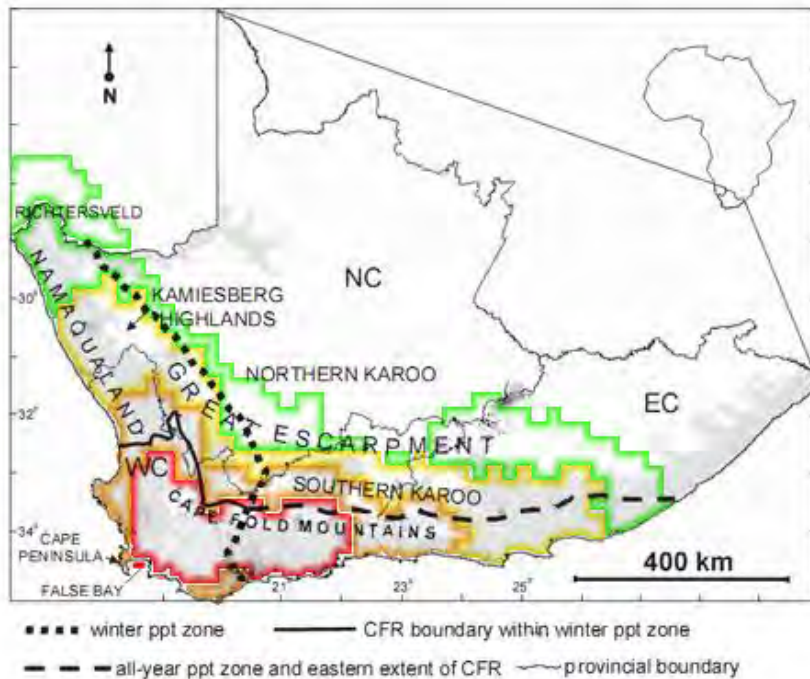


Fig. 6.10. Using a two-square neighbourhood algorithm shows a CFR centre of diversity, with diversity diminishing towards Namibia, the Eastern Cape, and more rapidly towards the interior (Fig. 6.8).

Using a two square circular neighbourhood algorithm (Fig. 6.9 and Fig. 6.10) generalizes the main areas of diversity even more. Here we see that the most diverse hotspot occurs within the boundary of the CFR, bordered on the north-east by the north-eastern extent of the Cape Fold Mountains. This region of highest diversity extends approximately an equal distance to the east of the winter-rainfall boundary, as it does to the west.

### 6.3.4 Turnover

The analysis of species turnover is provided in Fig. 6.11a-b, and Fig. 6.12a-b. Turnover is akin to beta diversity, providing a measure of the regions where the most relative change in alpha diversity is taking place between adjacent areas. The Elands Bay area on the West Coast has the highest turnover of 19-22 spp. (Fig. 6.11a). The Bokkeveld plateau in the Northern Cape around Niewoudtville and Calvinia has a high turnover, as does Matjiesfontein-Laingsburg and the Klein Karoo around Oudtshoorn. At a moderately rich level, two areas stand out: the Van



Rhynsdorp – Elandsbaai region, and the Klein Karoo. The latter is substantial in being contiguous and almost precisely contained by the boundaries of the Klein Karoo. This inland basin is thus considered a hotspot for turnover.

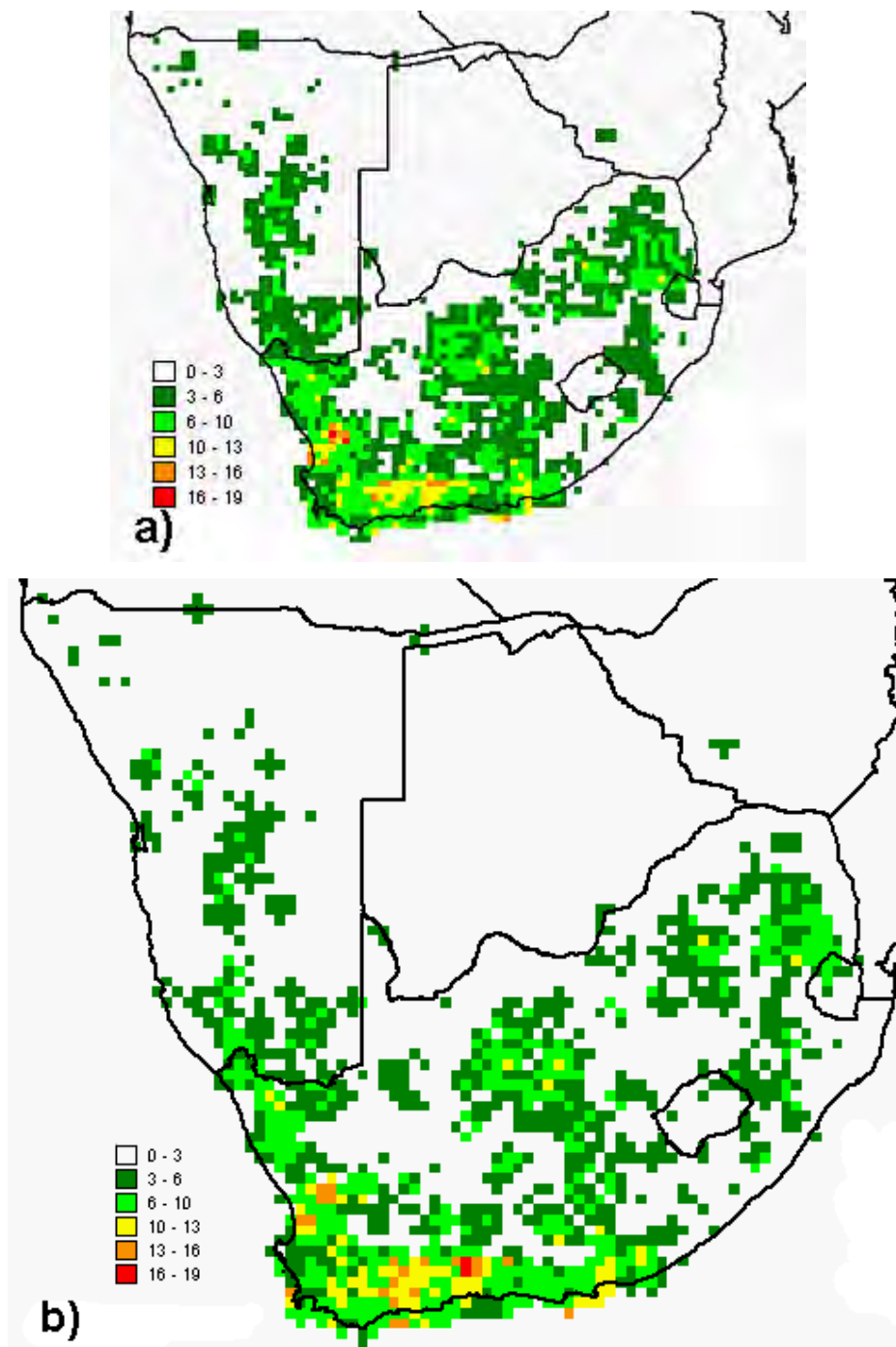


Fig. 6.11 Whittaker measure of turnover for *Hermannia* using a) queens case and b) rooks case.

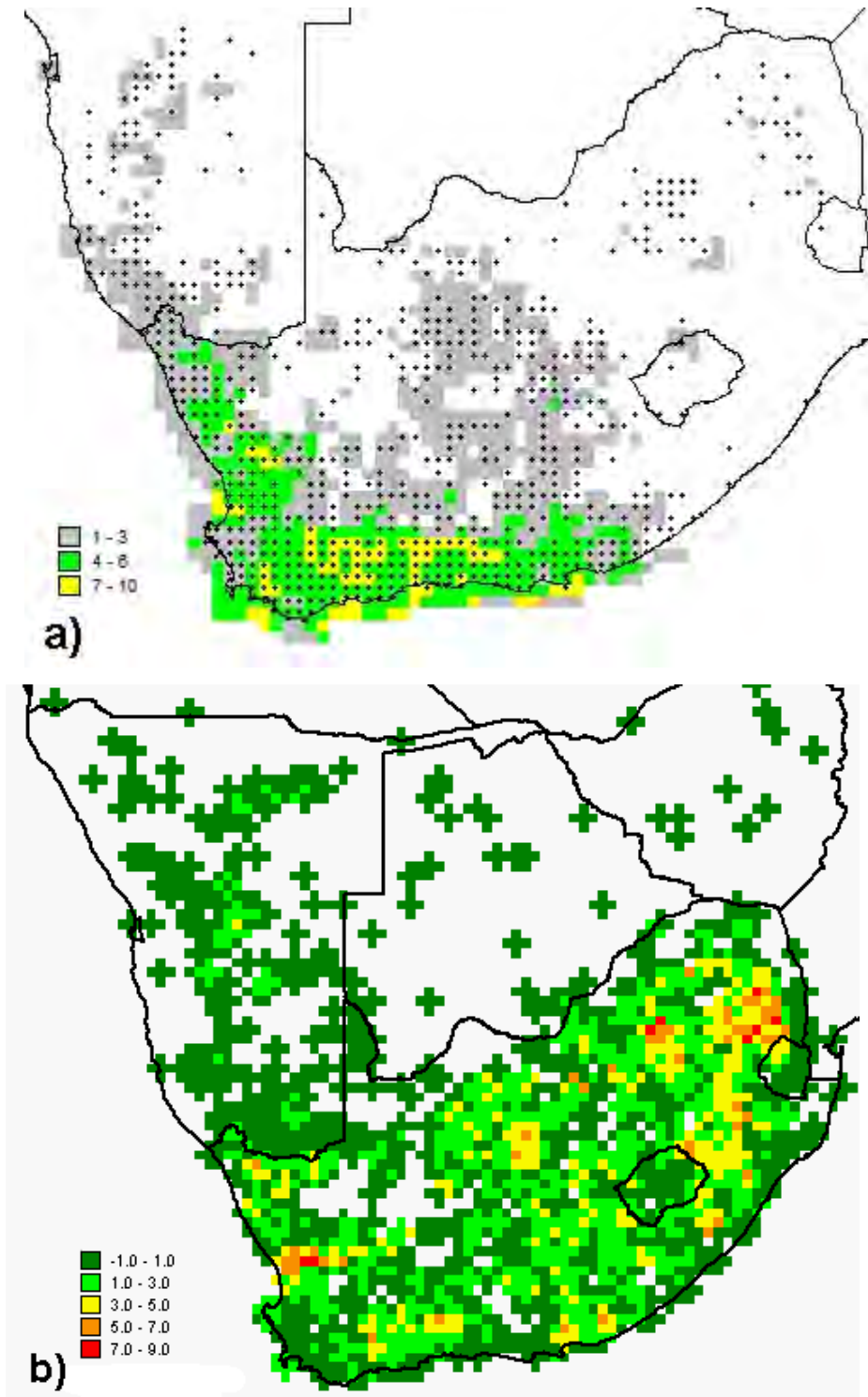


Fig. 6.12 Turnover using Whittaker a) for sect. *Hermannia* using a simple grid, and b) for the subg. *Mahernia* using the rooks case.

The queens case compares turnover from all adjacent squares, whereas the rooks case excludes the diagonally adjacent squares. The analysis of the rooks case (Fig. 6.11b) is therefore



more sensitive to change from the four major directions (N, S, E, W), and in this case the eastern Klein Karoo is the only exceptionally diverse hotspot.

The analysis of turnover for the sect. *Hermannia* (Fig. 6.12a) should be contrasted with that of subg. *Mahernia* (Fig. 6.12b) as these two groups are of roughly the same size. As mentioned above, sect. *Acicarpus* does not feature within South Africa, and the species are largely non-overlapping, so this section has been excluded from the analysis of subg. *Hermannia*. Although analysis of the sect. *Hermannia* (Fig. 6.12a) does not show any hotspots, the yellow blocks actually correspond with, and even exceed that of the hotspots of *Mahernia* (Fig. 6.12b). In general therefore, the turnover for sect. *Hermannia* is higher within the CFR and especially the Klein Karoo, than for subg. *Mahernia*. The greatest region of turnover for the subg. *Mahernia* is in the Gauteng region, especially near Lydenburg, with a smaller hotspot near Van Rhynsdorp. This hotspot shows a distinctive east-west extension inland, suggestive of a change of vegetation type running north-south.

### 6.3.5 Complementarity

The analyses of complementarity are provided in Fig. 6.13a-c & Fig. 6.13a,b, below.

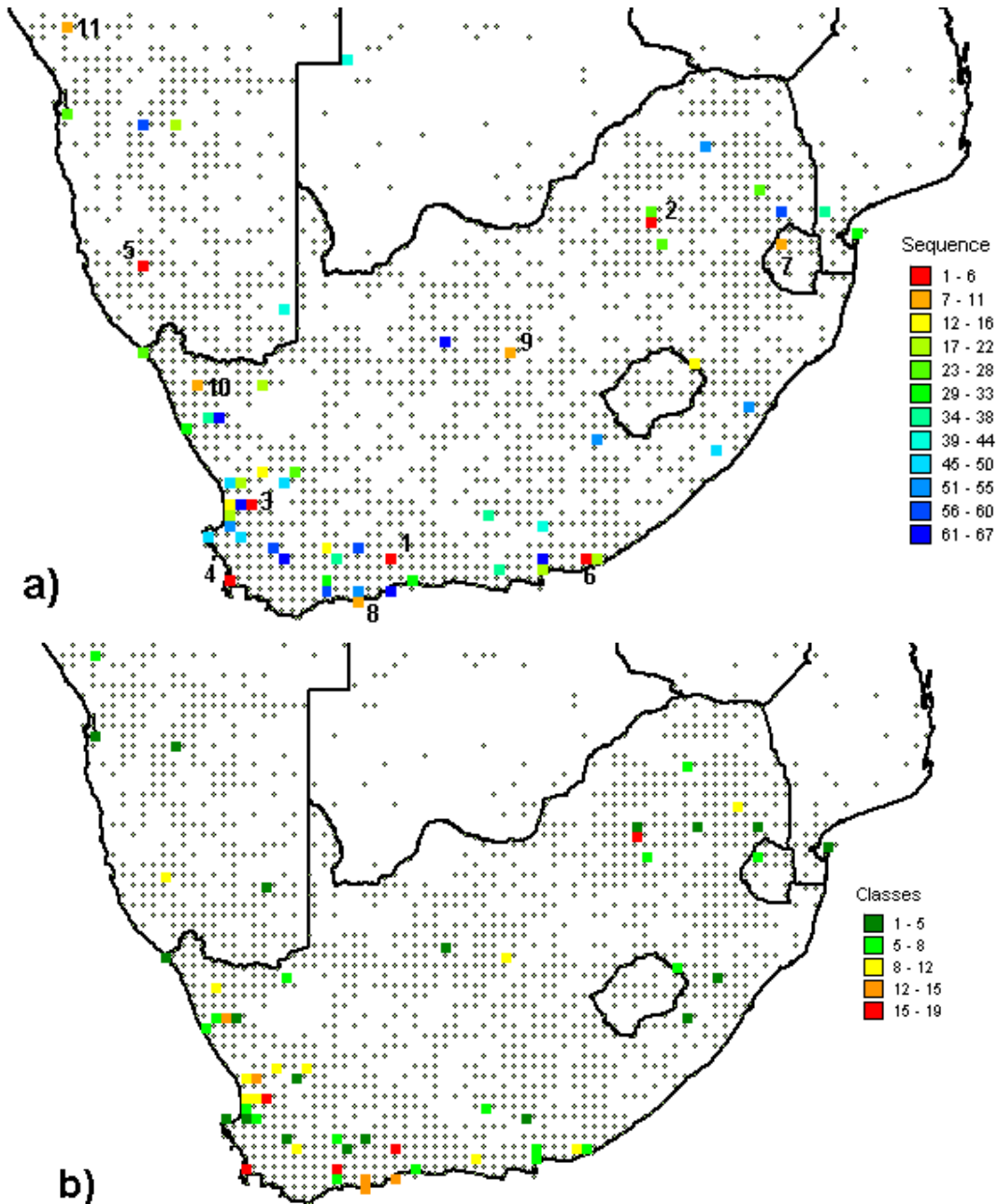


Fig. 6.13 Complementarity sequence of genus *Hermannia* with a) the sequence of the first 11 best reserves annotated and b) the number of species per QDS for all priority grids found by the algorithm.

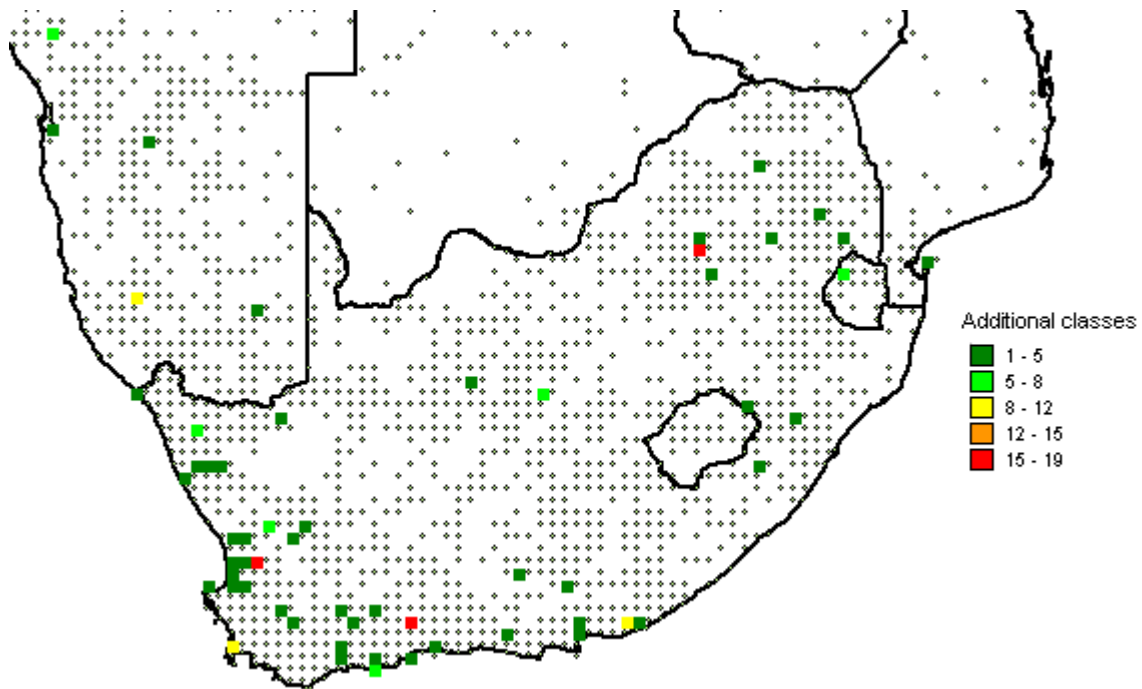
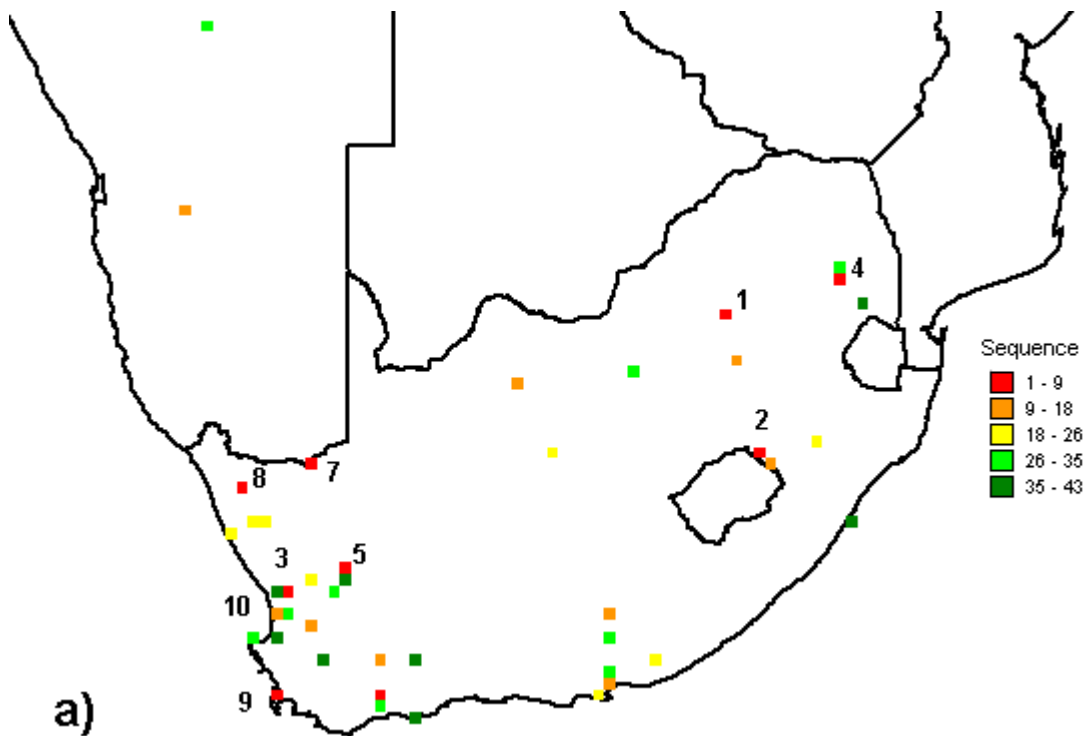
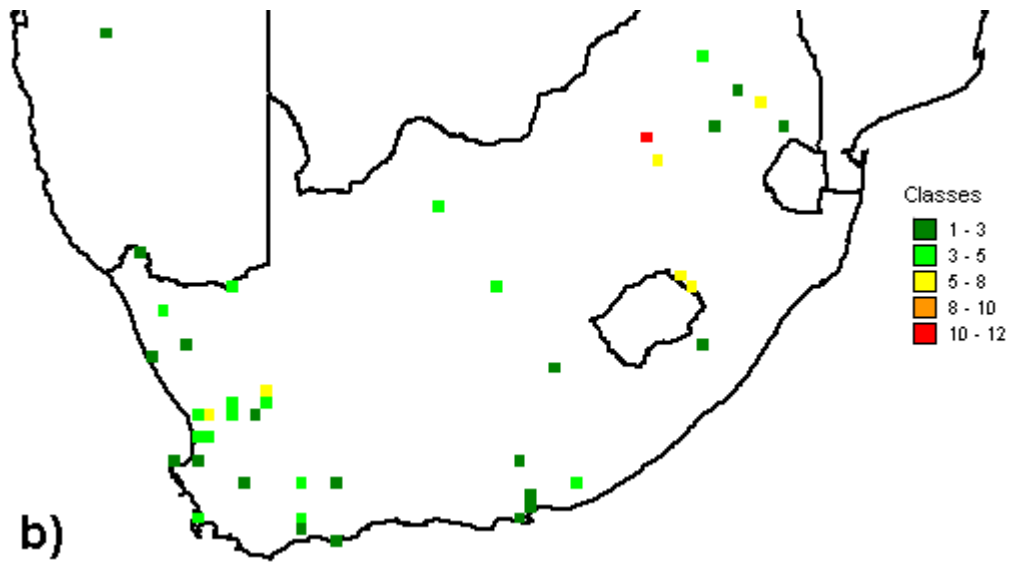


Fig. 6.14 Complementarity sequence of genus *Hermannia* with the number of different species gained from each subsequent selection.





**Fig. 6.15** Complementarity sequence for the subg. *Mahernia* with a) first 10 priority grids annotated, and b) number of species gained from subsequent selections.

The initial run on the entire genus was for 100 iterations with species given equal weight. Values for the run were 67 iterations with 217 unique observations captured. Fig. 6.13a shows that six of the top ten conservation-worthy areas are in the Greater CFR. As this algorithm maximizes species diversity, this illustrates the superior diversity and concentration of species within the CFR compared with the remainder of Southern Africa.

The result for the subg. *Mahernia* (Fig. 6.15a) is similar, but emphasises regions in the northern Greater CFR, and gives more importance to the summer rainfall regions. It is surprising that the area with the greatest conservation value is in the Gauteng region, not the Cape.

## 6.4 Discussion

### 6.4.1 Richness and diversity for *Hermannia*

#### 6.4.1.1 Summary of richness and diversity findings

Overall, the richness patterns derived via various instruments show a concentration of high richness of *Hermannia* in the CFR, extending also along the South Coast from Cape Town to around Oudtshoorn. Further patches of high richness are found along the West Coast, as well as near Kimberley, Pretoria and Lydenberg. The richness of sect. *Hermannia* is restricted to the CFR. Rarefaction methods corroborate these results. The regions of high diversity for *Hermannia* are similar to those of high richness, with an extension of the South Coast region from Oudtshoorn towards Port Elizabeth, and a more continuous stretch of high diversity from Cape Town towards Springbok. Similar patterns are found for the diversity of sect. *Hermannia*. Regions of high turnover for *Hermannia* are similar to the diversity patterns, although interrupted between Oudtshoorn and Port Elizabeth, while the region of high turnover for sect. *Hermannia* is restricted to a fragmented portion of the CFR. The regions of high turnover for subg. *Mahernia* are widespread across South Africa, and are especially concentrated around Clanwilliam, Pretoria and Lydenberg. Conspicuously, the CFR is not a centre of high turnover for subg. *Mahernia*. It is worth noting that the richness and diversity strongly correlate in all cases studied, suggesting that species richness for *Hermannia* is usually associated with a high variation of abundance of individual species.

#### 6.4.1.2 Identification of Cape element and concentration of diversity in the CFR

The diversity of *Hermannia* within the CFR is striking compared with other regions of the world in all diversity measures: richness, estimated richness, turnover, and diversity. The complementarity results confirm the unique diversity of the Cape, with five of the top ten best selections being within the Cape, despite the small area of the CFR relative to the total area occupied by *Hermannia*. This is particularly impressive given that the algorithm selects for the most dissimilar species, and that subsect. *Cristatae*, subsect. *Acicarpus*, and subsect. *Tomentosae*

are barely represented in the Cape. Unlike richness patterns observed in previously studied CFR groups (eg. *Cliffortia* (Whitehouse 2002), *Protea* (Rebelo 1995), *Erica* (Oliver 1999), Restionaceae (Linder and Mann 1988)), *Hermannia* species are concentrated in the lowlands, not the mountains. Thus centres of diversity for this genus do not relate to the Cedarberg, Table Mountain, and the Swartberg, but primarily to the lowlands around these mountains. The high diversity of flora in general in the CFR therefore cannot be explained solely by the sandstone mountains, but needs to take into account the high diversity in the lowlands as well, as evidenced by *Hermannia*.

Due to a high diversity concentrated in the CFR and along the South Coast, both *Hermannia* and sect. *Hermannia* qualify as Cape elements, while subg. *Mahernia* does not. While sect. *Acicarpus* has not been analysed, it cannot be a Cape element as it is poorly represented in the CFR. The subsect. *Tomentosae* is not a Cape element, for the same reason. The question of Cape elements will turn out to be of special importance if it can be established that *Hermannia* originated in the CFR. The character reconstruction of geography in Ch. 5 is not yet sufficiently well-supported to determine the geographic origins of the genus.

#### **6.4.1.3 The Klein-Karoo hotspot of diversity**

The Klein-Karoo hotspot showcases the massive contribution of this area to the diversity of *Hermannia*. More than forty species are found in this area, which comprises both endemic flora, and species or species complexes that have infiltrated the Klein Karoo. Elevated levels of turnover within the Klein Karoo are supported by the turnover analysis, with upwards of 10 species turnover per QDS across the entire Klein Karoo.

The Klein Karoo also provides a large, well-demarcated region of high turnover. Many species are shared with surrounding areas. The Klein Karoo represents a meeting point for winter and summer rainfall regimes, and a gradient from west to east from winter to summer rainfall. A large proportion of this turnover may thus be species that are constrained to a certain portion of the Klein Karoo by their narrow rainfall seasonality requirement. There is also a substantial south to north decrease in rainfall away from the coast. This further serves to separate species based on their annual rainfall requirements. The short dispersal ability of *Hermannia* seeds

means that species are seldom dispersed across length or breadth of the Klein Karoo, especially across the substantial east-west trending ranges of the Langeberg in the south and the Swartberg in the north. Combined with a rugged and dissected landscape, and with mountain-ranges acting as dispersal barriers, species tend to be limited to their areas of origin. i.e. species from the Agulhas plains tend to only be found in the southern portions of the Klein Karoo.

The analysis of species diversity of sect. *Hermannia* that utilizes circular neighbourhood averaging conveys a more general picture of the centres of diversity. As the Worcester hotspot is unexceptional at the QDS level, the circular neighbourhood analysis portrays the contribution of the dissimilar squares surrounding the hotspot. This thus represents a region of exceptional turnover. This is a meeting point between the fynbos to the west, the Ceres-Karoo to the north, the Robertson-Karoo to the south, and elements from the Klein Karoo to the east.

#### **6.4.1.4 The summer rainfall hotspot of diversity**

The areas of high diversity of *Hermannia* around Lydenberg are proximal to the Wolkberg and Sekhukhuneland Centres of Endemism. The summer rainfall area has been independently colonised by separate lineages of *Hermannia* on at least three occasions: by *H. cristata* from the subsect. *Cristatae*; from an early progenitor of the subsect. *Mahernia* with a very successful subsequent radiation; from the Cape element with two species, *H. oligosperma* and *H. malvifolia* that have survived only in the Drakensberg; and with at least one incursion from the subsect. *Acicarpus* (eg. *H. tomentosa*, *H. glanduligera*, *H. boraginiflora* and the annual species *H. modesta*). Only subg. *Mahernia*, especially subsect. *Tomentosae*, radiated successfully in this area, with possible links to Namibia via *H. stellulata* and *H. oblongifolia*.

In the summer rainfall hotspot as well as other hotspots experiencing predominantly summer rains, highly endemic species confined to small areas tend to occur more in mountains than the lowlands. Thus Graaff-Reinet, the Sneeuwberg, the Magaliesberg, and the Lydenburg area show up as hotspots and regions of high turnover. This suggests that unlike in the winter-rainfall areas where turnover and diversity are strongly linked to past refugia, in the east, mountains are acting as current refugia. The mountains experience higher rainfall and cooler temperatures, thus

serving as contemporary refugia for species that in the past glacial periods may have been in the lowlands.

#### **6.4.1.5 The Van Rhynsdorp-Elandsbaai hotspot of diversity**

The Van Rhynsdorp-Elandsbaai centre is located at an interchange between the Namaqualand flora and that of the S.W. Cape. This is also an area in which several distinct soils change over: tertiary sands along the coast, sandstones in the montane regions, Bokkeveld dolerites in the east, Namaqualand granites, Gariiep riverine sands and quartz plains to the north, and dolomite to the south. In all, many new species of *Hermannia* described in this thesis come from this area and are narrow endemics. The reasons for this high diversity of endemics should be investigated. It may relate to a high degree of substrate dissection fostering allopatric speciation, or acting as low-altitude edaphic refugia. The high turnover for subg. *Mahernia* found in the region of Van-Rhynsdorp-Elandsbaai consists of a short band running east-west. This suggests an intermediate zone of changeover of composition of subg. *Mahernia* species at this junction between the Namaqualand and S.W. Cape regions.

### **6.4.2 Understanding patterns of diversity in *Hermannia***

#### **6.4.2.1 Role of soil and elevation in colonisation by *Hermannia***

*Hermannia* species are generally not found in typical montane habitats, but rather tend to occur in lowland soils. For many species of *Hermannia* the range is limited and confined to the lowlands between mountain ranges. Within these lowlands, *Hermannia* is more commonly found on nutrient-rich soils such as shale, limestone, dolomite and dolerite than on nutrient-poor substrates such sandstone and tertiary sands.

Soil types form formidable constraints to the dispersal of plant species through time. Nearly complete turnover of species has been found on the Agulhas Plain for edaphically dissimilar, but climatically similar sites (Cowling 1990). Quint and Classen-Bockhoff (2008) use this soil constraint to date limestone species of Bruniaceae. *Hermannia* presumably has similar constraints, with both limestone and lowland shale species being unable to readily utilize



sandstone mountains as refugia through time, given the fact that most species are not found on sandstone.

#### **6.4.2.2 Diversity arising through limited dispersal**

As mentioned above, the majority of *Hermannia* species are apparently not adapted to growing on montane, nutrient-poor sandstone substrates and thus their range is confined to lowlands between mountain ranges. Assuming that these species typically have only short-range dispersal, such isolation would provide a mechanism for speciation and hence an increase in diversity in regions containing a high density of mountain ranges. This may account for the narrow range of distribution of such species as *H. albiflora*, which occurs in the lowlands between Montagu and Barrydale, *H. acocksii* which occurs in the lowlands of Robertson in the Karoo, and *H. atrofulminalis* which occurs through the lowlands of the Klein Karoo.

The concentration of *Hermannia* in the CFR could be partly accounted for by the high density of mountain ranges which would have led to isolation of species, as indicated in the preceding paragraph. In addition to this mechanism, it should be noted that the CFR is a region of high floral diversity in general. In order to understand this general phenomenon, it should be noted firstly that current environmental conditions in the CFR are not exceptional in a worldwide context (Milewski (2000)). Thus historical climatic factors are required to explain the speciation and persistence of species through time. This may be taken as support for Levyns (1964) who proposed that most of Africa experienced relative aridity during the interglacial periods. However, the S.W. Cape continued to receive rainfall from the regular cold fronts that served to ameliorate the harsh conditions. Taxa that were pre-adapted to tolerate a Mediterranean climate regime thrived, expanded and speciated, while those that could not were eventually lost.

#### **6.4.2.3 Survival in refugia as a contribution to diversity**

A further mechanism to explain the high species diversity in the CFR is that of refugia, whereby populations expanded into and among lowlands during mesic times, and retreated up mountains during arid periods, thus leading to the accumulation of species through time rather than the loss of species through extinction. It is difficult to assess whether *Hermannia* species

may have accumulated over time through survival in refugia, it is considered informative to examine evidence of contemporary refugia.

Currently, increased aridification is considered prominent on the western arm of the CFR, with increasing severity up to the Richtersveld in the north (Bergh, Hedderson et al. 2007). This region is considered to have been substantially wetter and cooler during the last glacial maximum approximately 18 000BP (van Zinderen Bakker 1976; Meadows and Baxter 2001). Some examples of taxa confined to mesic refugia may be *H. ballerunica* that is basal within

the sect. *Pinnatifidae*, and only found in the mesic forested ravines of Oorlogskloof where other palaeoendemics have been located (Conrad, Reeves et al. 2003). A second example may be the uncharacteristically broad-leafed *H. angelica* that is only known from a single high-altitude population near Leipoldt's Grave, Clanwilliam, that grows in the lee of sandstone boulders. This, together with its close relatives *H. disticha* and *H. Angelica*, occurs in sheltered ravines. Although this portion of the phylogeny is not resolved, *H. angelica* morphologically displays a close affinity to *H. disticha*, an endemic from the mesic riversides of Montagu, some 220km to the south-east of *H. angelica*. A third species described with smaller "wings" that is known from a single sandstone outcrop at the Heerenlogementsberg is that of *H. cherubim*. It is possible that an ancestor of these three apparently related species was once more widespread and that subsequently, due to aridification, it retreated, became isolated and speciated into the current refugia.

A third example cited in support of the phenomenon of more widespread ranges reduced in contemporary times, is that of *H. holosericea* and *H. pulchella*. *H. holosericea* is widespread in the Klein Karoo, but is known from a single collection in the Khamiesberg approximately 360km to the north of the Klein Karoo populations. This Khamiesberg region has been considered a refugium (Midgley and Roberts 2003) for a number of species including that of the single

**Renosterveld** directly translated means rhinoceros-field. It is a broad vegetation type that may derive its name from the dominant species, the renosterbos (*Elytropappus rhinocerotis*). It mainly occurs in the low lying valleys of the Cape which experience moderate winter - rainfall precipitation of 300-600mm per year. Renosterveld plants typically grow on nutrient rich, fine-grained clay or silt soils derived from shale or granite. It has amongst the highest diversity of bulbs in the world.

Source: Cowling 1992 – Fynbos: Nutrients Fire and Diversity

species most commonly associated with renosterveld vegetation, *Elytropappus rhinocerotis* (Bergh, Hedderson et al. 2007). Envelope models found fynbos to have been at its greatest extent during the last glacial maximum (LGM), some 18–12kBP, especially along the West Coast and the western interior where these *Hermannia* species occur (Midgley and Roberts 2003). From 12–6kBP the Succulent Karoo expanded with a subsequent shrinking in the range of the fynbos. Along the West Coast, these biomes may have shifted along a north / south axis during the Pleistocene due to climatic oscillations (Midgley and Roberts 2003).

#### **6.4.2.4 Areas of endemism with low representation of *Hermannia***

A number of regions of high endemism with Southern Africa are conspicuously lacking in *Hermannia* species. Examples of such phenomena can be used to test the hypothesis that, in general, species of *Hermannia* are unable to persist on nutrient-poor soil such as sandstone, and are generally confined to lowlands. In particular, a region of high diversity can be assumed to provide favourable conditions for flora in general to proliferate and diversify. Thus, if *Hermannia* is largely or completely absent from such an area, this points to a specific condition necessary for *Hermannia* species to colonise.

Perhaps the most obvious example is the Kogelberg. It is often considered to be the heart of the CFR due to its high diversity and number of endemics including palaeoendemics. Due to the sharp gradient from the coast on the western side of the Kogelberg, and the sandstone and limestone lowlands on the south side, mainly montane taxa are supported in this area. The only known species of *Hermannia* occurring in this mountain range are *H. salviifolia*, *H. grossularifolia* (possibly sp. nov.), *H. angularis* and *H. hyssopifolia* that occur in the mountains. In the lowlands surrounding the Kogelberg the near endemic, *H. rudis*, serves to link this flora with the Cape Peninsula, whereas on the limestone, *H. triflora* reveals a link to the South Coast. In general, the species richness is low in comparison to that of the CFR for a region of this size. This can be accounted for by the hypothesis mentioned above that *Hermannia* is generally poorly suited to montane, nutrient-poor environments.

A second example is the Pondoland Centre (PC) on the north-eastern border of the Eastern Cape which has been recognised as a centre of endemism, based on the largely endemic flora

that has adapted to the depauperate sandstone substrate of the Msikaba formation (Van Wyk and Smith 2001). These endemics include palaeoendemics that have speciated into neoendemics with a recognised Cape affinity (Carbutt and Edwards 2001; Cron, Balkwill et al. 2006). *Hermannia* is not known from this area. It should be noted that the region consists of a sandstone ‘island’, thus the majority of *Hermannia* species which are unable to colonise sandstone would have been excluded, and those Cape species which are sandstone specialists would have had to traverse an adverse nutrient-rich environment in order to colonise, which would have been improbable given the apparent limited mobility of *Hermannia* propagules.

A final example is the Drakensberg Regional Centre. As *Hermannia* is primarily a genus favouring nutrient-rich soils, it is interesting that the Drakensberg endemic species do not occur on the nutrient-rich basalt at the top of the mountains. *H. malvifolia* and *H. oligosperma* occur on the lower slopes at the base of the Talus. It has been suggested that as the high altitude basalt caps are subjected to low temperatures, the metabolism of plants and nutrient availability is low as a result (Carbutt and Edwards 2001). Thus climatological-altitudinal effects render these substrates effectively nutrient-poor, and thus unsuitable for the proliferation of most species of *Hermannia*, in particular species of subsect. *Tomentosae* that are proximal in the lowlands.

#### **6.4.3 Significance of *Hermannia* as a diverse lowland species in the CFR**

*Hermannia* is found to have a high level of diversity in the CFR, which is unusual for a genus largely occupying lowlands. This is significant both for the theoretic debate of factors contributing to the high diversity of the CFR and to conservation priorities for the region. It has long been known that the lowlands in the CFR contain many endemics, but the diversity for an individual genus has not been established. Thus the findings of this chapter provide further impetus for conservation of CFR lowlands affected by urbanisation; in particular, the Cape flats in suburban Cape Town. The high richness of *Hermannia* in the CFR may also be used to track changes to ecosystems due to urbanisation and climate change.

### **6.5 Conclusion**

The genus *Hermannia* is found to be a Cape element and has its main centre of richness and diversity in the CFR, as well as several other important centres across Southern Africa. A

mechanism has been proposed accounting for the patterns of diversity whereby many *Hermannia* species have speciated within narrow lowland ranges bounded by mountain ranges which act as barriers to dispersal. This mechanism is found to be consistent with the diversity patterns. Regions especially meriting conservation status have been defined and priorities using the method of complementarity. These regions are scattered across South Africa, with a concentration in the CFR.

## 7. Phytochoria and climatic influences upon *Hermannia*

### 7.1 Introduction

*Hermannia* occupies a vast area of South Africa, a multitude of habitats and encompasses a broad climatic and edaphic range. Detailed knowledge of the ecological and geographic distribution of species is fundamental to understanding the ecological and evolutionary drivers of spatial patterns of diversity (Elith, Graham et al. 2006). Field observations suggest that each species of *Hermannia* occupies a fairly limited environmental, altitudinal and edaphic range (pers. obs.). This implies that the considerable habitat variation that *Hermannia* occupies is a result of a composite of smaller species distributions. The distributions of these species are not evenly distributed in space, and are strongly partitioned by phylogeny. This is due to a combination of limited dispersal and speciation within a suitable habitat. This implies that phylogenetic constraint has limited the extent to which *Hermannia* can adapt to the environment. *Hermannia* contrasts with most other taxa studied from the Cape, in that unlike *Erica*, *Cliffortia* and *Protea*, the majority of species occur in the lowlands and thus can be expected to occupy different ecological niches. Ackerly (2004) asks the question: “which came first, the trait, or the environment?” He suggests that the phylogeographic pattern expected of adaptation is that taxa from multiple clades should be spread across the landscape. Alternatively, the pattern of spatial and temporal sorting of lineages across a heterogeneous landscape (Ackerly 2003), would suggest an ecological explanation for the current diversity of *Hermannia*. This prediction is tested for *Hermannia* in this chapter.

Species occupy a particular area in space and time due to environmental, edaphic, topographic, historic and genetic factors (Randin, Dirnböck et al. 2006). *Hermannia* has been divided into a number of clades based on the molecular phylogeny (Chapter 3), thus these factors of genetic similarity may be investigated to look for related patterns. The three most distinct clades, subg. *Mahernia*, subsect. *Acicarpus* and sect. *Hermannia* have been found to have distinct biogeographic signatures (6.2.3), especially when subg. *Mahernia* is split into the subsect. *Tomentosae* from the summer rainfall regions, and the subsect. *Mahernia* mainly from

the Cape. These major clades are assessed here to determine if these species distribution patterns are associated with dissimilar climatic preferences, and whether these preferences can be explained by phylogenetic inertia. If different in their climatic preference, it is expected that they will respond differently to climate change. This is assessed at the end of the chapter.

### **7.1.1 Phytochoria**

Phytochoria are defined by Takhtajan (1986) as floristic areas of any rank. Choria are areas that contain a suite of species in common (Whitehouse 2002). Typically clustering algorithms are utilized to both demarcate areas of similarity, and to show the relationship between these areas. The known distributions of South African flora have been used to produce maps of biomes (Siegfried 1989; Burgess, Hales et al. 2004), phytochoria (White 1983; Linder, Lovett et al. 2005), bioregions and ecoregions (Burgess, Hales et al. 2004). Whitehouse (2002) found UPGMA clustering algorithms useful for examining montane phytochoria within the Cape Floristic Region (CFR). This study of *Hermannia* provides a unique perspective for South Africa, in that it differs from the cited studies in that it examines a single genus that favours the lowlands, and extends beyond the boundaries of South Africa.

An extension of the CFR to incorporate the entire winter-rainfall region into a *Greater CFR* has been proposed (Jürgens 1991; Van Wyk and Smith 2001; Born, Linder et al. 2007). There may be support for this concept as there are species in common between the CFR and the extended portion of the CFR. An UPGMA clustering technique of species similarity is utilized here to establish whether the Genus *Hermannia* supports or rejects this concept of a Greater CFR.

### **7.1.2 Spatial and climatic modelling**

Climate envelope models (CEMs) and mechanistic models (MMs) have been used to understand biodiversity patterns, and to model past, present and future species distributions (Hijmans and Graham 2006). Gelfand et al. (2003) provides a review of spatial modelling within

South Africa and abroad. The climatic modelling approach uses a climatic model of an area, from which climatic variables are extracted for a set of points that are allocated to a spatial grid for further analysis. These points may either be for a particular taxonomic group, or for a dataset that includes multiple species from an area. Many studies derive localities from herbarium or museum specimens with haphazard geographical accuracy, making absences impossible to determine (Elith, Graham et al. 2006). In some instances, presence/absence datasets to one minute resolution have been available for particular taxonomic groups, such as that stemming from the Protea Atlas Project (Gelfand, Silander et al. 2003). A number of analyses make use of these datasets. Gelfand et al. (2003) utilized a Bayesian framework to examine the potential distribution of Proteaceae species. The most accurate study to date utilizes 8x8m plots to a locational accuracy of 2m, with 1m resolution Digital Elevation Models (DEMs) (Lasseur, Joost et al. 2006; Randin, Dirnböck et al. 2006; Engler, Randin et al. 2009). However, our study utilizes georeferenced herbarium specimens to only 15 minute or QDS accuracy, without the benefit of confirmed absences. As a result, General Additive Model (GAM) and Maximum entropy (Maxent) approaches are not appropriate. A comparison of models by Hijmans and Graham (2006) found the Domain model to perform poorly, strongly underestimating range sizes, and its use for predicting future species distributions was thus advised against. As a result this study has concentrated on the use of the Bioclim model (Busby 1991) that is a CEM appropriate for presence-only distribution data.

Environments vary through time, with major cycles having been identified that have predictable global implications over varying geological time-scales (Dynesius and Jansson 2000). In recent years anthropogenic greenhouse drivers have been causally linked to increases in temperature with associated changes in precipitation (Midgley, Hannah et al. 2002). Radical changes have been predicted for the Cape Floristic regions of South Africa, with large scale mortality for plant populations and in some cases entire species that cannot migrate sufficiently fast to persist in the equivalent climatic conditions (Midgley, Hannah et al. 2002). Dispersal and mobility is of particular concern for edaphic specialists constrained by limited substrate availability, or where substrate islands are separated by distances beyond the short-term limit of dispersability of the species confined to these substrates (Williams, Hannah et al. 2005). Empirical studies of population survival have shown that the most northern populations of the



quiver tree, *Aloe dichotoma*, have shown widespread mortality, although some populations in more southern regions have shown marginal increases in population numbers (Foden, Midgley et al. 2007). Translocation experiments across an altitudinal gradient have found that faster growing species are more susceptible to climate change, and that competition is an important factor that is difficult to account for (Agenbag 2007).

*Hermannia* provides an important dataset for analysis of climate change, as there are a number of properties that distinguish it from other genera. *Hermannia* is split into clades that have separate origins (i.e. Cape vs. Namibian origins), and these are largely confined to geographic, and hence presumably, climatic regions. Unlike the majority of the Cape Proteaceae and the genus *Cliffortia*, *Hermannia* seldom occur in the mountains. The genus *Hermannia* is distributed across most arid environments within South Africa, with probable origins in the Namibian desert [Ch. 5]. Thus, as climate change increases temperature and aridity within South Africa, *Hermannia* is a likely candidate for expanding into vacant niches left by more mesic taxa.

The Worldclim dataset is a global climate model based upon a variety of climatic data mostly derived from the period 1950-2000 (Hijmans, Cameron et al. 2005). It has an interpolated resolution of 1km, and has a number of precipitation and temperature derived outputs. It is least able to deal accurately with mountainous terrain, thus is best suited for climatic envelope modelling with lowlands taxa such as *Hermannia* (Hijmans, Cameron et al. 2005). Due to the low resolution of the herbarium data for *Hermannia*, the Worldclim dataset is sufficiently resolved for climatic modelling of the *Hermannia* dataset.

### 7.1.3 Objectives

- a) To determine whether *Hermannia* is suitable for examining phytochorological affinities.
- b) To ascertain the ecological range that *Hermannia* occupies.
- c) To determine whether the ecological range of the genus is due to the adaptability and variability of each species, or whether it is due to a composite of individual species with restricted climatic envelopes.

- d) To undertake preliminary climatic modelling given the existing dataset.
- e) To test the concept of the Greater Cape Floristic Region.

## 7.2 Methods

### 7.2.1 Phytochoria

Phytochoria maps were derived for *Hermannia* by producing a similarity matrix using the methodology of Linder & Mann (1988). Each QDS was scored for the presence or absence of each species. Single taxon grid squares were omitted from the analysis. Three geographic levels were examined: Southern Africa, South Africa and CFR. The Jaccard coefficient is the preferred method for calculating the similarity of the grids, as it does not account for shared species absences, which are usually an artefact of undersampling (Magurran 1988). The UPGMA algorithm is implemented in DIVA-GIS (Hijmans, Guarino et al. 2005) as for NTSYS 2.10q (Rohlf 2000). Trees with ties found using this algorithm were calculated using strict consensus to ascertain clustering patterns. In most instances the lowest numbered clusters from the dendrogram represented odd single QDS records with little or no affinity to other QDS, and thus have been manually removed from the tree.

All records of valid species were exported from BRAHMS (Filer 2005) collections management software as a *.shp* file. This was converted into presence and absence within a quarter degree square utilizing the point-to-grid method as implemented in DIVA-GIS (Hijmans, Guarino et al. 2004). The subsequent grids were converted into a stack and the clustering workflow worked through. Weighting was used for all subsequent analyses as it takes into account the rarity of a species. Comparisons of the results were then made between three algorithms:

Jaccard

$$(1-a) / (a+b+c);$$

Lance & Williams = Bray-Curtis

$$(b + c) / (2*a+b+c);$$

Dice = Czekanowski = Sorenson

$$1 - 2a / (2a + b + c);$$

where **a** are the species in common, and **b** & **c** are the species not in common.

The resulting distance matrices were visualized in a dendrogram, and pruned at various levels to explore the clusters. Pruning has the effect of grouping all cells that are attached below the pruned branch. The tree was then plotted on a map of Southern Africa which is where the majority of *Hermannia* diversity occurs. To explore the maps, several colouring options exist. For outputs of greater than 30 terminal tips, colours were randomly assigned to the tips. For less than 30 tips, colours were picked to maximize visibility. The latter was found to be the most effective, and colours/shades were chosen to highlight and separate major distinct clusters. The corresponding geographic regions were annotated on the dendrograms. This process was repeated for the section *Mahernia* and the subsect. *Acicarpus*. An initial run was also done using a 1 degree grid square.

### 7.2.2 Bioclimatic modelling

Diva-GIS provides a number of solutions for analysing georeferenced collections with respect to their inferred climatic attributes. Two sources of the climatic data were used, both with a 10° cell size: the current Worldclim dataset, and the future scenario Community Climate Model 3 (CCM3) dataset. Each record was plotted to the centre of the QDS, and the climatic values were extracted from the climatic values associated with this centre point. The climatic variables useful for analysis are obtained from the outliers.

An initial assessment of variation of climatic variables was undertaken for each group to determine the important variables determining distribution. The four most variable of these variables were utilized in subsequent analyses for frequency curves and bioclimatic envelopes. A 0.025 percentile is shown on the frequency curves and utilized in creating an envelope.

### 7.2.3 Prediction modelling

Two models, Bioclim and Domain, were run on the datasets of the major groups of *Hermannia* which were assessed as single classes (i.e. as a single unit). The two climatic models, Worldclim and CCM3 were assessed for seven different output variables: Bioclim, Bioclim true/false, Bioclim most limiting factor (MLF), Domain, Domain mean distance, Domain true/false, and Domain most limiting factor.

### 7.2.4 Datasets

Table 7.1 shows the variables used in climate analysis. The variables are from the Worldclim data model.

**Table 7.1 Climatic variables used in Worldclim and CCM3 datasets for bioclimatic analyses (Hijmans, Guarino et al. 2005).**

Variable # Temperature Variables		Variable # Precipitation Variables	
1	Annual Mean Temperature	12	Annual Precipitation
2	Mean Monthly Temperature Range	13	Precipitation of Wettest Month
3	Isothermality (2/7)(*100)	14	Precipitation of Driest Month
4	Temperature Seasonality (STD * 100)	15	Precipitation Seasonality (CV)
5	Max Temperature of Warmest Month	16	Precipitation of Wettest Quarter
6	Min Temperature of Coldest Month	17	Precipitation of Driest Quarter
7	Temperature Annual Range (5-6)	18	Precipitation of Warmest Quarter
8	Mean Temperature of Wettest Quarter	19	Precipitation of Coldest Quarter
9	Mean Temperature of Driest Quarter		
10	Mean Temperature of Warmest Quarter		
11	Mean Temperature of Coldest Quarter		

The dataset of localities and QDS for each record is in on the DVD in the file:

\appendix\collections extract file – 15K records.xls

## 7.3 Results

### 7.3.1 Phytochoria

#### 7.3.1.1 Results of clustering analysis

The currently recognised biomes of South Africa are portrayed in the map shown in Fig. 7.1 (Mucina and Rutherford 2006). This map represents a consensus of phytochoria derived from taxonomic and environmental layers. Climatic models of the biomes produced by Mucina and Rutherford (2006) predict their biomes with 65.1 – 86.7% accuracy for the CART method, and 63.2 – 91.8% for their Hand Constructed Linear Decision Tree (HCLDT). In the analyses described below, clusters are given geographic labels in the dendograms (where possible) in order to assist in identifying geographic relationships.

Analysis at one-degree scale excludes fine-level differences in species composition. Nevertheless, a considerable similarity is found between the Jaccard unweighted consensus for *Hermannia* (Fig. 7.2) and that of the Vegmap biomes (Fig. 7.1), notably a close correlation in the positioning of the Fynbos, Nama-Karoo, Albany Thicket and Grassland regions. Notable differences evident in the *Hermannia* map are that the Nama Karoo/Groot Karoo is combined with the Succulent Karoo in cluster 5, that the Elands Bay centre of endemism is isolated as cluster 4, a reduction in the extent of the Grassland region (cluster 2) and also in that of the Savanna region. Several “biomes” are recovered within Namibia, relating to a winter-rainfall phytochorion (cluster 8), a north-western phytochorion (cluster 9), a southern inland phytochorion (cluster 15), and a summer rainfall north-eastern phytochorion (cluster 16) that is shared with Botswana. Namibia is also represented in the northern regions by clusters 2 and 14, showing a link with the grassland and savanna respectively. *Hermannia* accordingly shows promise as a representative proxy for general vegetation, at least at the broad-scale.

Lowering the cutoff to 0.45 (Fig. 7.4) resolves 24 more clusters across Southern Africa. The finer-level phytogeographic groups begin to reveal themselves, though at the one degree scale are not sufficiently resolved to approximate the resolution of Mucina and Rutherford’s (2006)

bioregions, of which 35 occur in South Africa. It is now possible to distinguish between the western Karoo that includes the Klein Karoo and Roggeveld (cluster 12) and the Groot Karoo (cluster 9). There is also substantially more resolution along the West Coast, revealing a unique flora in the NW (cluster 7) that relates to the Namaqualand flora. Clusters 3-9 are all related and fall into a SW Cape cluster that includes the closely related Klein Karoo/Roggeveld and Groot Karoo regions. Cluster 10 is retrieved along with the Botswana/Great Karoo group (see Fig. 7.5). This cluster is located at the Botswanan border and comprises a single cell that is very dissimilar (in terms of the dendrogram) to its surrounding cells. The next most similar group is that of Namibia that includes 8 clusters (cluster 11-18). Clusters 19-26 form an eastern group, with the thicket and grassland forming a smaller group (clusters 19-22), and the Lowveld and Indian Ocean Coastal Belt (IOCB) (clusters 23-26) forming a distinct group. The Zimbabwean group is distinct and comprises clusters 27 and 28, but grades into the bushveld / highveld group (cluster 28-32) and the flora from northern Southern Africa (clusters 33-40). Considerable mixing is shown in Botswana, Zimbabwe and northern Namibia. This may be in part due to the undersampling of *Hermannia* in these areas.

The CFR is generally considered to include the Klein Karoo, here depicted in Fig. 7.4 as cluster 8. This cluster also includes the Roggeveld region and north-eastern portions of the CFR (*sensu stricto*). If cluster 8 is included with clusters 3-6, this would provide support for a Greater CFR. Clusters 3-6 themselves contain most but not all of the CFR, as they lack the north-eastern portions that are contained in cluster 8. Cluster 9, whilst appearing closely related to cluster 8 in dendrogram of Fig. 7.5, cannot reasonably be included in a Greater CFR since (at least at this scale of resolution) it encompasses primarily the Groot Karoo.

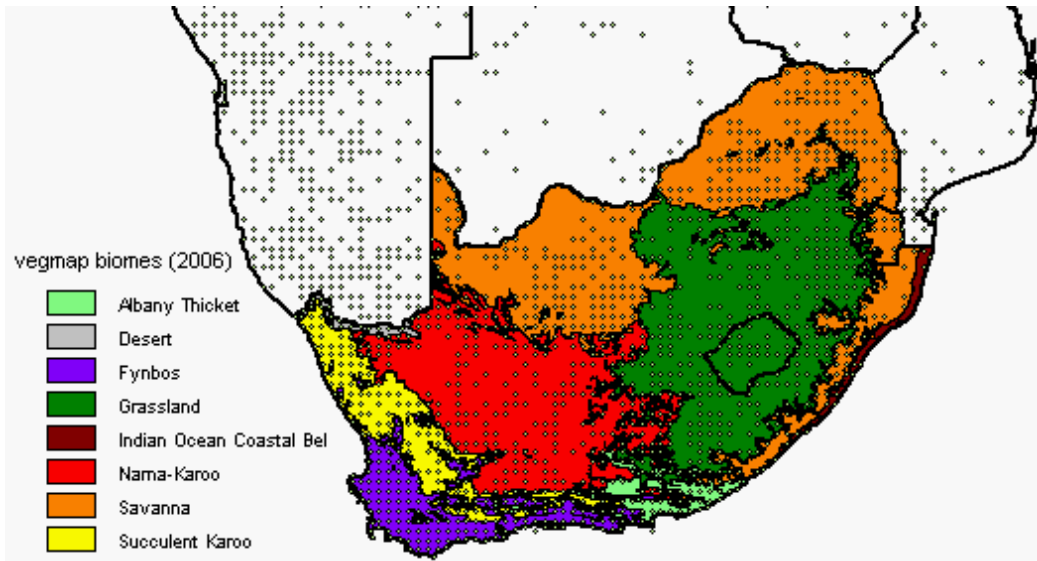


Fig. 7.1 The biomes of South Africa (forest excluded) as mapped by Mucina and Rutherford (2006). Data layer courtesy of SANBI.

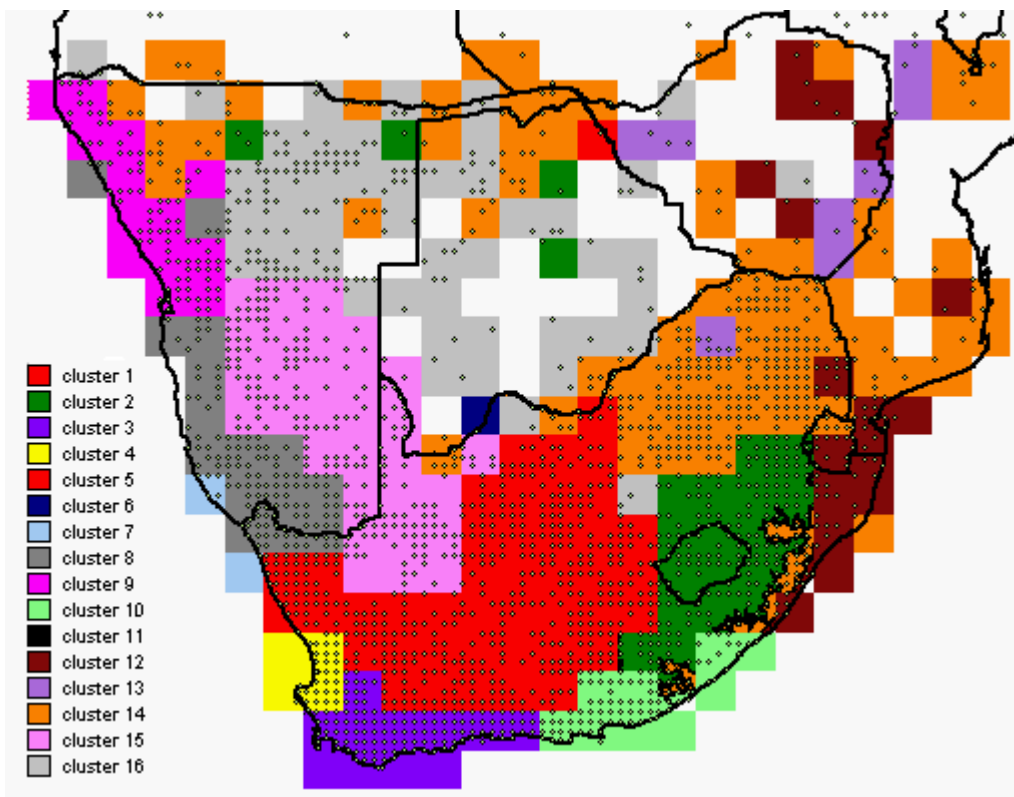


Fig. 7.2 A one degree map of *Hermannia* coloured to approximately match the biomes of SA. The map was derived from a Jaccard unweighted dendrogram pruned at a similarity level of 0.45617.



Fig. 7.3 Jaccard unweighted dendrogram for the map in Fig. 7.2 with a cutoff of 0.45.

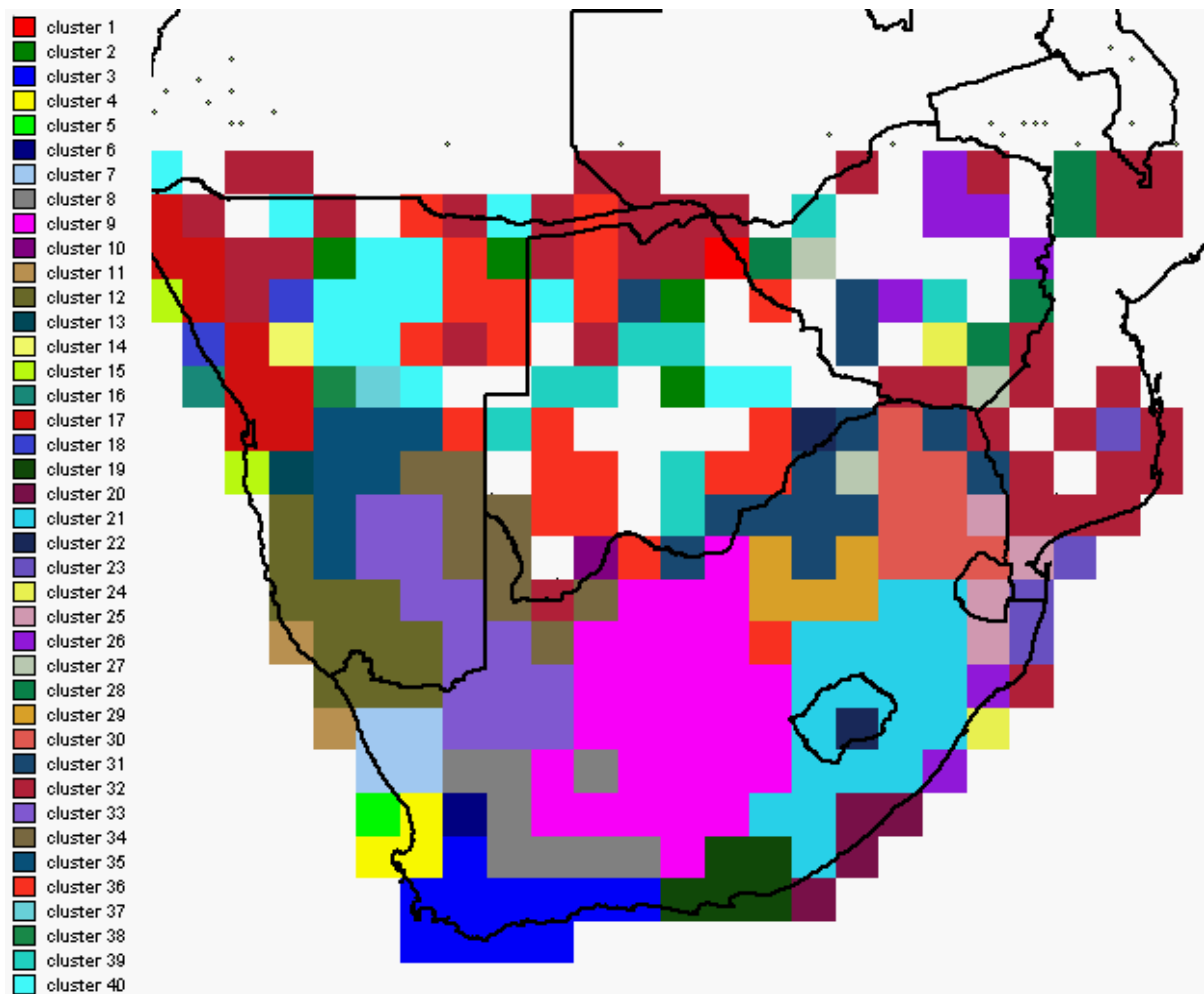
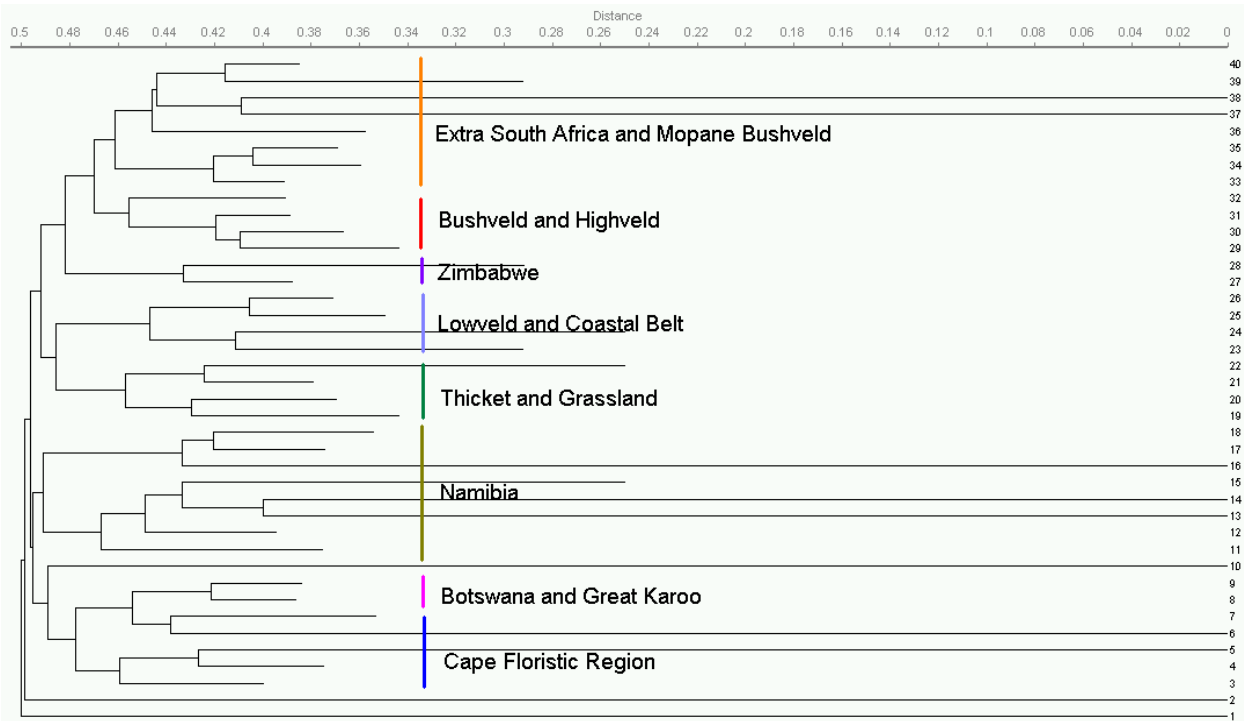
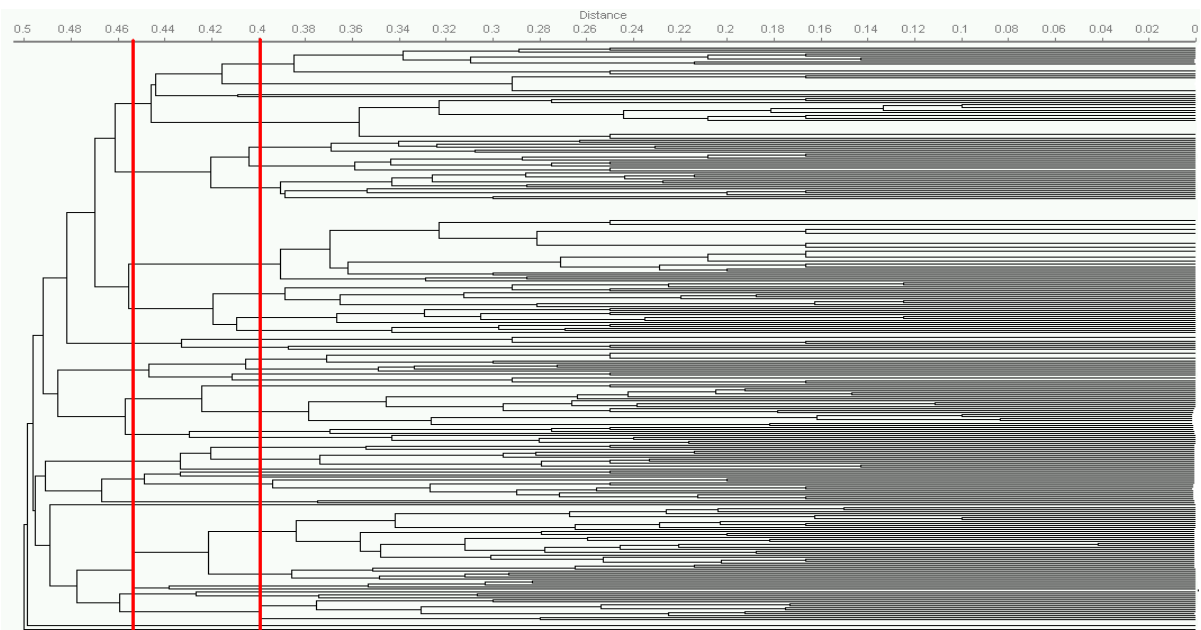


Fig. 7.4 Jaccard unweighted map for *Hermannia* at 1-degree resolution pruned at a cutoff of 0.4. The colours in the map and subsequent maps reflect the clusters in the associated cluster analyses.





**Fig. 7.5** Jaccard unweighted dendrogram for *Hermannia* corresponding to Fig. 7.4, with a cutoff of 0.4.



**Fig. 7.6** Jaccard unweighted and unpruned dendrogram for a 1 degree grid size, with the cutoffs for the 1 degree maps shown in red lines.

Fig. 7.7 has a large number of clusters (49) which are uniquely and randomly coloured. Thus a substantial area of contiguous colour suggests similar flora, and a good phytochorion. The CFR has four of these areas from cluster 31-40: a Cape Metropolitan Area (CMA) and West Coast; a South Coast belt; an inland Klein Karoo belt; and a Cedarberg belt. Further north, the Namaqualand region is fairly cogent, as is the SE belt that extends into the Drakensberg grasslands. Three contiguous patches occur in the NE of South Africa in the highveld.

Fig. 7.8 has a cutoff of 0.49, thus there are only 10 clusters. The clusters 9-12 form a group consisting of summer rainfall species. Clusters 13-14 form a putative Greater CFR region that includes the Klein Karoo, while cluster 15 includes a contiguous block in the Eastern Cape, spreading from there across the Groot Karoo and into Namibia. Clusters 16 and 17 are southern Namibian groups, and cluster 18 is in the northern and north-eastern portions of Namibia.

The map in Fig. 7.10 is the result of a weighted Jaccard algorithm, unlike the previous maps which are unweighted. Patterns are similar to those seen previously, with the most noticeable difference being that the areas are more discrete, reflecting the patterns observed in the field. For example, the Southern Cape flora extends further east, the SW CFR extends further inland, and Namaqualand forms a more contiguous patch.

Lance weighted analysis (Fig. 7.12) is similar to the Jaccard weighted analysis. The Dice analysis has a nearly identical output to the Lance analysis, and is therefore not depicted.

The concept of a Greater CFR is weakly supported at QDS level in Fig. 7.10 and Fig. 7.12 where the CFR clusters clearly extend into the Klein Karoo and Roggeveld, but are represented only as elements within a complex pattern. The Greater CFR is not discernable in Fig. 7.7, possible due to the large number of clusters resulting from the choice of cutoff. Fig. 7.8, with its cutoff of 0.49, displays very broad patterns. Its cluster 14 shows coherence between the Klein Karoo and Groot Karoo. However, at this coarse level of cutoff we do not expect to see fine level relationships between the CFR and Klein Karoo. Overall, the QDS analyses at these levels of cutoff show weak support for a Greater CFR compared with the strong support seen at 1-degree resolution in Fig. 7.4.

The Lance weighted map for subg. *Mahernia* (Fig. 7.14) shows that it agrees well with the patterns found for the whole genus. The limestone area of De Hoop (cluster 9) is substantially dissimilar to the surrounding area (cluster 10). The groups in Fig. 7.15 are annotated and form geographically sensible clusters. Cluster 19 extends from Swaziland to the Northern Cape, but is very different from the rest of the grassland group. Cluster 23 is exceptionally broad in its area and in the range of biomes it covers. The subg. *Mahernia* best represents the desert biome with cluster 18, although this cluster extends deep into Namaqualand.

The dendrogram for sect. *Acicarpus* forms only three major groups of clusters that are fairly closely related with a dissimilarity of less than 0.35 (Fig. 7.17). These groups correspond to the regions of NW Namibia, NE Namibia, Southern Namibia, the Cape, the Groot Karoo, and the bushveld as shown in Fig. 7.16. Cluster 14 portrays the desert biome in subsect. *Acicarpus*, with a lesser extension into Namaqualand than seen for subg. *Mahernia* in Fig. 7.14.

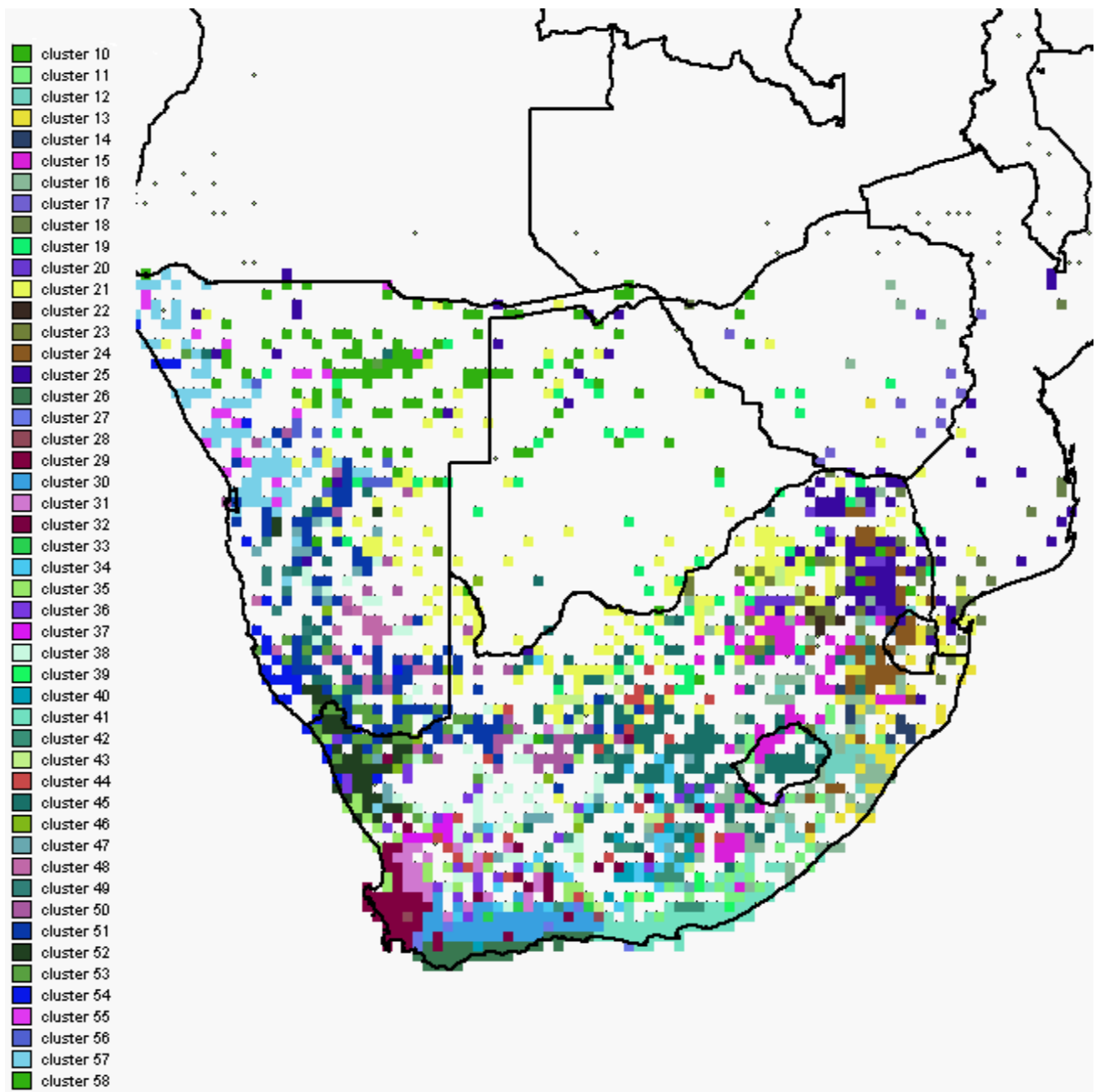


Fig. 7.7 Jaccard unweighted map for *Hermannia* at QDS resolution with a cutoff at 0.45817.

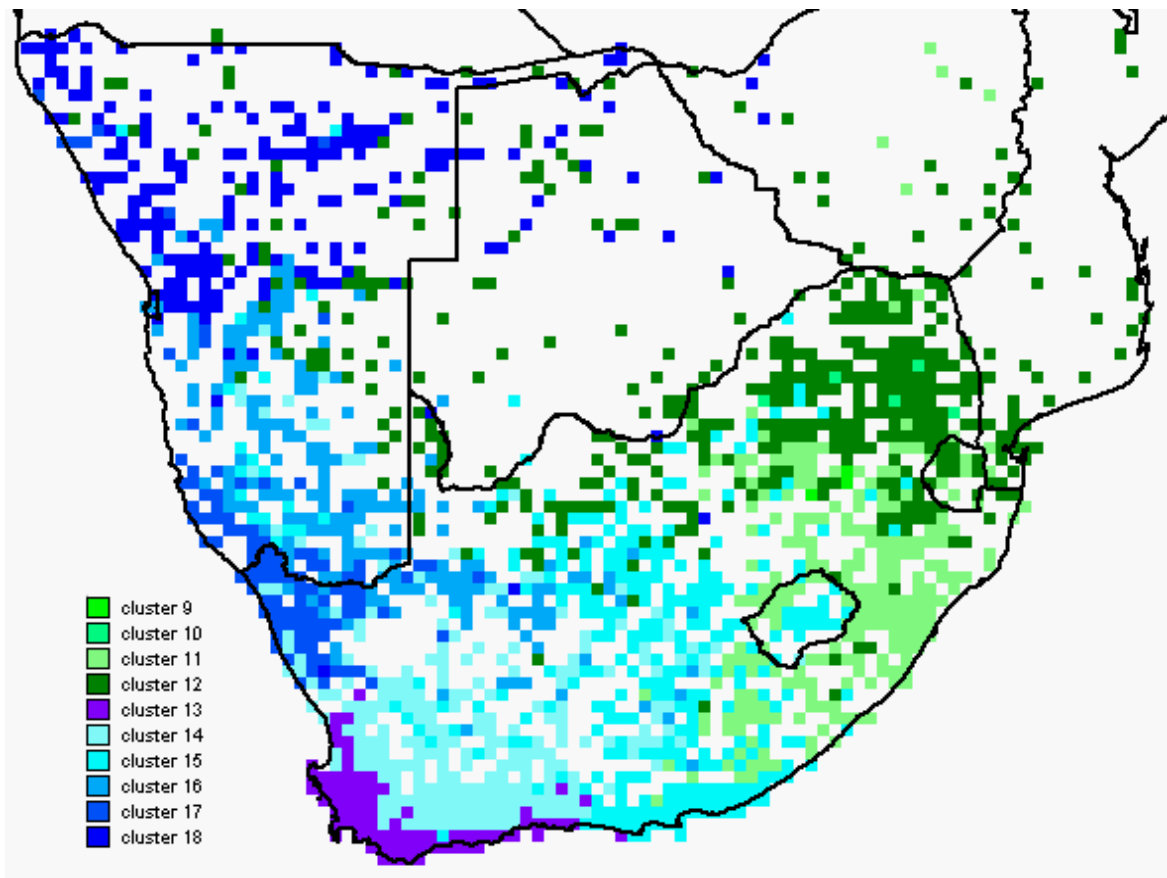


Fig. 7.8 Jaccard unweighted map for *Hermannia* at QDS resolution with a cutoff at 0.49.

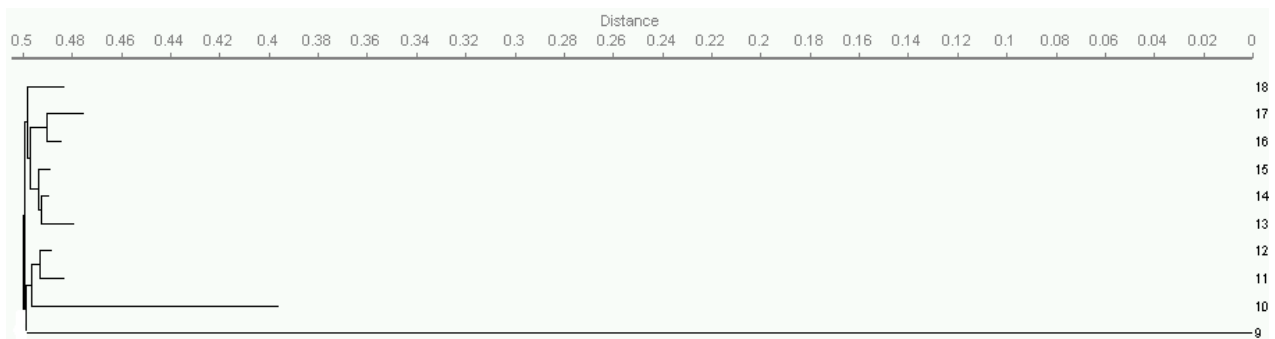
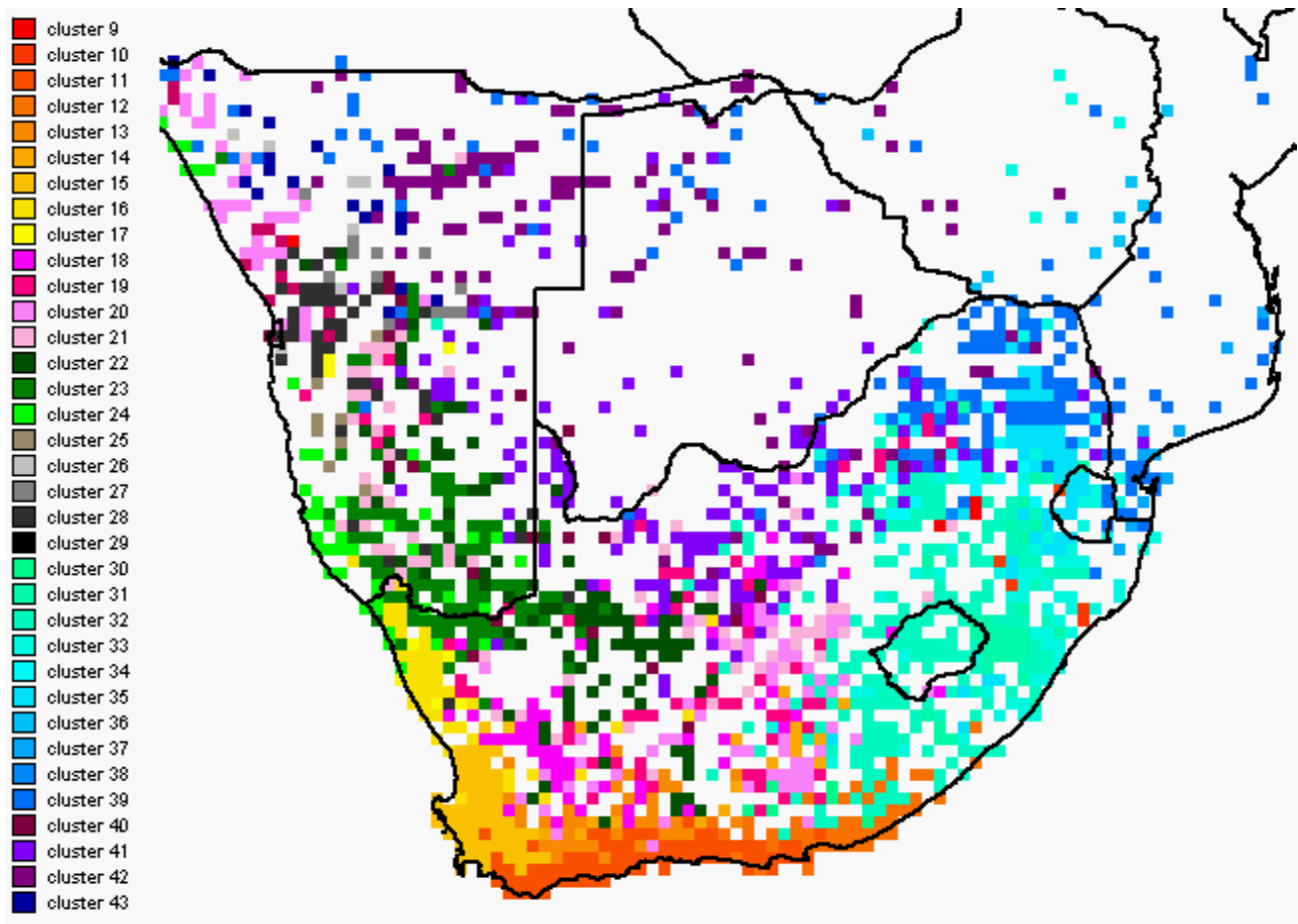
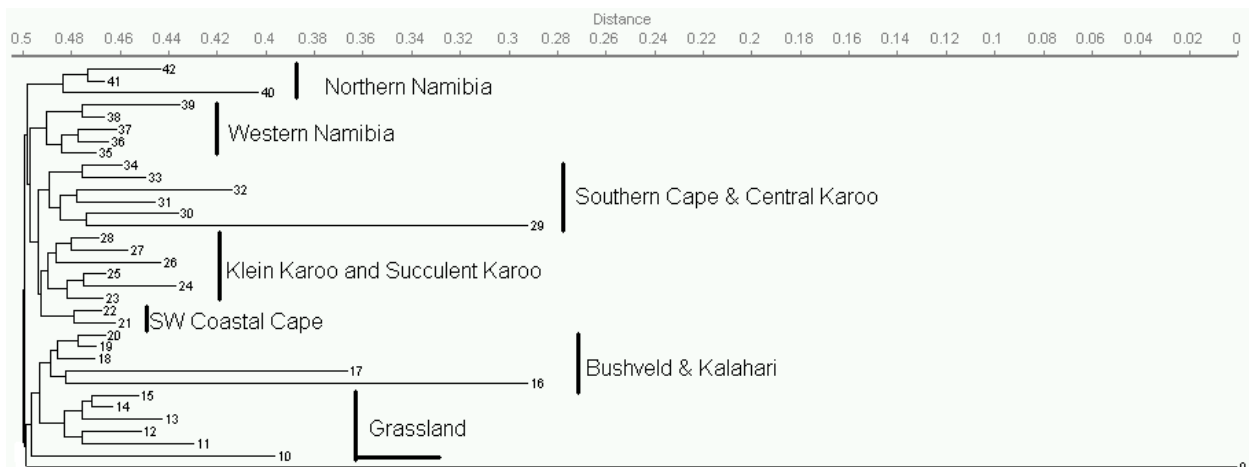


Fig. 7.9 Jaccard unweighted dendrogram of *Hermannia* corresponding to Fig. 7.8 with a cutoff of 0.49.



**Fig. 7.10** Jaccard weighted map of *Hermannia* at QDS resolution, coloured to reflect clusters, with a cutoff of 0.47.



**Fig. 7.11** Jaccard weighted analysis dendrogram for *Hermannia* with a cutoff of 0.47. Cluster 9 is included in grassland.

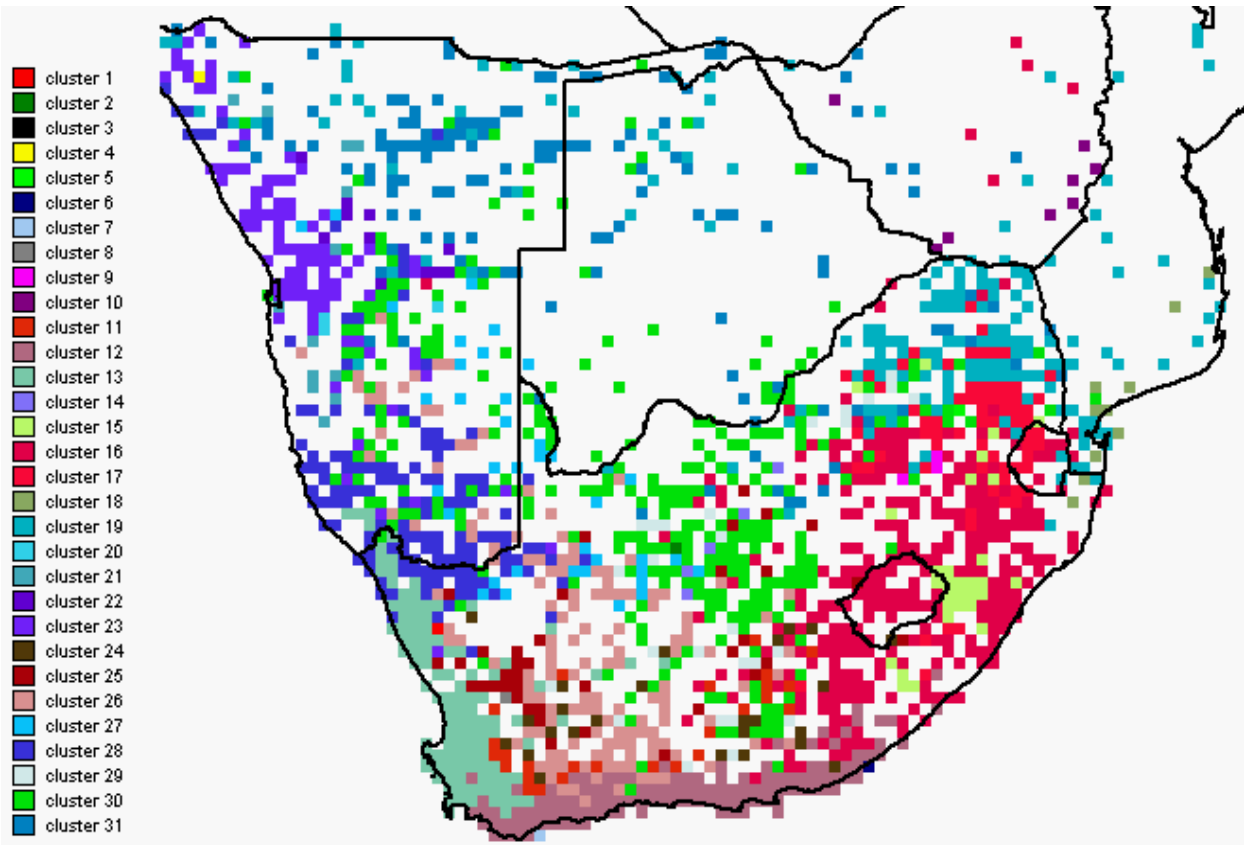


Fig. 7.12 Lance weighted map for *Hermannia* at QDS resolution with a cutoff of 0.47.

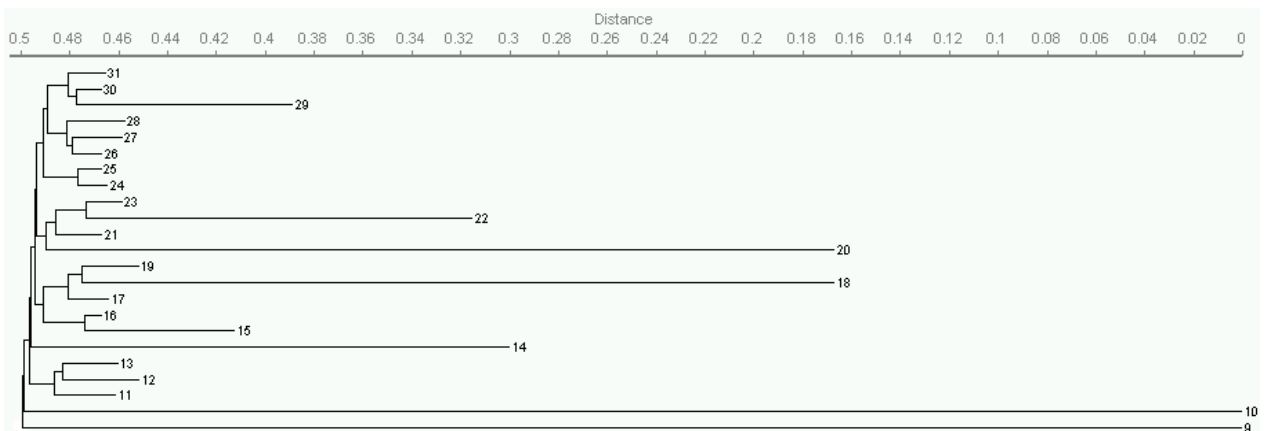


Fig. 7.13 Lance weighted dendrogram for *Hermannia* with a cutoff of 0.47.

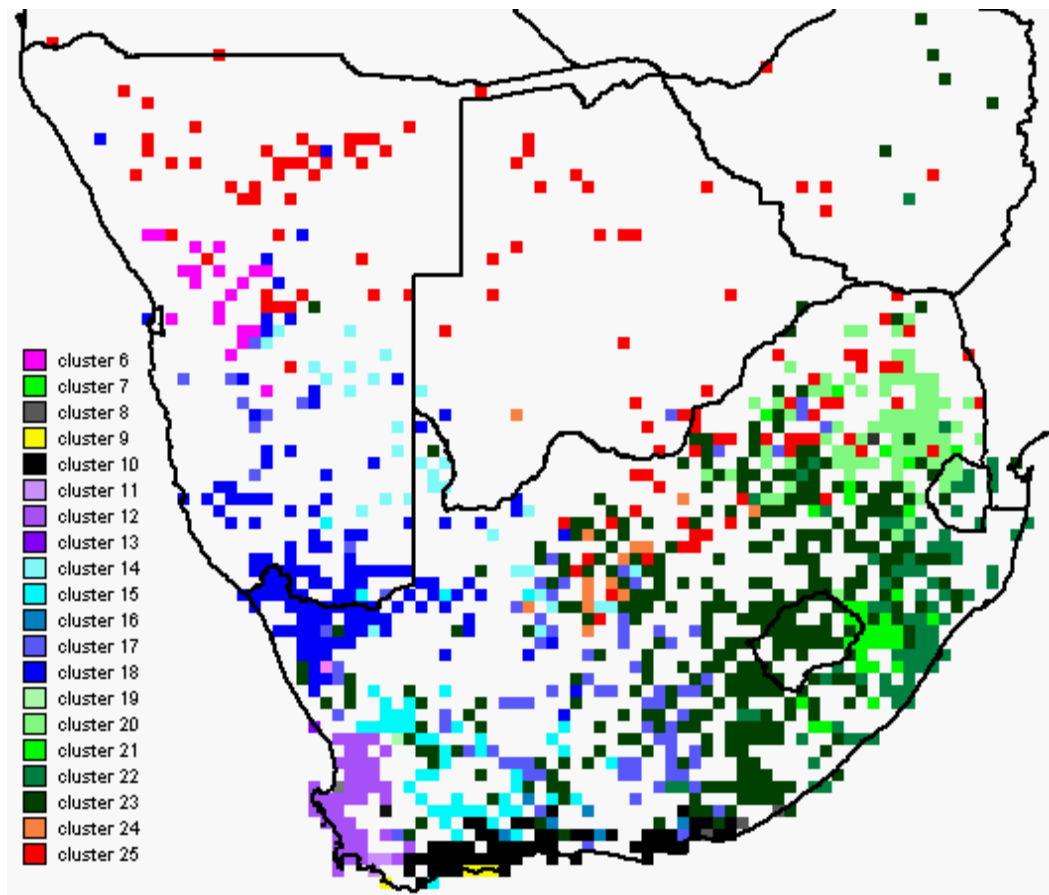


Fig. 7.14 Lance weighted map for subg. *Mahernia* at QDS resolution with a 0.47 cutoff.

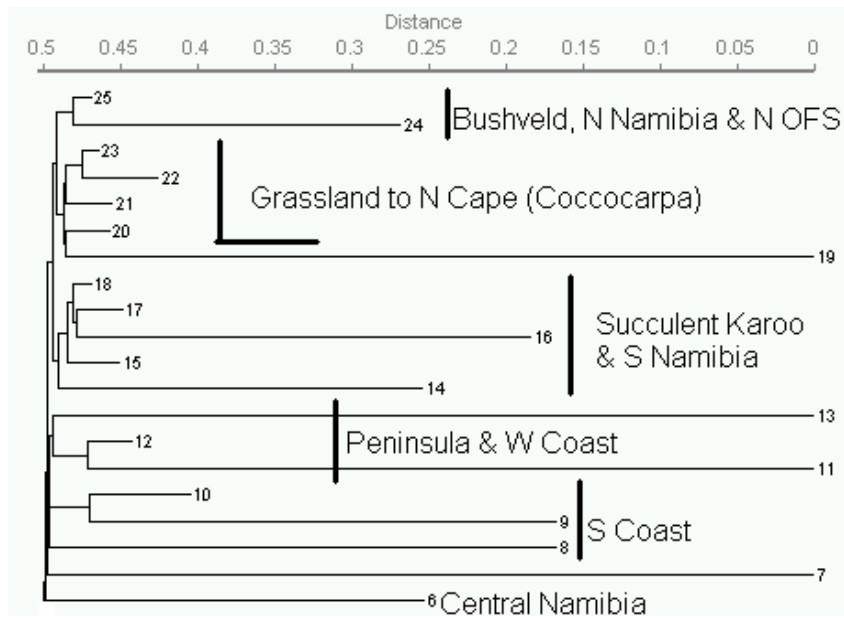


Fig. 7.15 Lance weighted dendrogram for subg. *Mahernia* at QDS resolution with a 0.47 cutoff.



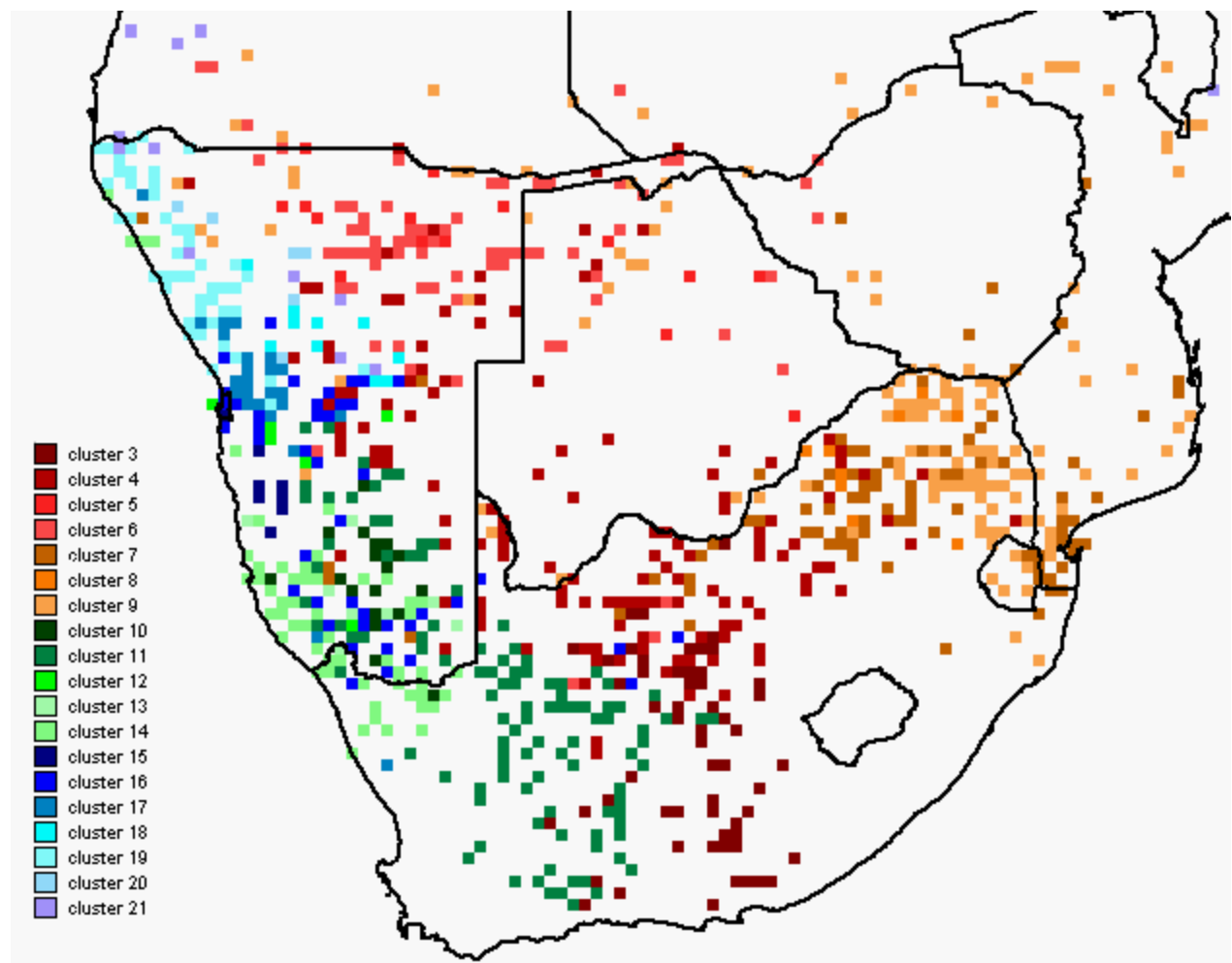


Fig. 7.16 Lance weighted map for subject. *Acicarpus* at QDS resolution with a cutoff of 0.4.

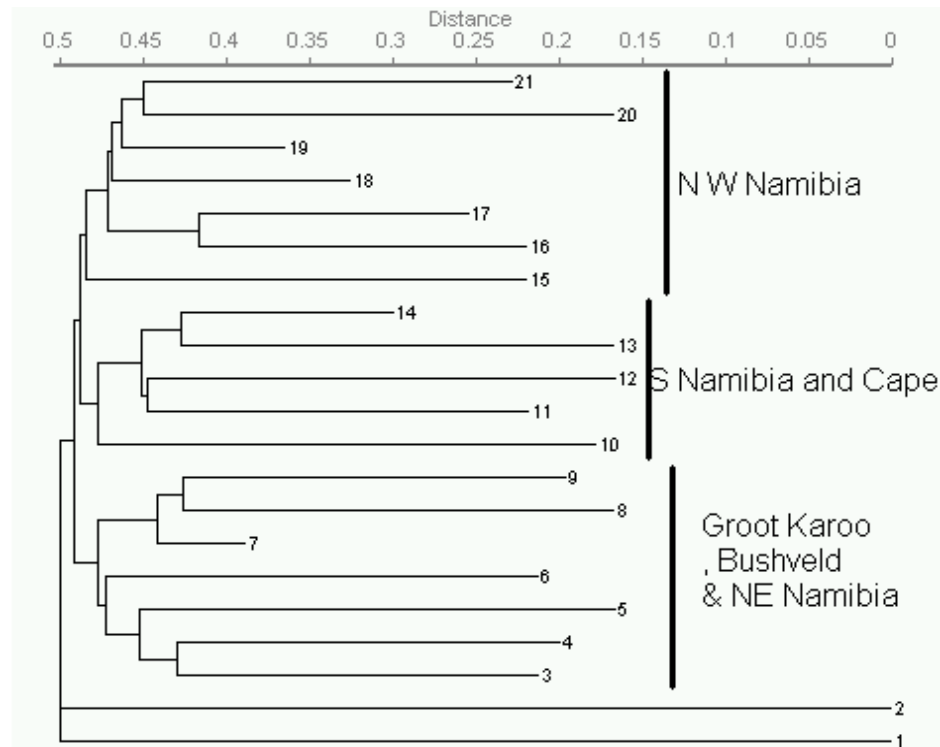


Fig. 7.17 Lance weighted dendrogram for subject. *Acicarpus* with a 0.4 cutoff.

### 7.3.1.2 Delineation of vegetation types

The fynbos region as defined by Vegmap corresponds well to cluster 13 in the Jaccard unweighted analysis shown in Fig. 7.8. Weighted Jaccard (Fig. 7.10) shows a broader concept of the fynbos region, extending further into the arid areas (cluster 15 and 11). There is a boundary between these fynbos clusters that separates the South Coast and West Coast flora. The Klein Karoo region contains various clusters, including a considerable representation of cluster 12 which is associated with the Southern Coast flora (Fig. 7.10). The Lance weighted map (Fig. 7.12) is not directly comparable as it utilizes a cutoff of 0.47, but shows a very similar distinction between the South and West Coast flora. In this instance the West Coast flora (cluster 13) extends up the West Coast slightly further, beyond the Namibian border. The border between the West and South Coast flora is seen also for subg. *Mahernia* (Fig. 7.14), although its position is shifted eastwards. This could be an artefact of the under-representation of this subgenus in the borderline area. These multiple sources (i.e. sect. *Hermannia* and subg. *Mahernia*) portray a fundamental distinction between the West Coast and South Coast flora. This boundary extends

from around Betty's Bay to either Worcester (Fig. 7.7) or to Caledon and Montagu (Fig. 7.10). This is considerably west of the fundamental east-west subregional boundary that separates winter-rainfall from non-seasonal rainfall (Cowling, Proches et al. 2009).

The Succulent Karoo (Fig. 7.1) does not show up clearly in the cluster analysis. For instance, in Fig. 7.10 no single cluster is contained within the Succulent Karoo. On the other hand, the Succulent Karoo contains a mixture of clusters. Thus *Hermannia* appears to define different phytochoria in the Succulent Karoo and its surrounding regions.

The Nama Karoo (Fig. 7.1) that can generally be recognised by cluster 9 in Fig. 7.4, is the arid aseasonal to summer rainfall portion of central South Africa. The identification of the Nama Karoo is generally supported by further analyses: clusters 18-22 in Fig. 7.10 (the Jaccard weighted map for *Hermannia*); clusters 26, 27, 29 and 30 in Fig. 7.12 (the Lance weighted map for *Hermannia*) and clusters 15 and 17 in Fig. 7.14 (the Lance weighted map for subg. *Mahernia*). In each case, the clusters are not contained completely within the recognized Nama Karoo region. For instance, in Fig. 7.10, cluster 18 overlaps with the Succulent Karoo; in Fig. 7.12, cluster 30 extends into the Grassland and in Fig. 7.14 cluster 15 extends into the Klein Karoo and Fynbos. In the Lance weighted map for subsect. *Acicarpus*, the Nama Karoo contains chiefly clusters 3 and 11, though these extend in a north-westerly direction through to southern and central Namibia (Fig. 7.16). In all, there is support for the Nama Karoo as a complex of composition types.

The Grassland region (Fig. 7.1) is perhaps the most obviously recognisable from the clusters. Again, Fig. 7.7 is too coarse to enable easy visualization of this flora, whereas in Fig. 7.8 it is easily recognisable as cluster 11, in Fig. 7.10 as cluster 31 and 32, Fig. 7.12 as cluster 15 to 17. The subg. *Mahernia* (Fig. 7.14) portrays the more coastal Natal region (cluster 22) as distinct from the more inland areas (cluster 23) and includes a further cluster (21) confined mostly to an area between Lesotho and the coast. The subsect. *Acicarpus* is noticeably absent from the grassland region (Fig. 7.16).

The savanna (Fig. 7.1) surrounds the grassland biome except to the south-west, with a narrow strip along the Natal East Coast adjacent to the Indian Ocean Coastal Belt (IOCB). Neither the narrow strip of savanna, nor the IOCB are obvious by cluster analysis, though the northern extent of the savannah is represented by cluster 39 in Fig. 7.10 and by cluster 31 in Fig. 7.12, while its north-western extent is represented by cluster 41 in Fig. 7.10 and by cluster 30 in Fig. 7.12. The clusters corresponding to the north-western extent of the savannah in Fig. 7.10 and Fig. 7.12 also occur in the eastern portions of Namibia, to the north of the Grassland and Nama Karoo biome, throughout Southern Africa. This is interesting in light of the finding of a southern distribution of the savanna biome (White 1983), and a more recent examination of the biome within Namibia (Irish 1994).

The Albany Thicket biome (Fig. 7.1) in the one degree map for *Hermannia* as cluster 10 in Fig. 7.2 and at the QDS scale as cluster 12 of Fig. 7.10 (Jaccard weighted map for *Hermannia*). However, in Fig. 7.12 (Lance weighted map for *Hermannia*) it appears as cluster 12 but is not distinguished from the remainder of the South Coast extending eastwards to the Cape Peninsula. Similarly, in Fig. 7.14 (Lance weighted map for subg. *Mahernia*) cluster 10 includes both Albany Thicket and the South Coast as far as Cape Agulhas. Thus there is general support for the Albany Thicket in this analysis.

The desert biome falls mainly within Namibia, and narrowly broaches the border of South Africa to the south. In Fig. 7.2 cluster 8 is covers a similar area to the arid-desert biome, as opposed to cluster 15 which more closely approximates that of the semi-desert biome (Mucina and Rutherford 2006). In Fig. 7.8, cluster 17 most closely approximates the area of desert, but extends to the Namaqualand region, while cluster 16 provides a fair representation of the semi-desert biome. In Fig. 7.10, cluster 24 approximates the desert biome while clusters 22 and 23 approximate the semi-desert biome (with some extension to Nama Karoo in the east). In Fig. 7.12 the desert biome is covered by cluster 28, with an incursion in its southern extent by the West Coast cluster 13. Overall, the evidence of multiple analyses broadly supports a desert biome centred around the south-western portion of Namibia that extends considerably north towards western Central Namibia. Related floristic clusters are found in Namaqualand and the Nama Karoo / semi-desert to the east.

The concept of a floristic region extending from western Central Namibia, to Damaraland in north-western Namibia is supported by cluster 57 in Fig. 7.7, cluster 18 in Fig. 7.8 (the latter extending eastwards into Botswana), cluster 23 in Fig. 7.12 and clusters 17-21 in Fig. 7.16. The Jaccard weighted map for *Hermannia* in Fig. 7.10 shows a complex pattern for this region. The subg. *Mahernia* (Fig. 7.14), is poorly represented in Namibia, and with cluster 6 partially covering the Damaraland region and cluster 25, a cluster that traverses a wide range across northern Namibia, Botswana and northern South Africa, also overlapping with the region in question. Cluster 18 in Fig. 7.8 also demonstrates this link into Botswana. Overall, there is some support from several of the analyses for a biome extending from the western parts of central Namibia to north-western Namibia.

### 7.3.2 Climate niche modelling

For all subsequent climatic modelling analyses, bioclimatic variables correspond to those Worldclim variables as provided in Table 7.1. The variation of climatic values for the major clades are shown in Fig. 7.18a-h. In this and the following figures, individual profiles for the accessions are overlaid, providing an overall picture of the variation. For all of the clades presented in Fig. 7.18, four distinct peaks of variation are visible, corresponding to variable temperature seasonality (4), annual precipitation (12), precipitation in the wettest quarter (16), and precipitation in the warmest quarter (18). Three lesser peaks are visible, with precipitation in the coldest quarter (19) being the next largest peak, followed by precipitation in the wettest month (13). Precipitation seasonality (15) is present at a low level in all cases.

In Fig. 7.18, the ratios of the heights of the major peaks are broadly similar for all but the last clade, namely *Hermannia*, sect. *Hermannia*, subsect. *Acicarpus*, subsect. *Acicarpus* sans east, sect. *Mahernia*, subsect. *Tomentosa* and subsect. *Mahernia*. In all cases, annual precipitation (12) is the dominant peak, followed by precipitation in the wettest quarter (16) and precipitation in the warmest quarter (18) which are roughly equal, and then temperature seasonality (4) the smallest of the major peaks. There are, however, some slight differences. The maximum peak height for precipitation in the wettest quarter (16) is greater than that for precipitation in the warmest quarter (18) in some cases, namely the genus *Hermannia*, and subsect. *Acicarpus*. Comparing

this to subsect. *Acicarpus* sans east (where the peaks are equal), it may be suggested that species of subsect. *Acicarpus* occurring in the east, as well as the group “*Mahernia*” (discussed below) may be responsible for the difference in peak heights for the genus as a whole. Under some of the peaks, a prominent ‘cavity’ is visible; this is especially noticeable for temperature seasonality (4) where it is present for all of the clades, especially for subsect. *Tomentosa* and subsect. *Mahernia*, both clades within subg. *Mahernia*. Precipitation in the coldest quarter (19) is present in most of the clades, though it is conspicuously sparse for subsect. *Tomentosa* and prominent for subsect. *Mahernia* where its peak height is similar to that of precipitation in the wettest quarter (16) and precipitation in the warmest quarter (18).

In Fig. 7.18, the profile of the informal group “*Mahernia*” is distinct from that of the other clades presented. It has a much higher peak for precipitation in the wettest quarter (16) than for precipitation in the warmest quarter (18), and its peak for temperature seasonality (4) is unusually low. It also has conspicuous ‘cavities’ under all the major peaks which are much more pronounced than for the other clades examined.

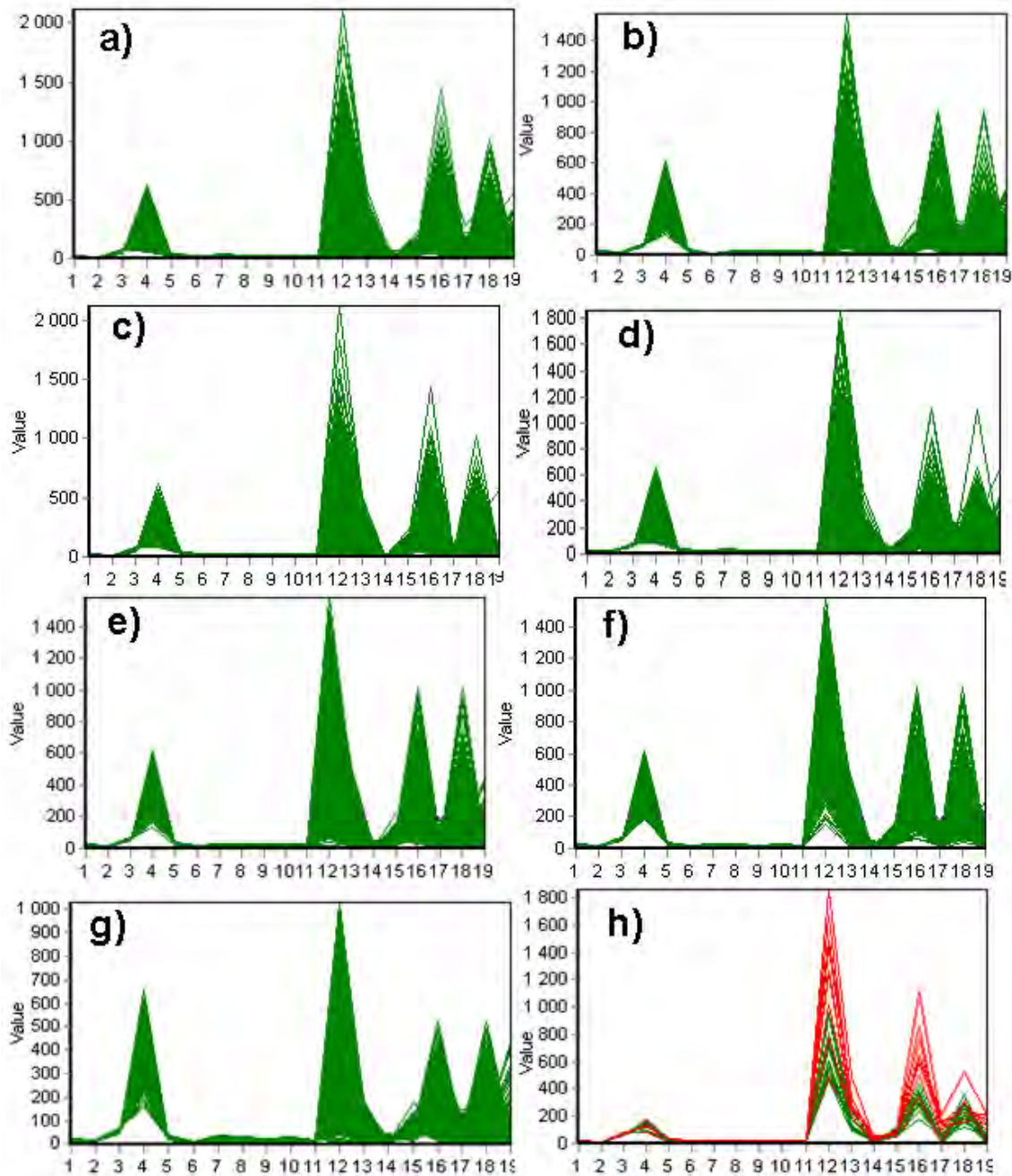


Fig. 7.18 Variation of climatic values for a) the genus *Hermannia*; b) sect. *Hermannia*; c) subsect. *Acicarpus*; d) subsect. *Acicarpus* sans east; e) sect. *Mahernia*; f) subsect. *Tomentosae*; g) subsect. *Mahernia* with sect. *Pinnatifidae*; h) “*Marehnia*”. The numbers on the X-axis of all graphs refer to Worldclim bioclimatic variable numbers: 4 is temperature seasonality, 12 is annual precipitation (ppt), 16 is ppt of wettest quarter, 18 is ppt of warmest quarter, 19 is ppt of coldest quarter, and the remaining values are given in Table 7.1 of the Methods. On all climatic niche graphs, the red lines represent “outlying” species from the 95% clustering within the climatic envelope, and the y-axis represents the “strength” of the variable.

### 7.3.2.1 The western *Mahernia* (subject. *Mahernia*) and the sect. *Pinnatifidae*

Examining species profiles assists in understanding the profiles of the major groups to which the species belong. In considering subg. *Mahernia*, the annual precipitation values for the lowland species (Fig. 7.19a and Fig. 7.19b) are found to be nearly identical, with a low at factor 18 and a high at factor 19. The arid montane species, *H. cedarbergensis* (Fig. 7.19c), has a similar profile, except with an exceptional temperature seasonality peak (factor 4) that is higher than that of the annual precipitation (12). The Drakensberg species, *H. malvifolia* (Fig. 7.19d) experiences rainfall in the summer rather than the winter, and differs from *H. cedarbergensis* in having a peak for precipitation in the warmest quarter (18) and no peak for precipitation in the coldest quarter, and also in having a low peak for temperature seasonality (4), despite the fact that both are montane species. The summer rainfall species from the Groot Karoo (Fig. 7.19e and Fig. 7.19f) have similar profiles to *H. malvifolia*.

### 7.3.2.2 The subject. *Tomentosae*

The subject. *Tomentosae* is most typically represented by the profiles shown in Fig. 7.20. The first four species shown all have similar profiles, all typical for sect. *Mahernia*, with the largest peak for annual precipitation (12), followed by roughly equal peaks at an intermediate height for precipitation in the wettest quarter (16) and in the warmest quarter (18) and for temperature seasonality (4). It is interesting to note that of these species, *H. stellulata* (Fig. 7.20d) extends to Namibia while *H. rautanenii* (Fig. 7.20c), an endemic from Namibia is distinguished by having a minor peak for precipitation seasonality (15). The latter also has a relatively low contribution of warmest quarter precipitation (factor 18) compared with the wettest precipitation quarter (factor 16). *Hermannia veronicifolia* (Fig. 7.20e) has a narrow profile typical of the southern summer rainfall area. It is similar to the typical summer rainfall profile, but with an elevated relative precipitation in the driest quarter (factor 17) and the coldest quarter (factor 19). *H. saccifera* (Fig. 7.20f) has the same profile, but with substantially more variation especially in the last four factors demonstrative of its greater east-west distribution. For the latter two species, the annual precipitation peak (12) is more pronounced.



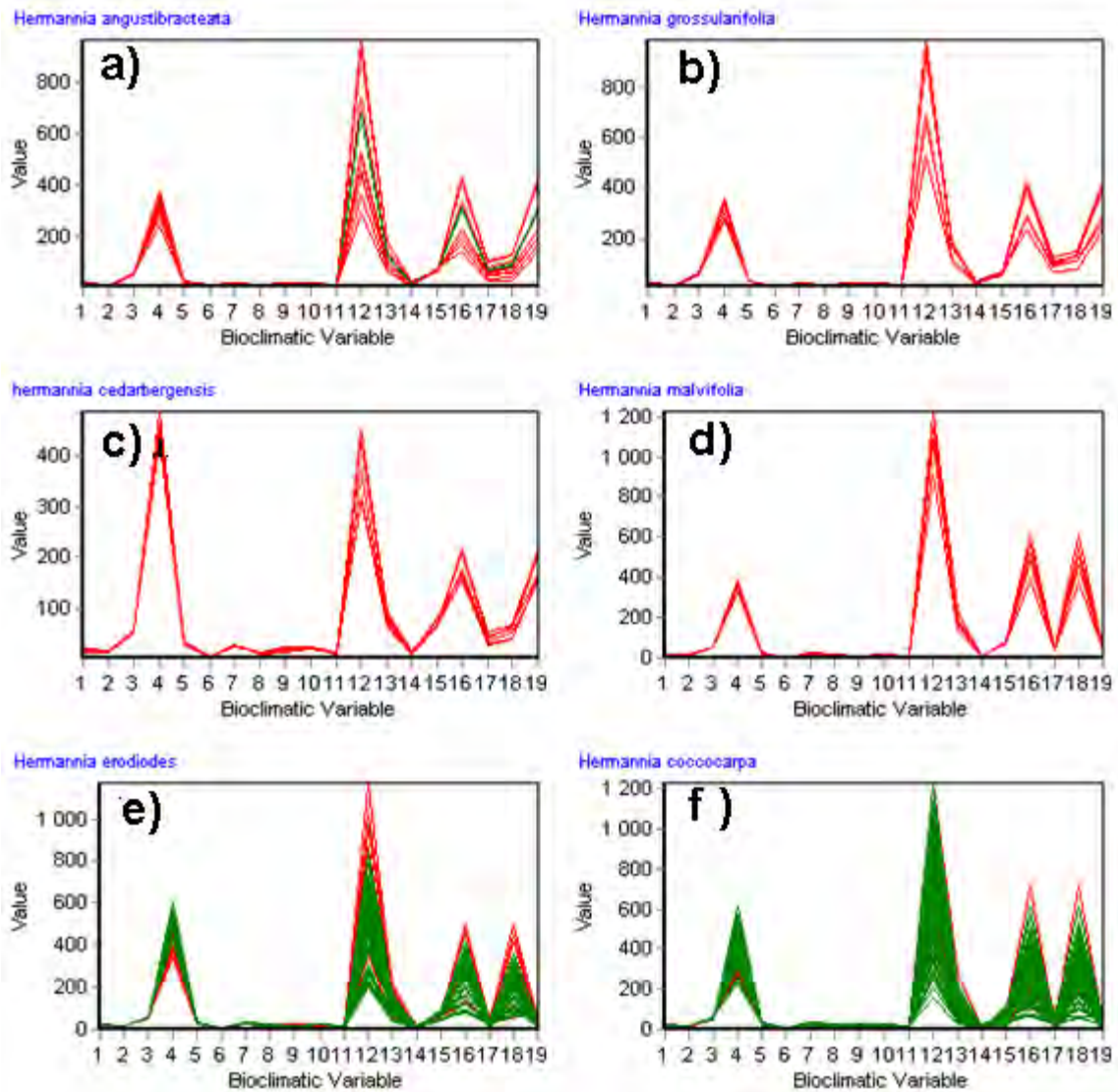


Fig. 7.19 Contrasting profiles of species from the sect. *Mahernia*: Two SW Cape lowlands species: a) *H. angustibracteata*, and b) *H. grossularifolia*. Two montane species: c) *H. cedarbergensis* from the Western Cape, and d) *H. malvifolia* from the Drakensberg. Two widespread, primarily Groot Karoo species: e) *H. erodioides*, and f) *H. coccocarpa*. The numbers on the X-axis of all graphs refer to Worldclim bioclimatic variable numbers: 4 is temperature seasonality, 12 is annual precipitation (ppt), 16 is ppt of wettest quarter, 18 is ppt of warmest quarter, 19 is ppt of coldest quarter, and the remaining values are given in Table 7.1 of the Methods.

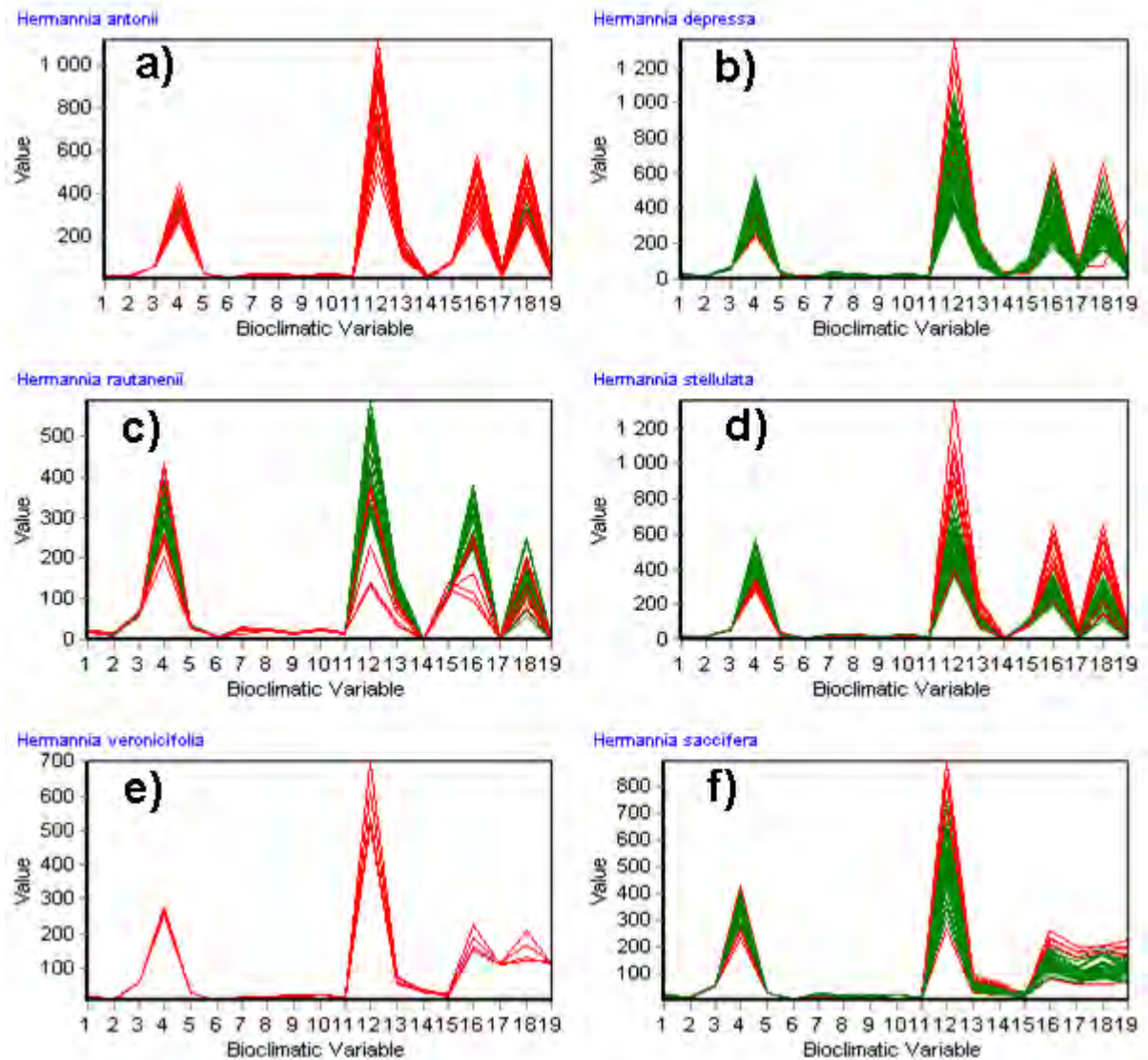


Fig. 7.20 Profile of summer rainfall species from the subsect. *Tomentosae*: a) A typical species *H. antonii* and b) a widespread species *H. depressa*. Profile of two species extending to Namibia: c) *H. rautanenii* and d) *H. stellulata*. Profile of two southern species: e) *H. veronicifolia* from the Eastern Cape and f) *H. saccifera* which extends to the western parts of the Southern Cape. The numbers on the X-axis of all graphs refer to Worldclim bioclimatic variable numbers: 4 is temperature seasonality, 12 is annual precipitation (ppt), 16 is ppt of wettest quarter, 18 is ppt of warmest quarter, 19 is ppt of coldest quarter, and the remaining values are given in Table 7.1 of the Methods.

### 7.3.2.3 The subsect. *Acicarpus*

The subsect. *Acicarpus* is represented by typical profiles as shown in Fig. 7.21a-b. There is generally an full range of values (lacking a ‘cavity’ for precipitation factors, and a very high temperature seasonality (factor 4), frequently higher than factor 12, as well as a conspicuous peak for precipitation seasonality (factor 15). The southern species *H. gariepina* and *H. trifurca* that extend into South Africa (Fig. 7.21c-d) have somewhat different profiles from each other, as they are in different biomes, Nama-Karoo vs. Succulent Karoo / Coastal thicket respectively. The former strikingly has a greater peak height for precipitation seasonality (factor 15) than factors 16 and 18. *Hermannia trifurca* has an unusually prominent peak for precipitation in the coldest quarter (factor 19). The summer rainfall species of this clade have profiles like that of the subsect. *Tomentosae*: a relatively low temperature seasonality peak, a very high annual precipitation peak, and generally approximately equal peaks in the wettest and warmest quarters (factor 16 and 18).

### 7.3.2.4 The sect. *Hermannia*

The sect. *Hermannia*, shown in Fig. 7.22a-f, is considered a CFR clade as it has its centre of diversity and radiation in the CFR. Typical species experience moderate amounts of winter-rainfall precipitation, which relates to factor 19 (precipitation in the coldest quarter). This is evident in all the species presented in Fig. 7.22 with the exception of *H. erecta* and *H. comosa* which have peaks for precipitation in the warmest quarter (18) and not for precipitation in the coldest quarter (19). The northern species, *H. comosa* from the Nama Karoo and *H. amoena* from the succulent Karoo (shown in Fig. 7.22c and Fig. 7.22d respectively), have the highest temperature seasonality peaks (4) relative to their annual precipitation peaks (12). In the case of *H. amoena*, the peak height of temperature seasonality (4) is exceptionally pronounced, being three times that of annual precipitation (12). The southern Cape species *H. hyssopifolia* and *H. flammea* (Fig. 7.22e-f) both have a moderately low temperature seasonality peak (4), a relatively high annual rainfall peak (12), and irregular precipitation peaks (16, 18, 19) reflecting distributions that cover a wide variety of habitats.

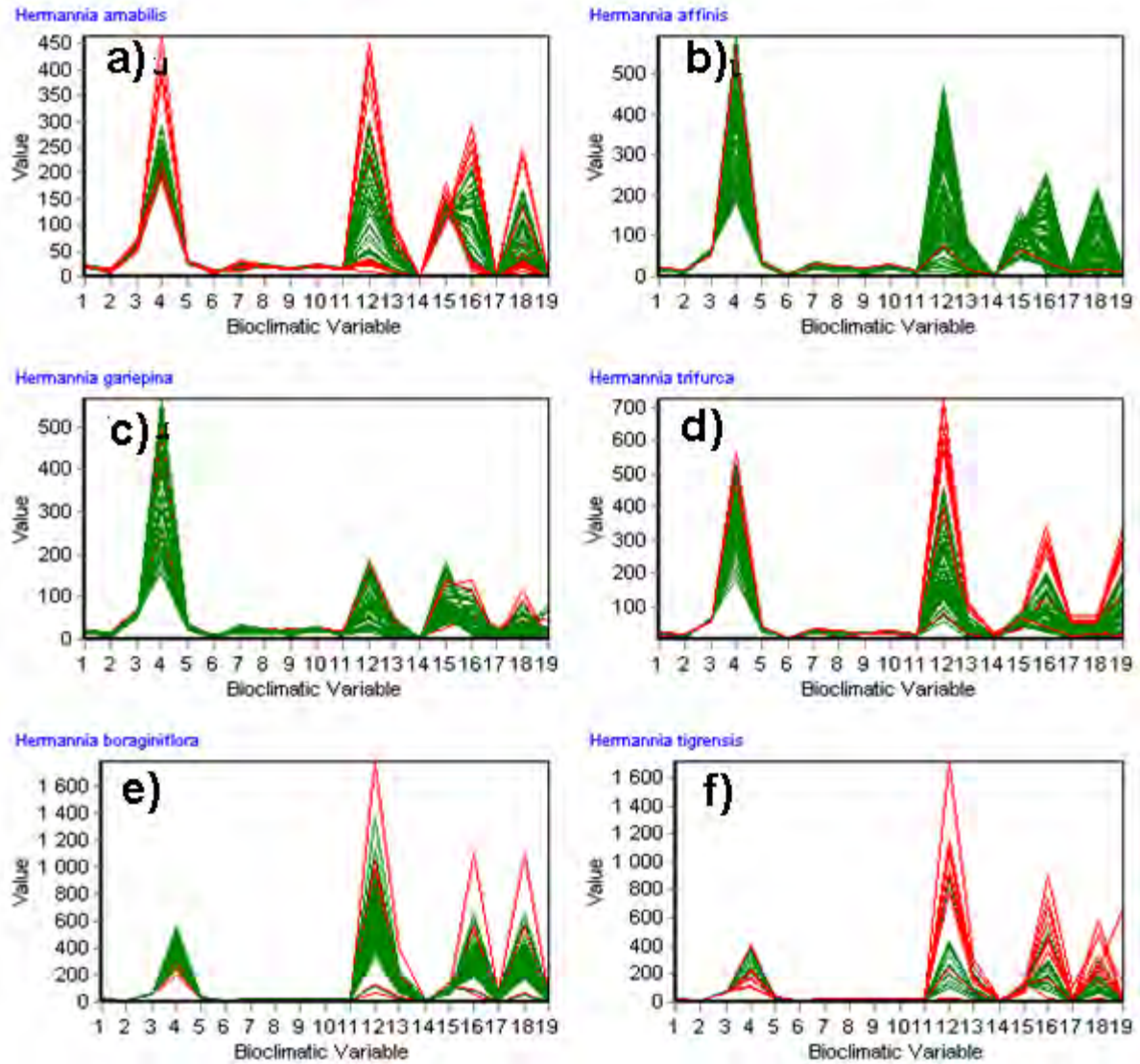


Fig. 7.21 Members of subsect. *Acicarpus*: a) *H. amabilis*, b) *H. affinis*, c) *H. gariepina* (similar to *H. engleri*, *H. fruticulosa* and *H. squarrosa* – not shown), d) *H. trifurca*, e) *H. boraginiflora* (similar to *H. micropetala* – not shown) and f) *H. tigrensis*. The numbers on the X-axis of all graphs refer to Worldclim bioclimatic variable numbers: 4 is temperature seasonality, 12 is annual precipitation (ppt), 15 is ppt seasonality, 16 is ppt of wettest quarter, 18 is ppt of warmest quarter, 19 is ppt of coldest quarter, and the remaining values are given in Table 7.1 of the Methods.



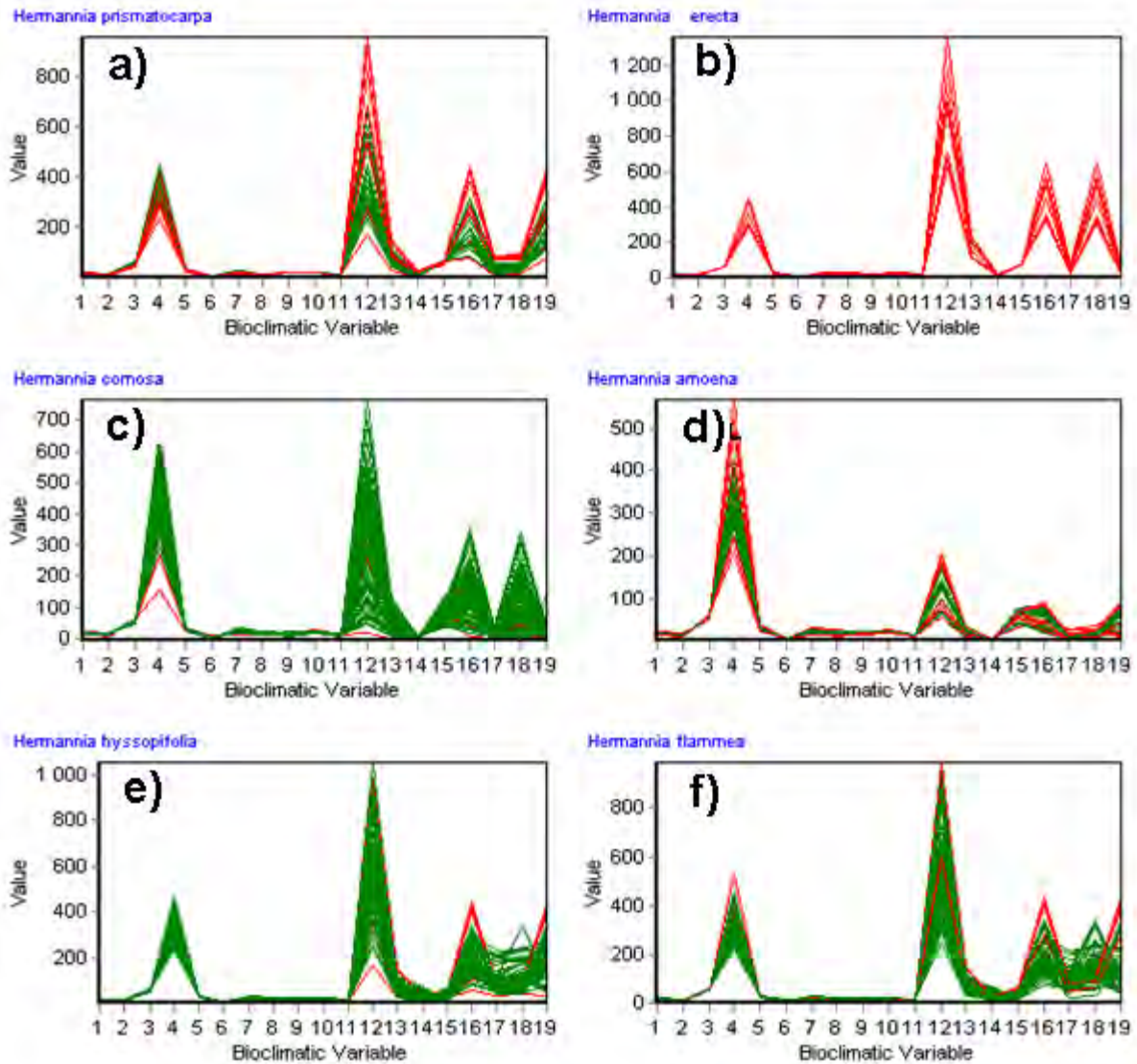


Fig. 7.22 Members of the sect. *Hermannia*: a) *H. prismatocarpa* from SW Cape, b) *H. erecta* from the extreme north-east of the extent of sect. *Hermannia*, with a typical summer rainfall profile, c) *H. comosa*, a Northern species from the Nama Karoo (similar profile to *H. bryoniifolia*, *H. bolusii*, *H. abrotanoides* - data not shown), and d) a typical Namaqualand species, *H. amoena* (similar profile to *H. macra*, *H. paucifolia*, *H. pfeilii* - data not shown) from the Succulent Karoo biome. Species of sect. *Hermannia* with a southern distribution: e) *H. hyssopifolia* (similar profile to *H. holosericea*), and f) *H. flammea* of the red-flowered *Flammea* group. The numbers on the X-axis of all graphs refer to Worldclim bioclimatic variable numbers: 4 is temperature seasonality, 12 is annual precipitation (ppt), 16 is ppt of wettest quarter, 18 is ppt of warmest quarter, 19 is ppt of coldest quarter, and the remaining values are given in Table 7.1 of the Methods.

### 7.3.3 Climatic predictions

The Bioclim model was chosen to provide an overall predicted current and future distribution of *Hermannia* based on climatic models derived from the Worldclim dataset. This model has been found to perform adequately well with outcomes only marginally worse than more complex algorithms (Jimenez-Valverde, Lobo et al. 2008). Fig. 7.23a provides a current estimate of the distribution of *Hermannia*, compared with the future year-2050 CCM3 model (Fig. 7.23b). There is a general reduction in all regions except for the Klein-Karoo and eastern Namaqualand that increase in the probability of occurrence from high, to very high probability with portions of excellent suitability. The majority of the distributional probability is high to very high in Namibia, Botswana and Zimbabwe, and this is reduced to low probability over most of this region in the CCM3 scenario. A drastic increase in unsuitable areas appears in the Mozambique region in the CCM3 scenario.

Examining the species individually shows a far more drastic reduction in distribution under the CCM3 scenario. *Hermannia coccocarpa*, an inland widespread species across the Groot Karoo (Fig. 7.24a) has the potential distribution reduced southwards by about a third, with the higher probability distributions decreased by about two-thirds (Fig. 7.24b). A similar effect is seen for the arid-adapted species *H. grandiflora* (Fig. 7.25a and Fig. 7.25b). The reduction of coastal species is even more drastic, with the more northerly species, *H. pfeilii* losing nearly its entire distribution (Fig. 7.26a and Fig. 7.26b). *Hermannia prismatocarpa* fares marginally better in the south, with the distribution shrinking, fragmenting and losing the region of ‘\_excellent’ potential for occurrence (Fig. 7.26c and Fig. 7.26d).

In Fig. 7.27 shows the current predicted distribution for the arid portion of *Hermannia*, namely subsect. *Acicarpus* without its more mesic eastern species. This distribution is centred around Namibia and Botswana, while under a CCM3 scenario the potential range is shrunk by almost half, with much of Botswana, Zimbabwe and the north-eastern portions of Namibia, predicted to become uninhabitable. The upper potential for distribution is reduced to ‘\_low’ for much of Namibia, but interestingly increases in area in much of the Cape.

As shown by Fig. 7.23a, according the model there is climatic potential for *Hermannia* to occur within Madagascar, and across much of the Zambeziaca region. Simulating the effect of a five degree lower temperature using a Bioclim model considerably shifts the potential distribution of *H. tigrensis* (Fig. 7.29a) across new areas in eastern Africa (Fig. 7.29b). This simulation will be discussed further below.

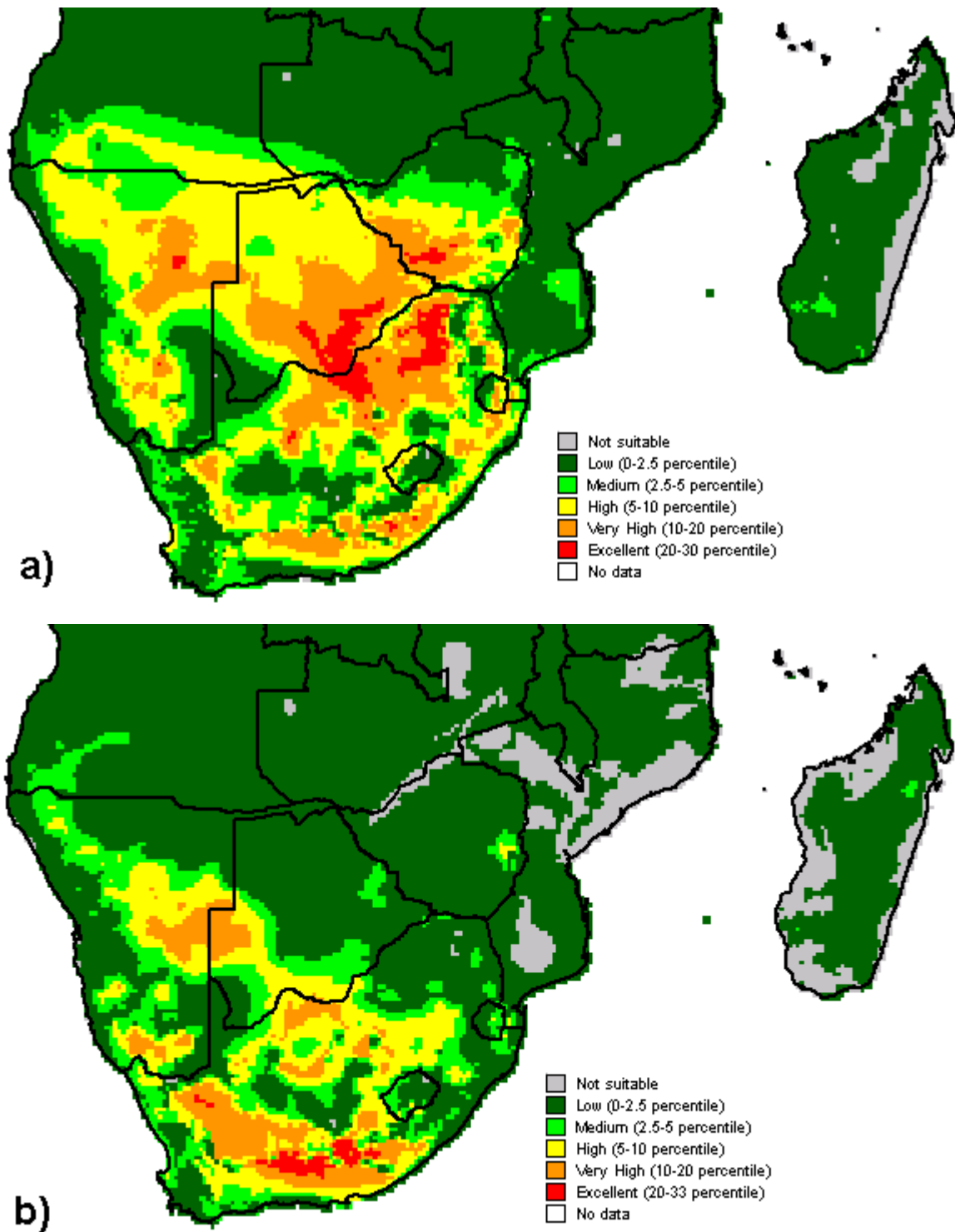


Fig. 7.23 Bioclim for *Hermannia* model based on a) Worldmap data, and b) CCM3.



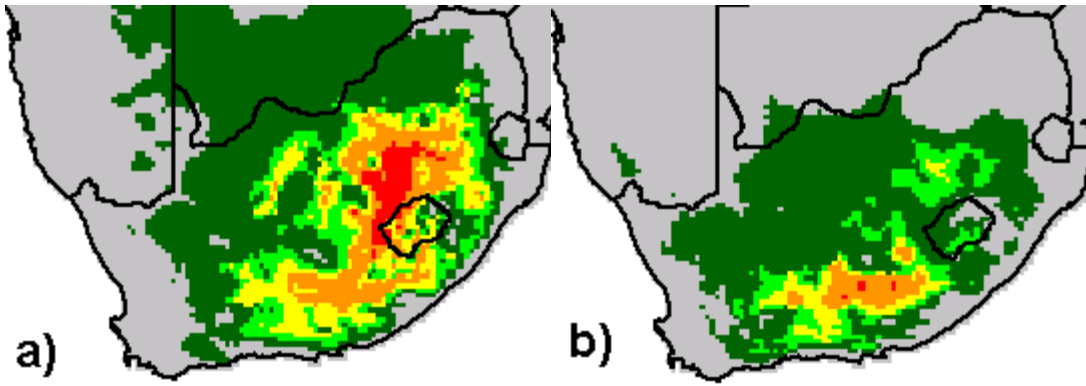


Fig. 7.24 a) Bioclim model for *H. coccocarpa*; contrasted with b) the CCM3 predicted area.

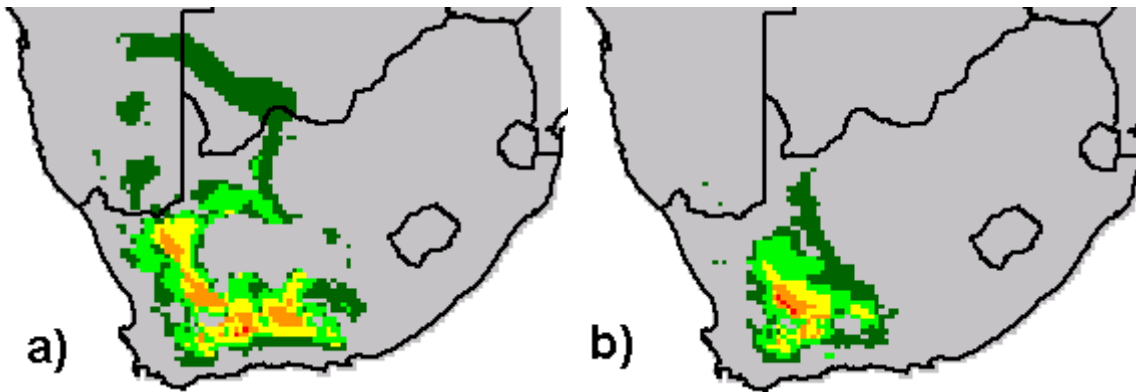


Fig. 7.25 a) Bioclim model for *H. grandiflora*; contrasted with b) the CCM3 model.

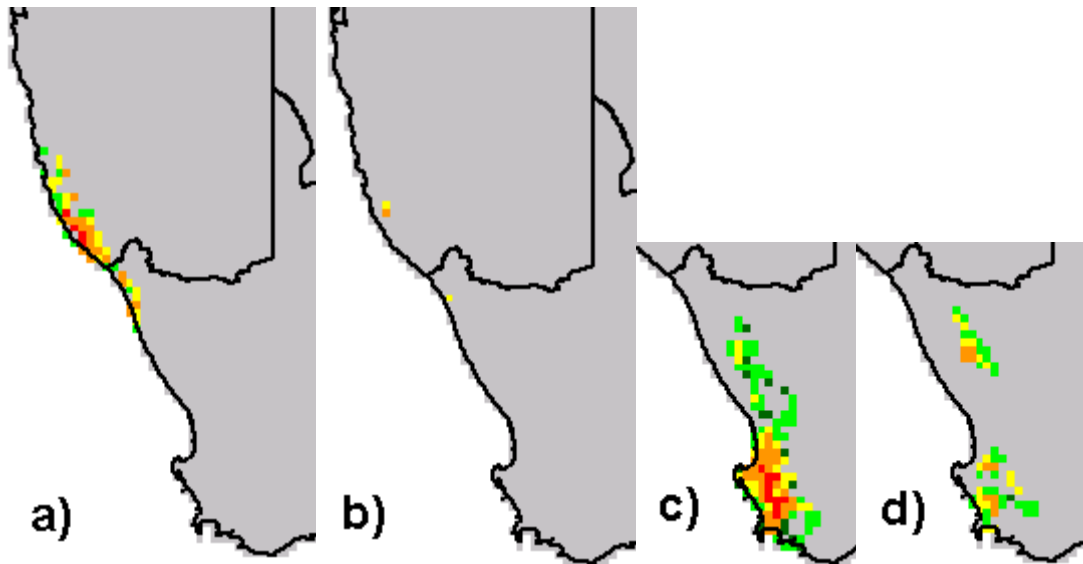


Fig. 7.26 West Coast species: a) & b) *H. pfeilii* and c) & d) *H. prismatocarpa* under a) & c) current predictive models and b) & d) CCM3 models.

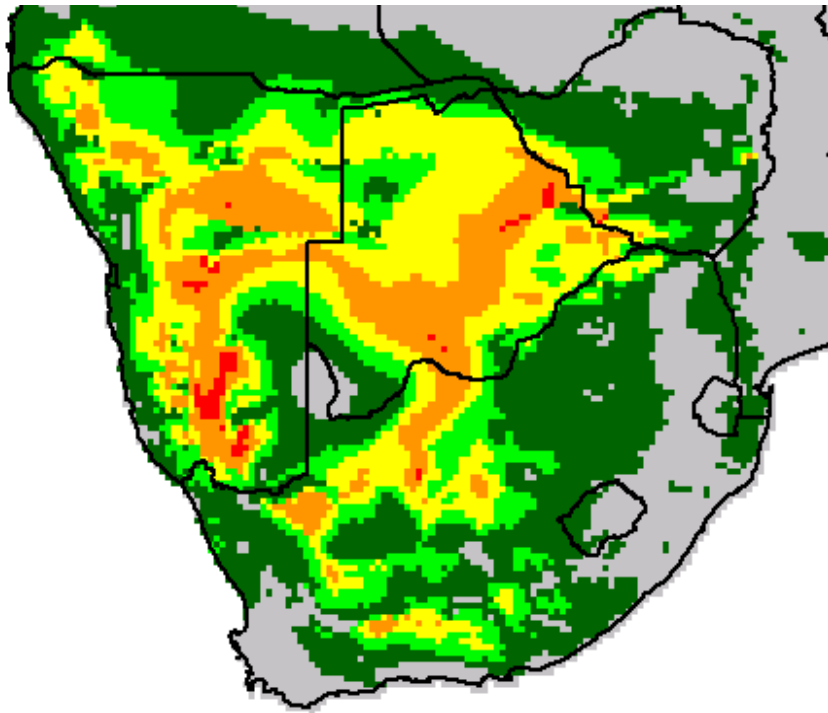


Fig. 7.27 Current predicted area for subject. *Acicarpus* excluding the eastern species.

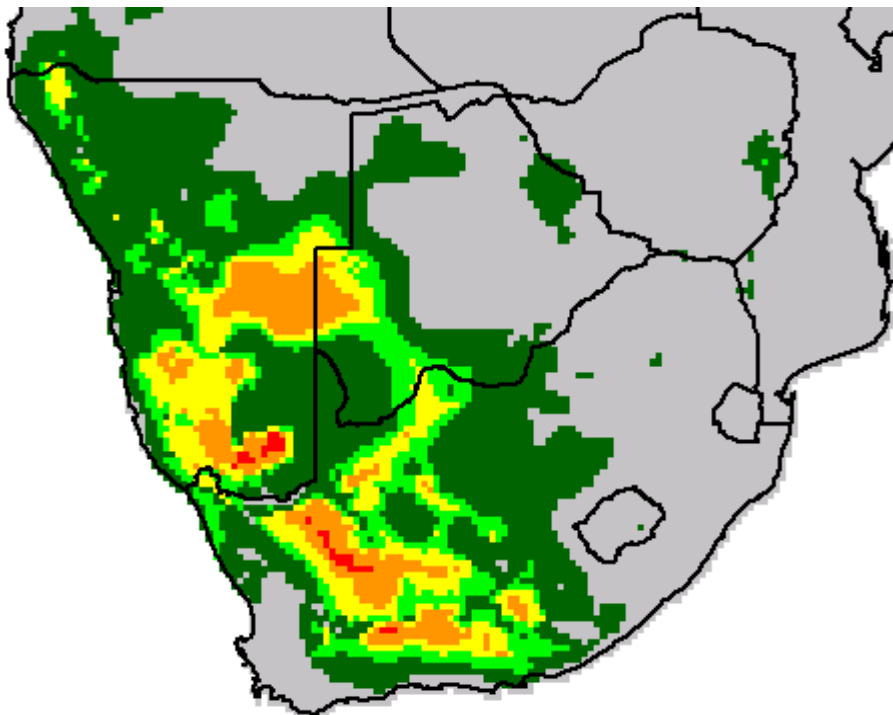


Fig. 7.28 Future predicted area for subject. *Acicarpus* CCM3 excluding the eastern species.

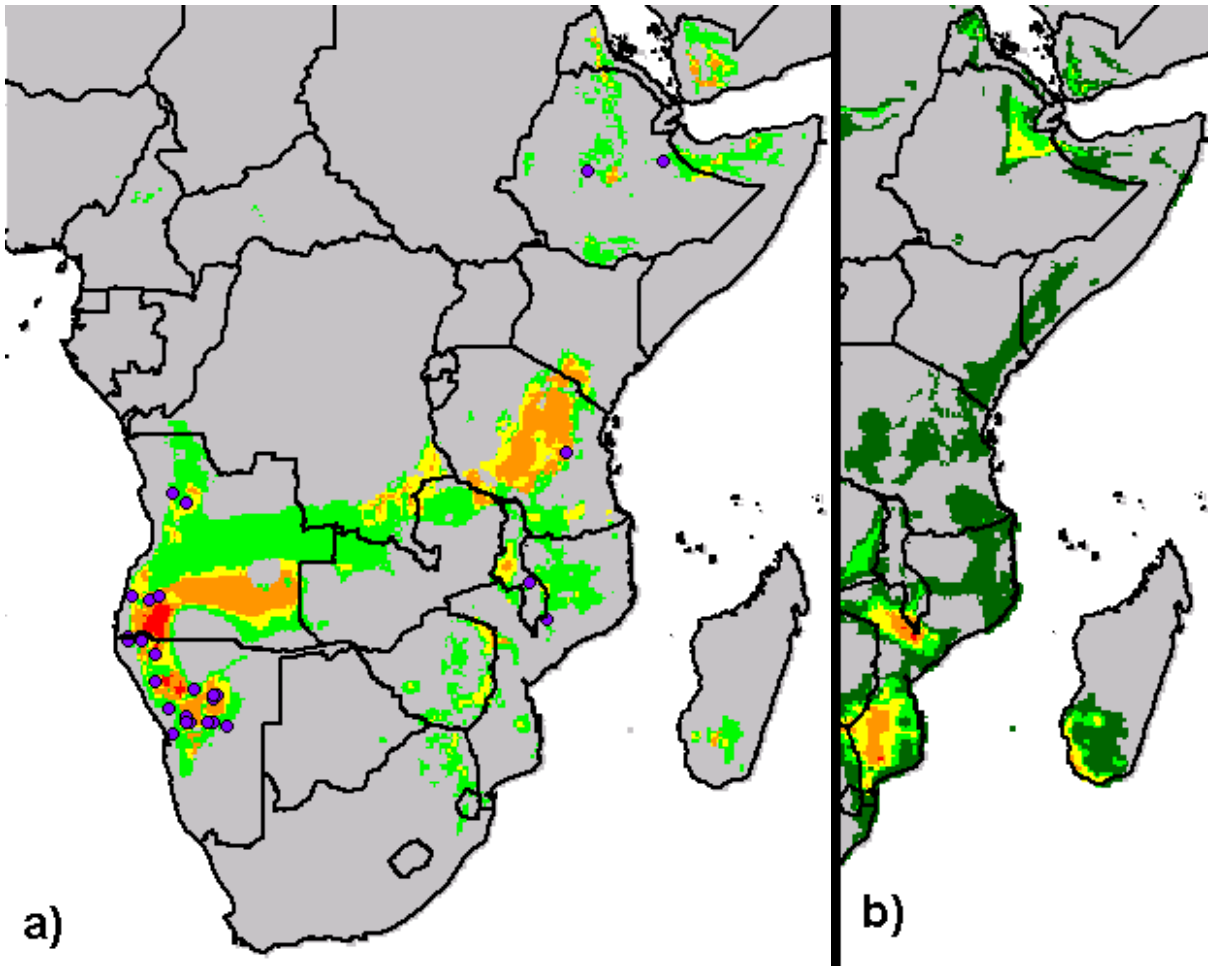


Fig. 7.29 a) Current potential distribution of *H. tigrensis*; with b) the effect of a 5°C lower temperature overall.

## 7.4 Discussion

### 7.4.1 Phytogeography and cluster analysis

In evaluating *Hermannia* as a genus suitable for defining phytochoria, it is important to assess the degree of separation between areas defined by clusters or groups of associated clusters. It is also important to assess the relationship between these areas and known regions of defined vegetation.

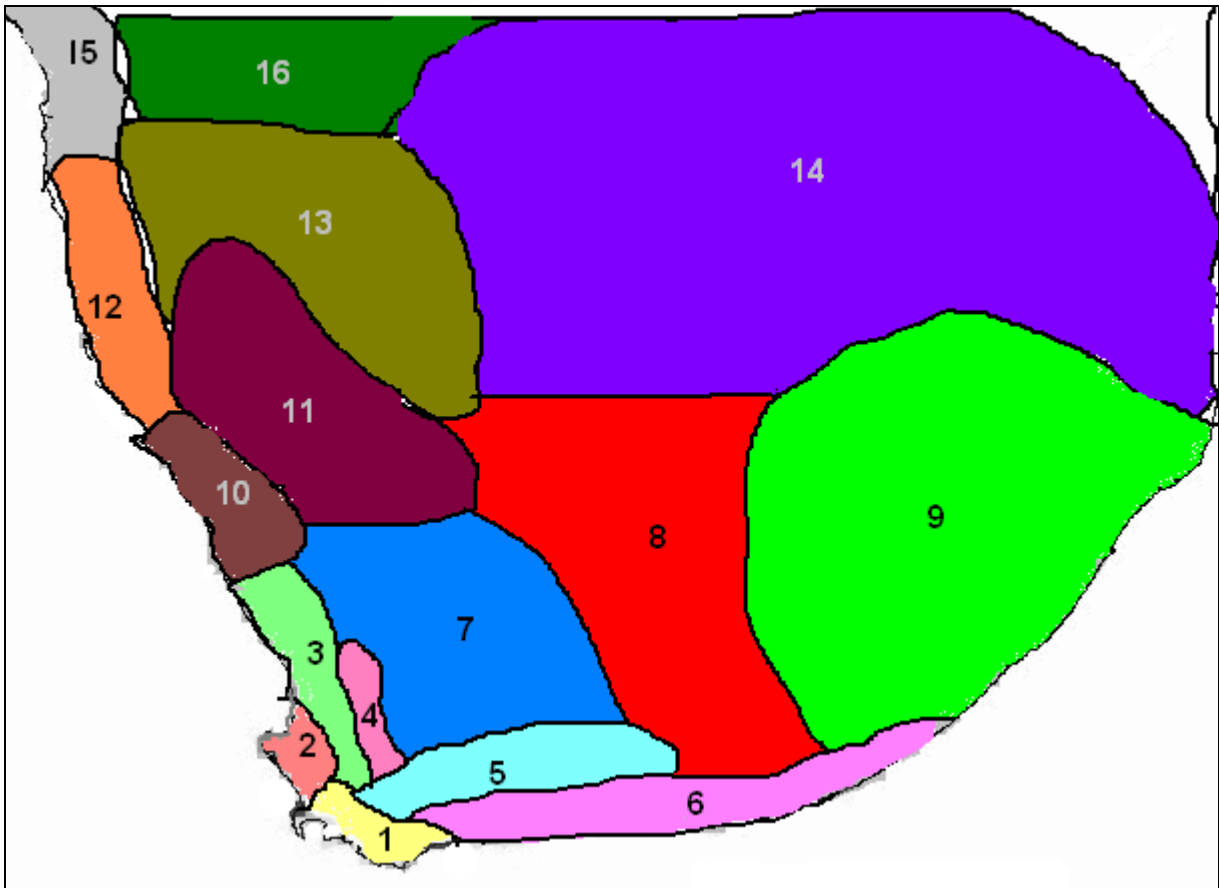
#### 7.4.1.1 Suitability of the data set for cluster analysis

As noted in the results, the cluster analysis, at appropriate choices of cutoff, produced maps for which most of the region assessed (southern Africa) could be identified as consisting of a coherent cluster or set of clusters. Furthermore, analyses at lower cutoff produced finer information, showing nuanced variation within phytochoria, while analyses at higher cutoff produced broader products and were in some cases more applicable for testing hypotheses such as the Greater CFR (discussed further below). It is significant that clearly defined regions could be identified, since a phytochorial study needs in the first instance to be based on strong data before the phytochoria produced can be compared with known biomes.

The overall patterns provided by cluster analysis show that species and hence clusters seem to at least partially reflect particular biomes. The cutoff level for the dataset needs to be fine-tuned to the scale of the question. At broad levels approaching 0.5 (Fig. 7.8), around nine clusters are resolved within Southern Africa with the major biomes being resolved. A cutoff of 0.47 allows for a better resolution of regional vegetation, as well as allowing for links to floristically similar areas. Experience shows that weighting the maps improves the coherence of clusters and hence regions, thus the majority of maps were weighted. The different algorithms (Jaccard and Lance) provided similar outcomes, with the Dice algorithm portraying an almost identical output to Lance, at least for this dataset. The results from the algorithms are largely congruent, and thus only the output of the Lance algorithm has been shown to display cluster maps of subg. *Mahernia* and subsect. *Acicarpus*. Most species of subg. *Mahernia* have a smaller distribution than subg. *Hermannia* species occurring in the same area. The similar boundaries and patterns of

phytochoria seen for the subg. *Mahernia* and that of the entire genus shows that the regions obtained through this cluster analysis are fairly robust and that subg. *Mahernia* is a good proxy for the genus. A difficulty in interpretation is that the northern parts of Southern Africa appear to have far more phytochoria than the more diverse regions of South Africa. This is likely to be a product of low species numbers in the region forming several distinct terminals that are little united by shared species.

The general phytogeographic regions obtained are depicted in the schematic Fig. 7.30, below, as an aid to synthesizing the results. This is an extremely coarse estimate, especially over Namibia. Significantly more sampling would be needed to obtain a more accurate depiction.



**Fig. 7.30** A schematic map highlighting the general phytogeographic areas that have emerged from the phytogeographic analysis. The regions roughly correspond to 1) SSW Coast; 2) SW Coast; 3) W Coast; 4) Cedarberg and Roggeveld; 5) Klein Karoo; 6) S Coast; 7) W Groot Karoo; 8) OFS; 9) E summer rainfall; 10) N Namaqualand; 11) S Namibia; 12) SW Coastal Namibia; 13) Central Namibia; 14) N. summer rainfall (Botswana, Zimbabwe and Mozambique); 15) N Coastal Namibia; 16) N Namibia.

#### **7.4.1.2 Relating clusters to the South African biomes**

The cluster analysis, at a 1-degree scale, produced maps showing considerable similarity to the Vegmap biomes (Mucina and Rutherford 2006). In particular, most of the major biomes occurring in South Africa can be matched, though not identically, in relative positions. These include the Fynbos, Nama Karoo and Albany Thicket (all of which quite closely match) as well as the Succulent Karoo, Grassland and Savanna.

The boundaries of these areas of homogeneity produced by the cluster analysis vary based on the cutoff value and the algorithm used. At a lower cutoff (see for instance Fig. 7.10), the Fynbos and Succulent Karoo regions can be identified, though these are found as distinct West Coast and South Coast regions with a boundary at the Cape Peninsula, which is different from the boundary occurring halfway up the West Coast in the Vegmap. The Grassland region is very well matched between the cluster analysis and the Vegmap, with Savanna split into two cluster types and absent from the East Coast (as is the Indian Ocean Coastal Belt). The Albany Thicket is also absent at this level of cutoff and resolution.

In the cluster maps, it is possible not only to distinguish regions but also to measure how related one region is to another based on the dendrograms produced. In doing so, one finds that the grassland and bushveld/savanna are typically strongly separated from the remaining arid or winter-rainfall flora. The bushveld/savanna is usually distinguished from the Grassland. The fynbos region is generally closely allied to the Succulent Karoo and Southern Cape flora. This lends credence to the concept of a Greater CFR (Van Wyk and Smith 2001; Born, Linder et al. 2007), that includes the SW portions of the Succulent Karoo. The Klein Karoo clusters with the Succulent Karoo and the South Coast fynbos, but not the West Coast fynbos. The Klein Karoo is not entirely contiguous at a QDS scale, but comprises elements from Karoo, fynbos and the South Coast. Support for the concept of a Greater CFR also comes from the fact that a region is identified bordering both the CFR and partially overlapping with it, and this region resolves as distinct from the Groot Karoo at 1-degree resolution. The evidence for this is much weaker at

QDS level but this may be due to the fragmentation that occurs as one analyses with lower cutoff.

Further relationships obtained from the dendrograms include the Southern Cape, most closely related to the Central Karoo flora (Fig. 7.10), the latter extending in a band to the southern portions of Namibia (see cluster 26, Fig. 7.13). The Albany Thicket region is well-represented in the Grassland region (Fig. 7.7). This explains the extension into the Southern Cape of *H. saccifera*: the only member of the subsect. *Tomentosae*. Western Namibia and Northern Namibia, are related, but in all analyses come out separately. The Northern Namibian flora tends to be distributed across to Zimbabwe, and into the Mopani Bioregion in the north-east of South Africa.

Analysis of subg. *Mahernia* produces many of the same phytochoria and patterns as seen for *Hermannia*. Thus subg. *Mahernia* may adequately represent the broad patterns of the genus as a whole. This widespread distribution is indicative of long-term diversification, coupled with the species spreading to occupy a narrow climatic envelope. Cluster 23 in Fig. 7.14 and Fig. 7.15 occupies a large range of climatic zones. This cluster includes *H. coccocarpa* which is a species complex that has diversified across a number of habitats and regions. Including species complexes serves to weaken the distinctness of the clusters, and form artificially broad links between disparate habitats and regions containing those complexes. Thus much of our resolution in this area may have been lost through the inclusion of the *H. Coccocarpa* species complex.

In most analyses there are as many as 9 unresolved clusters at the base. They are found across Southern Africa, typically in or close to known areas of endemism. Areas in which they fall include Khamieskroon, Niewoudtville, Kimberley, and NW Namibia and Cape Agulhas. These may represent areas with many endemics and few shared species such that the algorithm does not link them to any other flora. Remaining points in the Eastern Cape and Botswana may be artefacts of the algorithm as they do not appear to be sites of special significance or endemism.

The eastern Namibia flora shows strong association with the Northern Province of South Africa, Botswana and in the eastern extent into Zimbabwe. This corresponds with a mainly

bushveld biome. These links provide likely routes for dispersal of the subsect. *Acicarpus* (Fig. 7.18a), from Namibia in the west to Mozambique in the east. This directionality is supported by both a higher species number in Namibia, and the multiple basal species occurring in Namibia.

#### 7.4.2 Climate Analysis

The climate analysis profiles for the genus *Hermannia* reveals clear peaks for four of the climatic variables (4, 12, 16 and 18 – corresponding to temperature seasonality, annual precipitation, precipitation in the wettest quarter and precipitation in the warmest quarter) and a further three minor peaks (13, 15 and 19 – corresponding to precipitation in the wettest month, precipitation seasonality and precipitation in the coldest quarter). This general pattern is found, with variations, in most of the analyses – including those for various clades and for most of the individual species considered.

The variations found between clades, and within a clade, are in the relative heights of the peaks (the climatic ‘signature’). These differences are interpreted as indicating different levels to which climatic variables determine distribution within *Hermannia*. For instance, the variable 19 is barely present in the profile of subsect. *Tomentosae* while it is prominent in subsect. *Mahernia*, suggesting that precipitation in the coldest quarter is an important climatic element determining the distribution of the latter but not of the former. Similarly, for the group ‘*Marehnia*’ the peak for temperature seasonality is very small relative to the others, suggesting that in this group, temperature seasonality does not strongly determine distribution.

When studying the profiles for individual species, we find that the minor peaks – for climatic variables 13, 15 and 19 – are present in the profiles of some species and absent in others. This gives a better understanding of the overall profiles for clades, that they are not uniform across the clade but rather come from subtle variations amongst the species that make up that clade. For instance, the species of sect. *Mahernia* studied all have the same basic profile but they differ in that each one has a peak either for precipitation in the warmest quarter (18) or precipitation in the coldest quarter (19), but not both. This separation cannot be discerned from the profile for sect. *Mahernia* as a whole.



Further interesting observations are that species displaying a prominent peak 19 are generally associated with winter-rainfall, and that peak 4 is found to be dominant only in species of sect. *Hermannia* and subsect. *Acicarpus*. Furthermore, the peak 15 for precipitation seasonality occurs most prominently in species of subsect. *Acicarpus*. This is particularly striking in the case of *H. amabilis*; see Fig. 7.21.

In conclusion, we find that similar climatic signatures are associated with clades within *Hermannia* and that variations from the basic signature for a particular clade are sometimes uniform across that clade and sometimes accounted for by variations of the signature between species within the clade. The existence of a basic signature is significant as it can be understood to reflect the degree of versatility of the genus in adapting to different climatic conditions. In particular, the general lack of association with temperature-related variables (except for variable 4) and the high degree of association with precipitation-related variables (most notably the greatest peak 12 for annual precipitation) suggest that clades within genus *Hermannia* are generally more constrained by precipitation conditions and less constrained by temperature variability, with subsect. *Acicarpus* a notable exception to this rule. Finally, the existence of a climatic signature makes *Hermannia* a suitable genus for making climatic predictions, both current and future.

### 7.4.3 Climatic predictions

The current climatic predictions shown (Fig. 7.23a) show a geographical envelope generally appropriate for the known distribution *Hermannia*, encompassing Southern Africa. However, CFR, one of the centres of diversity, is assigned low suitability. Thus it appears that factors than climate play a dominant role in determining the presence of *Hermannia* in the CFR and are thus not taken into account in the model. It should be noted that the CFR is a primarily winter-rainfall area and it may be that the model is not able to accommodate this exceptional climatic profile within a predominantly summer rainfall regime.

The year 2050 predictions based on CCM3 data indicate a considerable reduction in suitability across much of the distribution range of *Hermannia* (Fig. 7.23b). Examining the

individual species shows the extent of the potential reduction in area, with western species such as *H. pfeilii* being the most radically reduced. In the case of *H. prismatocarpa* (Fig. 7.26c and Fig. 7.26d), the distribution is split into a region on the West Coast, and one in inland Namaqualand. This is a very similar pattern to the current actual distribution of *H. althaeifolia* in which a disjunction of over 150 kilometres is found between the Khamieskroon mountains and the West Coast populations. This serves to corroborate that the model may be correctly indicating this northern region as a refugium through time.

Examining the potential distribution of *H. tigrensis* that has a disjunction between western Southern Africa, east and north-east Africa, shows the existence of a potential corridor from west to east. Although only a first-attempt, modelling a reduction of 5°C does shift and change the eastern portions of the distribution, extending a potential corridor up the east coast into Somalia (Fig. 7.29b). This suggests that under favourable past conditions, *H. tigrensis* and other *Hermannia* species may have utilized a corridor similar to this. The dating of the annual species of *Hermannia* and *H. uhligii* (Fig. 3.7) suggests the arid corridor may have been open in a far earlier glacial cycle than that exploited by contemporary annual species (eg. *Heliophila*) that are widely distributed across Africa (Cowling, Proches et al. 2009).

It may be postulated that arid-adapted species may profit from the increased aridity predicted for South Africa by spreading in area. This was not found for individual arid species such as *H. grandiflora* (Fig. 7.25a and Fig. 7.25b) which also experiences a reduced potential future distribution. Indeed the subsect. *Acicarpus* (Fig. 7.27) appears even more drastically impacted by climate change than the genus as a whole, with much of the northern extent of the range becoming uninhabitable. However, both the genus as a whole, and the subsect. *Acicarpus* show increased suitability within portions of the Cape, particularly around the eastern portions of the Klein Karoo, and the south-western parts of the Groot Karoo. This implies that these regions could be important refugia for arid species, provided they can shift sufficiently through space and time. It is difficult to ascertain to what extent interspecific competition has led to the current extent of species, and even more uncertain how changes in these dynamics will affect future distributions. Success in growing *Hermannia* species under glasshouse conditions under uniform soils and a high moisture regime, suggest that soil may not be a limiting factor in itself, nor high

rainfall. Rather it is the combined effect of soil type with other factors, and likely high rainfall with competition that may limit the spread of *Hermannia*. Thus the possibility of *Hermannia* spreading under future conditions of relaxed interspecific competition due to increased aridity and temperature, are not ruled out by the diminishing distributions demonstrated by the Bioclim predictions.

The dispersal ecology of *Hermannia* is important to the survival of the species, and there are several causes of concern for future sustainability of species. If plants are passively dispersed as appears to be the case for much of the genus, they are not likely to keep up with the demands placed on them by rapid climate change. This situation is exacerbated by several species which are restricted to scarce geologies. If Janzen's (1984) "foliage as fruit" dispersal mechanism proves pertinent for *Hermannia* (as indicated by the attributes of general palatability and many species presenting their fruit above the foliage) then this may provide the necessary distance for a species to cover the distance needed to stay within its climatic envelope. Nonetheless, such dispersal would be further compounded by the large portion of land in South Africa covered by farming, and the associated fencing that limits movements of potential herbivores. In short, further research will be essential to determine dispersal processes in *Hermannia* and the outcomes of such research will enable more accurate predictions of the effect of climate change on *Hermannia* populations.

## 7.5 Conclusion

In the introduction to this chapter, a set of predictions were stated in Ackerly (2003) whereby it could be determined whether the pattern of species distribution is likely due to recent speciation or ancient dispersal. Ch. 4 reveals the strong geographic structuring of clades of *Hermannia*. In the current chapter, the environmental characteristics of these species and regions have been explored. The cluster analysis reveals distinct phytochoria corresponding to known regions of vegetation types. In addition, a strong association is found between the fynbos region and the Succulent Karoo. This result supports the concept of a Greater CFR (Van Wyk and Smith 2001; Born, Linder et al. 2007), that includes the SW portions of the Succulent Karoo.

The distinct climatic profiles demonstrate that the vast majority of species are climate specialists, with very few generalists. Thus each species is very much constrained by the climate. This is demonstrated by their strong response to climate modelling. Further evidence of this is that in Ch. 5 we can see that clades are largely structured by biome. It is suggested therefore that strong geographic lineage patterning is indicative of pre-adaptation to a broad environment. Subsequent recent adaptation has assisted in differentiating on a more local environment.

*Hermannia* is an ecologically and climatically diverse genus that has tremendous scope for potential experiments in future climate change and reconstructing past environments and corridors. It has a number of major clades that have dissimilar climatic characteristics, allowing for interesting potential contrasts between the evolution of these clades. These clades also originate in different regions, but also frequently overlap, such as in the CFR where sect. *Hermannia*, subg. *Mahernia* and subsect. *Acicarpus* occur. Species are particularly worthy of more intensive study and mapping, often being confined to small edaphic islands. This climatic assessment has therefore provided an interesting starting point for a study of the current and future potential distribution of *Hermannia*. Predicting species distributions may also be better undertaken using complex mapping methods that have been found to outperform simple envelope models, such as Maxent, GARP and MARS (Elith, Graham et al. 2006).

This study was also undertaken by utilizing primarily herbarium records that were georeferenced to a quarter degree scale, and their climatic envelope derived using a 10 minute Worldclim dataset. A new atlas of *Hermannia* could map localities to unprecedented accuracy of position and altitude using the Galileo global navigation satellite system that is set to be activated in 2014. Enhanced climate change outcomes would be possible through integrating this atlas with more accurate climatic models such as the 3 minute Worldclim dataset, and improved climate-change scenarios. An atlas would allow for presence and absence data to be modelled. Tying this atlas in with remote sensing and ground-truthed atlas of geology would also aid in our understanding of the potential for future climate change, and new insight into the speciation of an edaphically constrained group.

## 8. Future work

### 8.1 Molecular dating of *Hermannia*

The initial exercise in molecular dating has provided dates for radiations and diversifications of numerous clades. The date found of  $c\pm 60$  Mya for the divergence of *Hermannia* from *Waltheria* is significantly different from that of  $\pm 40$  Mya found by Verboom (2009), and this warrants further confirmation and investigation using more gene regions. Jan Saunders (pers. comm.) suggests that the selection of the form of *Waltheria indica* may influence this date. Saunders adds that her morphological analysis suggests that *W. virgata* from Australia appears to be basal to the Hermanniae, with the remaining *Waltheria* species being derived and monophyletic. The inclusion of *W. virgata* in the analysis would therefore likely yield an even older date. The Namibian clade: sect. *Acicarpus*, has a diversification age of  $\pm 27$  Mya that coincides with the start of the Oligocene. This period is characterised by the expansion of arid, alpine and grassland biomes (Crisp, Arroyo et al. 2009). The subsect. *Cristatae* initiated  $\pm 17$  Mya, with the split between *H. cristata* (South Africa), and *H. uhligii* (Kenya) dated to  $\pm 14$  Mya. The “Marehnia” clade provides additional evidence for the arid corridor being between  $\pm 17$  Mya (Galley, Bytebier et al. 2007) and  $\pm 8$  Mya (Schrire, Lavin et al. 2003). There are currently few studies that examine the age of this important link between northern and southern Africa, with the annual species of *Hermannia* dated to  $\pm 10$  Mya, close to the  $\pm 11$  Mya found with the north African species of *Indigofera* (Schrire, Lavin et al. 2003).

The divergence of the summer rainfall species belonging exclusively to the subsect. *Tomentosae* initiated  $\pm 6.6$  Mya, an age that should be compared with other genera to determine if there is a common period associated with Cape Clades extending to the summer rainfall regions. The separation of the Drakensberg endemics and the Australian species from the remainder of the Cape Clade has been dated to  $\pm 4.5$  Mya and  $\pm 3.8$  Mya respectively. This date should also be compared with other endemic disjunct Cape relics from other genera. All clades except for sect. *Acicarpus* radiated primarily in the last  $\pm 6.6$  Mya, with a strong bias towards more recent radiations. This ties in well with analyses of other clades (eg. Verboom, Archibald et al. 2009) providing an independent confirmation of recent radiations not just in the Cape, but in the summer rainfall regions as well.

## 8.2 Future refined phylogenies

As phylogenies form the basis of most systematic studies, a resolved phylogeny creates a platform for many avenues of research, such as the role of pollination in speciation. Future phylogenies should aim to find variable primers from both chloroplast and nuclear regions. The addition of more species will also serve to capture more variation within the genus.

De Winter cited hybridisation as the explanation for specimens that did not fit neatly into his species concepts. He claimed that these dubious entities frequently possess “intermediate characters” between affirmed species, leading him to assign them as species ‘of hybrid origin’. Hybrids may contribute adaptive variation to existing species and constitute a suitable source for new recombinant species (Barton 2001). Hybridization has generally been considered of widespread importance for adaptation and evolution (Arnold 1996). Six mechanisms were listed by Grant (1981) that lead to the fixation of hybrids. With the inclusion of a chloroplast dataset, a future study could evaluate the role of hybridization leading to speciation, particularly in the light of Grant’s proposed mechanisms.

Phylogeography has traditionally been the preserve of animal systematists due to rapidly evolving mitochondrial DNA. With more rapidly-evolving gene regions having been found for plants, progress is being made into understanding long-term population expansion and contraction within the Cape flora (eg. Bergh, Hedderson et al. 2007). Phylogeographic approaches that typically utilize multiple samples of a species, have helped elucidate the processes behind evolution and speciation (Avice 1998; Hewitt 2001). Due to the considerable number of species within *Hermannia*; I have prioritized uncovering the infrageneric patterns of the genus. Primarily, priority has been given to sampling the range of variation of *Hermannia*, and resolving major clades within the genus that reflect the products of evolution.

Several complexes exist within *Hermannia* which hold promise for further phylogeographic study. Perhaps the most widespread and thus useful complex would be that of *H. cuneifolia* that is widespread in the Western Cape in both arid and mesic areas. *H. modesta* and *H. kirkii* are two

closely related species that are spread from South Africa through to Saudi Arabia and Kenya respectively. A phylogeographic analysis of these species may allow for reconstruction of timing and directionality of the arid corridor through eastern Africa.

### 8.3 Diversity

The biogeography of this widely distributed genus has been facilitated by the data capture of some 16000 herbarium specimens from seven herbaria, and subsequent georeferencing to an accuracy of QDS. This effort has corrected many of the errors and omissions from previous efforts on PRECIS, allowing for the generation of comprehensive distribution maps. These localities have been further utilized in examining diversity and richness measures (Ch. 6). The initial results from the analysis of richness and diversity measures of *Hermannia* have shown many important hotspots, despite being done at a crude QDS resolution. Given a more accurate dataset, *Hermannia* may prove an exceptional group for studies of distributional response to climate change. The highest diversity and greatest richness of *Hermannia* species is found in the CFR, a pattern enhanced when smoothing algorithms are applied. A high diversity is also found in the Gauteng region due to a concentration of members of the subsect. *Tomentosae*, with an unexpected region of diversity in the Free State around Kimberley. The Free State hotspot needs to be verified with further studies and other genera. Turnover was a particularly revealing measure of biodiversity change, with a region of particularly high turnover located between Van Rhynsdorp and Elands bay. This edaphic boundary likely distinguishes taxa from the more arid north region from those of the mesic south. The Klein-Karoo region was also found to have exceptional turnover, interpreted as a meeting zone for component floras from the mesic south coast, the arid Karoo to the north, the summer rainfall east, and the winter-rainfall west. A similar scenario, with a particularly high richness was found for the small region around Worcester. This area is highly threatened by urban spill-over from the City of Cape Town, viticulture and other agriculture, and is proposed to be considered a region of high conservation priority.

A useful contribution towards conservation is that of the complementarity approach (Rebello and Siegfried 1992) that ranks sites according to their uniqueness and richness relative to other

areas. If *Hermannia* is indicative of overall plant species diversity as Fig. 7.2 would suggest, and the diversity, richness and uniqueness are considered the most important for conservation, then most conservation efforts should be focussed on the Cape. Nonetheless several regions outside the Cape are also highlighted. Table 6.2 provides a summary for the importance of the hotspots identified in this analysis. It shows that the top three most important regions are in the South Coast, Oudtshoorn and the Pretoria area. The Khamieskroon and the Clanwilliam area are the next highest priority.

#### **8.4 Phytochoria and climate change**

The analysis of phytochoria (Ch. 7) and particularly Fig. 7.2, has demonstrated remarkably similar patterns to overall biome patterns produced using Vegmap (Rutherford, Mucina et al. 2006). The details of phytochoria retrieved have proven sensitive to the chosen level of cut-off (i.e. the percentage similarity between nodes), yet relatively insensitive to the algorithm utilized. The results provide numerous broadly recognisable ‘vegetation types’ based on the composition of species within a QDS. Results show support for both the concept of the CFR, and more importantly for the Greater CFR (Born, Linder et al. 2007). Cluster analysis reveals a sharp disjunction in the CFR around the Cape Town area, with flora of a different composition to the north and the south/east of Cape Town. This disjunction is likely due to climate, as analysis of the climatic profiles shows that climate plays a major role in determining the distribution of *Hermannia* species. Timing of rainfall is particularly important, with there being little overlap between species occurring in summer- and winter-rainfall areas. The specificity of species for particular soils and climate most likely explains the narrow ranges and endemism of most *Hermannia* species.

As with most genera examined from South Africa, considerable range shifts and contractions have been found under climate change scenarios. Response to a changing climate was modelled for clades that display considerably different environmental characteristics, but although the magnitude and details of the change differed, all distribution ranges shrink. The climate modelling also demonstrated that a lowering in temperature could induce a corridor of probability similarly situated to the hypothesised arid corridor. While the climate change study



undertaken here is initial, it provides an incentive for future studies on datasets containing finer coordinates for the accessions of *Hermannia* specimens.

## 8.5 The significance of *Hermannia* in the CFR

*Hermannia* is found to be a Cape element, with sect. *Hermannia* fitting the description of a Cape clade. Due to the ubiquity of *Hermannia* in Southern Africa, and its predominant habitat being lowland areas, this genus should prove to be an important taxon for studying theories of the origins of diversity in the CFR.

Table 10.1 demonstrates the importance of primary taxonomy. Prior to this study, the Malvaceae with 91 species were not recognised as an important component within the CFR. The updated *Hermannia* species taxonomy now promotes the family to 17<sup>th</sup> most speciose family within the CFR. The statistic at generic level is even more startling. Prior to this thesis, *Hermannia* did not feature in the top 20 largest genera within the CFR. Now it may be considered the 6<sup>th</sup> largest genus after *Phyllica*. This strongly reinforces the general call for considerably more investment in field work and alpha taxonomy within botany.

In view of the importance of *Hermannia* in CFR, and the concern for the future of the CFR under climate change, there is great impetus to make use of the genus in future climate modelling projects.

## 8.6 The need for a comprehensive revision of *Hermannia*

The need for a more comprehensive revision of *Hermannia* is clear. There are over 600 names within the literature for *Hermannia* and *Mahernia* species, and 30 groups of various ranks. There are some 52 new species mostly in subg. *Mahernia* that have been prepared for publication as new species, all of which are readily identifiable as distinct species. I have not described species from species complexes within *Hermannia* from which several species could be erected. Furthermore, a considerable number of species from Namibia have yet to be described, as demonstrated by Colleen Mannheimer's single e-mail contribution of four unrecognised species. Herbarium specimens show there to be several species within the "Marehnia" complex in East

Africa that also require description. A recent visit to the Schweikerdt Herbarium in Pretoria has uncovered a further ten or so unrecognised entities. The number of new species found, illustrates that the discovery of new *Hermannia* species within Africa is far from exhausted.

## 8.7 Potential for pollination and dispersal studies

Little is known about the pollination and dispersal of *Hermannia*. There is considerable indication that the dispersal of *Hermannia* is primarily through endozoochory. It survives many ecological pressures such as drought, grazing and fire through various mechanisms, and provides great potential for further studies in evolution and adaptation. The diversity of flower colour and shape, combined with observations by Gess & Gess (Gess and Gess 2004; Gess 2005) and I have observed that there may be both generalist and specialist pollinated species and syndromes. This diversity of syndromes demonstrates the potential for pollination studies, research which is to date non-existent. Pollination syndromes should also be incorporated into theories of the evolution and diversification of *Hermannia*. For instance, the species of subg. *Mahernia* are likely to be more specialist pollinated (Gess and Gess, 2004), which may explain the greater genetic diversity within this subgenus compared with subg. *Hermannia*.

## 8.8 Tools developed for further work on the genus

The above review of literature and previous research on *Hermannia* [Ch. 1] reveals that most literature was limited to taxonomy and horticulture. A noteworthy foray beyond taxonomy was Engler (often with Schumann) who between 1900 and 1921 published 38 new species, erected several sub-generic groups whose concepts still hold, and discussed the biogeography of both the species and the major groups. Subg. *Mahernia* has been largely neglected, with the largest treatment of this subgenus including just 28 species (Engler 1904). To put this in perspective, a thorough conspectus of the CFR, Cape Plants (Goldblatt and Manning 2000) recognises just 8 species in the subg. *Mahernia*, with a further two unnamed species. The revision of subg. *Mahernia* has been attempted, with images of types from over 36 herbaria having been referenced in the nomenclatural section. This revision recognises 122 distinct species within the CFR – 78 species in subg. *Hermannia*, 43 in subg. *Mahernia*, and *H. trifurca* in the sect. *Acicarpus*. All types belonging to subg. *Mahernia* currently in Aluka have been

examined, with over 200 names having been dealt with for this subgenus. Nonetheless, types for c. 60 names need to be found, before publication of the c. 70 manuscript species that have been recognised in this study can be effected.

To facilitate this undertaking, there are a number of tools and datasets provided to facilitate further research and interest into the genus *Hermannia*. Being able to diagnose species is a high priority for individuals interested in pursuing *Hermannia* further. A good starting point is to browse the plates for all the species recognised in this study. These have been provided both in alphabetical order within each subgenus, and as a set of field-guides with species grouped by region for easy reference. As *Hermannia* can nearly always be identified to species level by macroscopic features alone, a full-set of colour plates with distribution maps have been provided. If the species is in the subg. *Mahernia*, the quickest means of identification may be to utilize the electronic key, Intkey. Once the set of possible species is narrowed down sufficiently, the user can examine: the colour plates; the scans of dissections of the flower; the species description; and the diagnostic characters. A dichotomous key to all *Mahernia* species is provided in Ch. 10 for those without access to a computer. Descriptions of many of the new species, and all currently recognised species of subg. *Mahernia* have been provided on the accompanying DVD accessible directly or through Intkey.

## **8.9 Towards a *Hermannia* atlas**

The ultimate outcome of this research would be the undertaking of a *Hermannia* Atlas. The Protea Atlas project headed by Tony Rebelo was open to the public for ten years. In this time, ten new species were found, with many important re-discoveries. It served as a springboard for many amateur botanists, and gave meaning in life to many others. The localities recorded during the atlas have been used in many scientific studies both as data and to obtain DNA material (eg. Barker, Vanderpoorten et al. 2004; Williams, Hannah et al. 2005; Valente, Reeves et al. 2010). They have provided breakthroughs and the best available datasets in the field of climate change within the Cape (Midgley, Hannah et al. 2002). The localities have also been utilized to inform the red-list of endangered species, and to facilitate the collecting of material for DNA studies. Nonetheless, this study took place over 10 years ago, before GPS became sufficiently accurate

for use. Now, the maturation of online mapping software (eg. Google Earth), the ubiquity of GPS, and the widespread adoption of digital cameras and email, allows for many more people to contribute records significantly more efficiently and accurately than for the Protea Atlas project.

*Hermannia* has a number of characteristics that make it complementary to the Protea Atlas. The species are largely confined to the lowlands, whereas *Proteaceae* are mostly montane. No *Proteaceae* occur in the very arid areas of South Africa and Namibia, whereas *Hermannia* occupies all these areas, including the mesic areas in which *Protea* occurs. This makes it useful for climate change comparisons. The phenology shows that the pollination syndrome may affect the flowering time of a species. An atlas would also allow for more evidence of flowering time and pollinators. This could prove useful in an analysis of flowering time related to pollination syndrome, and in a meta-study of pollination time relative to biomes.

Further characteristics make *Hermannia* a suitable group for public involvement in atlassing and identification. The species are readily identifiable by photograph. Most species of *Hermannia* are palatable resprouters, and thus many species may be found on farms. This provides an incentive for farmers to get involved, thereby engendering the possibility of the farmers becoming custodians of the flora. Despite being such unassuming plants, there is great potential for this genus to contribute to conservation and botany within this country. In research, as a group promoting conservation and education, and as a public-spirited atlas, *Hermannia* fulfils many of the criteria needed to further botany, and botanical collaboration, within Africa.

The tools for this *Hermannia* Atlas are nearly in place, and may currently be viewed at [www.casabio.org/informer.php](http://www.casabio.org/informer.php), with both the login name and password `_david_`. `_Informer_` is a module that allows one to efficiently contribute images of plants including *Hermannia* species to a central database (Fig. 11.0.1, at the end of the appendix). It has been made quick and simple to group images of a plant at a locality, forming a photographic species unit (Fig. 11.0.2). This unit may then be associated with one or more localities using the mapping feature (Fig. 11.0.3). There are then several tabs to allow the association of additional information including habitat, population size, and vulnerability due to various threats (Fig. 11.0.4). Upon completion of data

input one is taken to the browser [www.casabio.org/casabio.php](http://www.casabio.org/casabio.php) where further identification can be done by comparing the images with other photos and type specimens. Any *Hermannia* species will then be earmarked for my attention to make or confirm the identification.

Several features separate this software from existing atlases and online herbaria. The photos are grouped into initial photo units based on time intervals with optional manual refinement. Instead of photographs being attached to information, information is attached to a unit or groups of units. This makes it very quick to attach a locality, habitat type or additional information to an entire selection of units or part thereof. Instead of working with the images online, Informer makes use of images from the hard drive. This makes it very responsive, and assures a minimum of delays. These features makes the atlas quick and intuitive to work with. In much of Africa, bandwidth is limited and expensive, or non-existent in the rural areas. A new software innovation allows for images and associated information from Informer to be sent to a DVD or external hard drive, where it can be uploaded where or when more bandwidth is available. Identifications and new information from the server may then be synchronised with these computers either online or via DVD updates. Future updates will include the ability to tag pollinators and associated plant species to create webs of interactions.

## 9. References

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## 10. Appendix including a key to an overview of datasets and identification tools

### 10.1 Introduction

An excellent working key along with descriptions to each species were produced by Verdoorn (1980) for the Southern African species of the subg. *Hermannia*. In her revision she dealt with 290 out of approximately 650 species names including synonyms of *Hermannia*, of which five taxa were mentioned as requiring further attention. The single shortcoming that has resulted in the general lack of knowledge of this genus by current botanical professionals and enthusiasts alike, is the lack of images or drawings to accompany the descriptions. Thus, with the exception of De Winter and myself, no other person has a working knowledge of species concepts within *Hermannia*. However, De Winter published relatively little on *Hermannia*, and has not worked further on the genus since his retirement. This has necessitated the current revision, with the inclusion of plates of all currently recognised species.

To summarise this knowledge and to provide a series of identification and taxonomic / nomenclatural aids, a DVD is included with the following:

1. An electronic key
2. A summary of nomenclatural research completed to date, including
  - a. a tagged collection of protologues and associated literature;
  - b. an ordered collection of type specimens.
3. Image folders for each species containing
  - a. images of all species photographed to date in the field;
  - b. images of specimens of all herbarium specimens extracted from Jstor Plants;
  - c. images of specimens sent from herbarium requests and my own photographs of herbarium specimens.
4. An Excel spreadsheet with my determinations as well as georeferenced label information from +16 000 herbarium specimens.

5. An addendum including containing observations on the ecology of *Hermannia* and proposed open questions regarding pollination, dispersal and adaptation.

Each of these components is summarised below, with instructions on accessing them where appropriate.

## **10.2 Methods**

### **10.2.1 Capturing information from herbaria and georeferencing records**

Six months were spent in Pretoria which included some crucial input on the fundamentals of *Hermannia* and discussions of taxonomy with Dr. De Winter. This time was spent developing species concepts particularly for the summer rainfall species, encoding their characteristics into DELTA, and capturing the labels into an Excel worksheet. Details captured include the collector and collector number, collection date, locality, flower colour if mentioned, extra details such as habitat information, and whether the plant was in flower or fruit, and any taxonomic notes. The spreadsheet was then combined with specimen records from other herbaria, ordered by species, and a quarter-degree square (QDS) assigned to each record. QDS were obtained by using a combination of Google Earth, various gazetteers and atlases eg. Skead (1993), and the South African Geographical Names System (<http://sagns.dac.gov.za>) that contained 15196 records (2010). The resulting georeferenced Excel spreadsheet together with the incorporation of records from other herbaria was then imported into BRAHMS (Filer 2005). Species were then grouped into formally recognised groups, as well as informal groups before being exported into DIVA GIS (Hijmans, Guarino et al. 2004). Maps were derived to depict both formal and informal species groups. Where more than one overlapping species per QDS was depicted at a time, symbols were chosen that visually optimized the visibility of all species within the QDS. Although optimized for readers with full colour vision, the use of differing symbols should aid the colour-blind reader in distinguishing species. Maps were saved as JPEG files for incorporation into or alongside species plates, and for use within various chapters of the thesis.

### 10.2.2 Encoding vegetative states into DELTA

The method of encoding into DELTA is explained in 3.2.7. Species were then arranged by alphabetical order. The Action Set > layout' file was edited, with various tweaks including the linking of character states to create a reasonable output. The Action Set > Mark-up for RTF output' was edited to add bold, italics, or specify a font. The Action Set > translate into natural language' was then used to create a description file in rich text format (RTF). The descriptions of states of hairs and several other sections that could not be modified sufficiently by editing the layout' file to create a satisfactory automatic output, were manually edited within the resultant description file. This file was then integrated with the nomenclature and the plates. The Intkey file was generated by using the Action Set > Intkey tab > Intkey initialization file.

### 10.2.3 Creating species plates

Two kinds of species plates were created: photographic plates and plates using scanned specimens. For the photographic plates, the best images of each species were opened with Irfanview cropped to highlight important features including habitat, habit, leaves, inflorescence, flower (from the side and below), and the capsule. Irfanview ~~–drawing tools~~” were used to annotate and highlight features where necessary, and the ~~–thumbnails~~” feature then used to incorporate five images and the appropriate map into a single plate. This was then imported into Powerpoint for annotation. The final plate was screen captured, saved as a Jpeg file in Irfanview, and incorporated into species plates for the descriptions, and into the INTKEY electronic key.

For the plates of scanned specimens, fresh specimens were obtained from the field. In the field, the scanner was attached to an inverter, and a laptop used for capturing the scans. For the scan of the branch, the plant was scanned with the lid open creating a black background if the plant was not too 3-dimensional. If the plant was stiff and 3-dimensional, the plant was compressed using a moderate amount of pressure, and scanned with the lid closed. This typically created a variable grey background that necessitated considerable effort to extract the image from the background and remove shadows cast upon the lid.

A typical workflow to extract the object from the background involves importing the scanned image into Photoshop 5.0; selecting the majority of the background using the *magic wand tool*

set to a value of between 8 and 30 with the *contiguous* option unselected; zooming into the details and removing the background by either using the *magic wand* tool with the *contiguous* option selected, using the *quick selection* tool, or manually using the *eraser*. Once deemed satisfactory, the branch was saved as a layer, and duplicated to a new A4 sized 600 dpi image. The process was then repeated for dissected organs of the flower.

Where informative, adaxial and abaxial surfaces of organs such as the stipules, leaves, petals, calyx, and stamens, and the lateral and anterior view of the flower scanned. The background of the images was then selected using the *magic wand* tool, and the image refined with a *smoothing* value of 2, and *shift edge* value of 30%. The *mask selection* was then *inverted*, and a *new layer* created. This layer was then cleaned using the *eraser* before being copied to the A4 master document. Plant parts were arranged, and scaled to fit with either 50%, 100% or 200% reduction in size. The images were finalized with annotation of the various organs and the name and details of the plant. One major difficulty encountered in reproducing the plant, was the loss of detail encountered as plants faded into a black background with the lid off. This necessitated a novel approach to extracting hidden colour information by compressing the *levels* of a copy of the background of the image to highlight the differences between the upper and lower layers. The missing areas could then be manually replaced using the *history brush*. This was also found to be a useful technique in manually reconstructing hairs and bristles that had been lost during the *magic wand* or *refine* process.

The final images of the plates were then saved as a JPEG file. These files were added to a MS Powerpoint 2010 document to create the field guides, or imported directly into the nomenclature document.

## **10.3 Products**

### **10.3.1 Electronic key to the species**

On the attached DVD, a link to the INTKEY file entitled “Electronic Key to *Hermannia*” will be found. Upon opening the executable file, it will be seen that the 311 characters are in “best”

order, i.e. the order that best diagnose the species. It may be easier to use the “Natural order”, by clicking the square button to the left of the green intersecting circles button. From here, characters can be selected, and the appropriate states entered until several species remain. Double-clicking on a species reveals the *species description*, the *diagnostic description*, the *species plate*, and the *scan of the floral dissection*. The electronic key contains details for nearly all species of subg. *Mahernia*, and most of the new species of subg. *Hermannia*. Since 2013, to ensure that a description of each species possible was included in the taxonomic treatment, coding into DELTA was abandoned in favour of directly writing the description. This was done due to time constraints, because encoding into DELTA, converting to a description, and correcting the resulting description takes over five hours instead of three hours for a manual description.

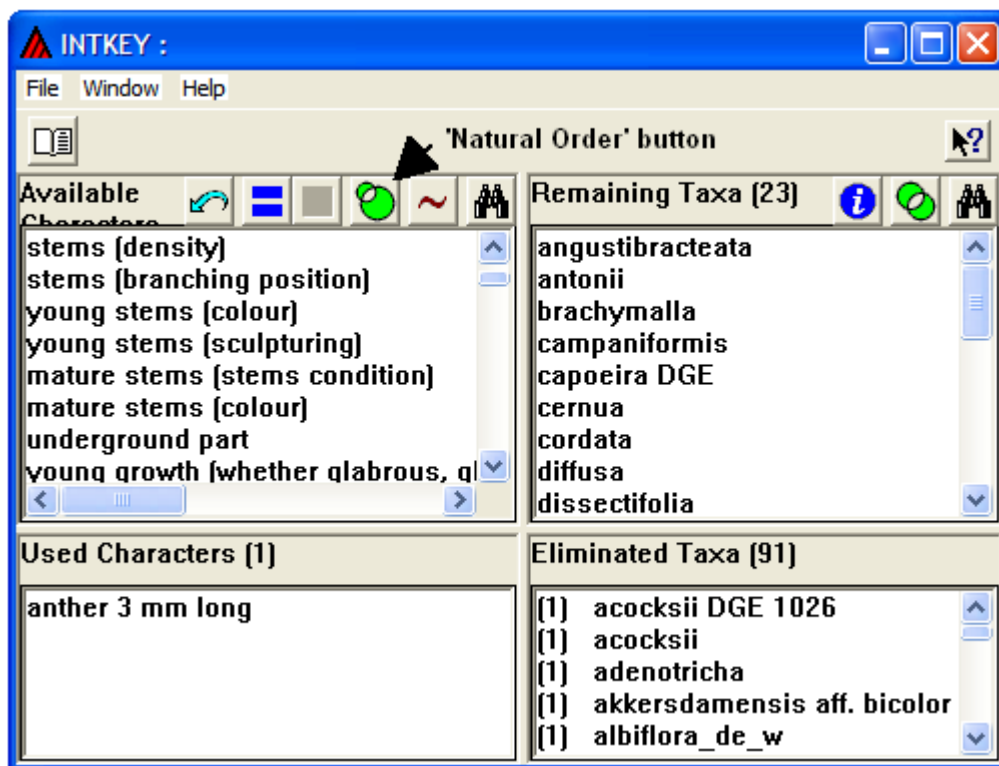


Fig. 10.1 Example of Intkey use. Clicking on the „natural order“ button as indicated will arrange the characters in the order they occur in the character list. Clicking on a character in the left panel will allow one to select a character state. In this example, selection of an anther length of 3mm left 23 taxa remaining (right upper panel), and omitted 91 taxa (right bottom panel).



Fig. 10.2 A selection of the floral dissections available from Intkey. The dissections are mounted on standard glass microscope slides of 75mm x 25mm. From top to bottom, with organs of decreasing size: *H. elliotiana*; *H. stipitata*; *H. akkersdamensis*; *H. biniflora*. In the latter case the stamens have been enlarged to show their filamentous filaments. The petals are just above the stamens. In *H. akkersdamensis*, the candy-like bicolored nectar guides are visible, which lend the group the name “Candiflorae”.



**azurea Gwyn. & van den Berg**

*Lorraine van den Berg 06.04.2010/1 (holo!, Bol).*

Dwarf herb; 3–7 cm tall; 3–5 cm wide. Stems herbaceous; ascending.

**Indumentum** inconspicuous; glabrescent to dense; consisting of glandular hairs with occasional stellate hairs. *Glandular hairs* conspicuous; consisting of sessile to shortly stalked, minute and medium sized, sparse to dense glandular hairs. Stalked glandular hairs medium sized; very sparse to moderately dense; stalk shorter than, to as long as the apical gland; terete or conical; the apical cell clear to pale brown, globose, mushroom shaped, or disc shaped. *Stellate hairs* very sparse (only rarely found on the abaxial leaf surface); medium sized; fine; more or less uniform in size; appressed; sessile; transparent. Stellate hair branches bristly; few (2–6) armed; not significantly reduced.

**Stipule** one on each side of the petiole; 1.7–2.8 mm long; 1.3–2 mm wide; stipules entire; oblanceolate.

**Leaf petioles** 7–13 mm long; 0.4 mm wide; with a distinct groove adaxially. *Leaf blade* not lobed or lacerate; lanceate-elliptic to elliptic-oblong; 7–22 mm long; 4–9 mm wide. *Margin* distinctly; finely; shallowly; irregularly; crenate; across the entire margin except for base. *Base* acute. *Apex* obtuse and rounded.

**Inflorescence** single flowered or paired cymes; arising from young branches; 22–38 mm long. *Peduncle* 15.5–27 mm long; geminate cymes 16–21 mm long; moderately densely to densely; covered with globose sub-sessile glands. *Bracts* two; sub-glabrous; 1.8–2.5 mm long; 1.4–2 mm wide (measured for both bracts at the base); connate; narrowly triangular; hooded; joined to around half the length of the bracts; margin glabrous or occasionally fimbriate with fine single or paired crisped hairs, possibly derived from stellate hairs. *Pedicels* 7–10 mm long in non-geminate cymes; densely covered with globose sub-sessile glands. Upper pedicels 6–8 mm long in geminate-cymes; lower pedicels 1.3–1.7 mm long.

**Flowers** tumbler-shaped (generally straight lines petals with a slight outwards angle); not flared; dark purple to dark blue, becoming brown with age; 2.5 mm diameter; with the narrowest portion at the calyx; 2.5 mm in diameter in the throat. *Calyx* 4 mm long; *lobes* 2 mm long; 1 mm wide, triangular; apex elongated; margin fringed with bristles.

*Petals* 3.3 mm long; 1.2 mm wide; oblanceolate to narrowly obovate; glabrous abaxially and adaxially. *Claw* 1.5 mm long; 0.9 mm wide.

*Stamens* 2.6 mm long. *Filaments* 0.8 mm long; free; linear without any widening; broadly linear; glabrous. Arms poorly developed, barely kite-shaped; somewhat removed from the base of the anther; with a weakly developed flange; the filament barely thickened. Arms moderately densely hairy; stellate bristly; on the arms. *Anther* lanceate-acuminate; 2 mm long; 0.4 mm wide; bristly on the sutures; with a few stray bristles forming the beard, with a flattened beard, and with a large distinct sac; sparse; c. 10 beard bristles (very small bristles); with anthers forming long submembranous horns; 10–16 total bristles (excluding the beard); short bristles on the sutures; without stellate bristles.

*Ovary* densely; covered with minute and barely-stalked globose sessile glands and stellate bristles (very rare small stellate bristles with up to three arms); indumentum even all over. *Style* style absent from specimens. *Capsule* obloid to ovoid; 6–7 mm long; 3.5 mm wide; sessile; moderately densely; covered with a mixture of; globose subsessile glands and stellate hairs; smooth to bumpy; angles or ribs glabrous to same indumentum as walls. *Seeds* seeds unobtainable.

*Flowering time* March, or April, though likely rain-dependent. **Habitat** Flat pans. **Abundance** Scattered plants in depressions. **Affinities** with other species Nearest *H. coccocarpa* from which it differs in the shorter petals. **Distribution** Only known from near Beaufort West on the Nelspoort road, on the farm Montana. **Notes** This is likely a perennial species which goes dormant between rains, as there leaf base scars visible on the stem. **Diagnostic characteristics** The dark blue flowers are unique, especially when combined with the diminutive size of the flowers and the short petals. The annual appearance of the plants is also unusual, with numerous flowers appearing on very short plants.

Fig. 10.3 Example of a description available through Intkey. The name and author are in bold, the collector and collector number in italics, and the type and herbarium where lodged are in brackets. Distinct portions of the plants are highlighted in italics or bold throughout the description.

### 10.3.2 Character list

The character list (illustrated in Fig. 10.4, below) is an output from DELTA that could facilitate encoding of future *Hermannia* and related projects into a similar framework. This provides a structure for discussing changes and improvements to the methodology of encoding. The full file is available on the DVD in the file: *Character List From Delta.doc*.

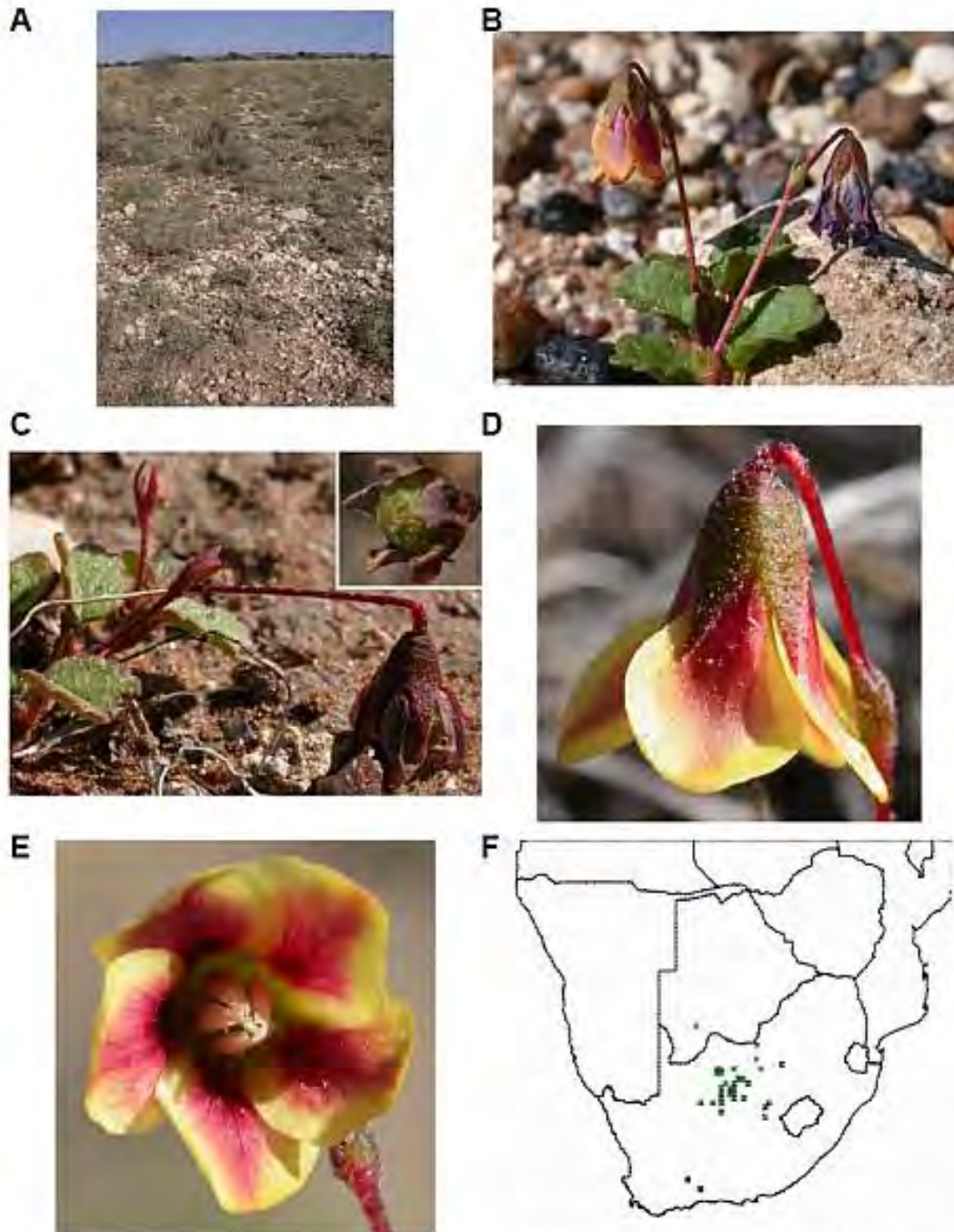
Character List	
#1. Synonyms/	
#2. <Longevity of plants>/	
1. Perennial/	
2. Annual/	
#3. <Habit, whether compact or loose>/	
1. compact/	
2. cushion-shaped/	
3. loosely branched/	
#4. <Habit>/	
1. herb/	
2. dwarf shrub/	
3. shrub/	
4. suffrutex/	
#5. Height <plant>/	
cm/	
#6. Diameter <plant>/	
cm/	
#7. Stems <firmness>/	
1. herbaceous/	
2. sub-herbaceous/	
3. sub-woody/	
4. woody/	
#8. Stems <taproot>/	
1. from a central taproot <lying flat>/	
2. arising annually from a perennial rootstock/	
#9. Stems <direction>/	
1. straggling/	
2. sprawling/	
3. decumbent/	
4. procumbent/	
5. ascending/	
6. erect/	
7. virgate/	
8. divaricate <wide-angled branching>/	
#10. Stems <whether slender or robust>/	
1. slender/	
2. robust/	
#11. Stems <density>/	
1. sparsely branched/	
2. densely branched/	
#12. Stems <branching position>/	
1. branched from the base/	
2. branched in the upper part/	

Fig. 10.4 An example of the Character list to found on the DVD. „#“ indicates the characters, „<>“ enclose invisible comments that are not output, and numbered items are the states.

### 10.3.3 Regional field guides to all species.

On the attached DVD, in the directory *Field Guides*, field guides are provided in PDF format (Fig. 10.5, below). *Foxit PDF Reader* is recommended freeware that may be used to view the field guides. The field guides are provided as separate files for the two subgenera within each region, namely: Cape Town area; Cedarberg, Tanqua and Western Mountains; Groot Karoo; Klein Karoo; Namaqualand; Namibia; the summer rainfall region of South Africa; and tropical east Africa, America and Australia. These plates are also provided in separate subgenera in alphabetical order, and in high-resolution files and low-resolution files for internet purposes.



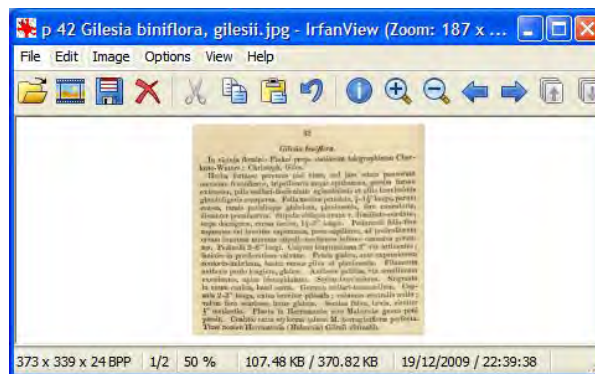


*H. linnaeoides* showing the habitat and habit on a limestone pan near Danielskuil (A,B); inflorescence and leaves (C); flower (D); flower from below (E); and distribution map (F). The leaves and form of this species are similar to *H. erodioides* that has pink flowers, and *H. argillicola* that has white flowers.

Fig. 10.5 A page from the field guide that follows the typical layout: A) a habitat shot; B) the whole plant; C-E) various aspects of the plant including close-ups of flowers from above and below, inflorescences and capsules. F) a distribution map with the main distribution in green, and dubious records in red.

### 10.3.4 Protologues

On the DVD within the directory *\Protologues*, over 1600 pages of literature (including 98% of all protologues) are provided. The species names in these images have been indexed and appended to the filename. Occurrences of a species name in the literature can therefore be searched for using the supplied freeware *Everything* (Carpenter 2009). It is recommended that the supplied software Irfanview is used as described in the caption to view the images (Fig. 10.6).



**Fig. 10.6** This screenshot is of the Irfanview interface. Basic keys are: „Enter“ to toggle full-screen; arrow keys to move between images when in full screen mode, or scroll around the image when not in full-screen mode. „+“ and „-“ zoom in and out respectively. „R“ turns the image to the right, and „L“ to the left. „S“ saves the image as its current name, and „Ctrl+S“ saves it to a specified location.

**Table 10.1 Statistics for the most important families of the CFR, adapted from Manning and Goldblatt (2000). “Existing” shows the figure for diversity in the year 2000, “updated” represents the current level of knowledge using manuscript taxa. After this revision, Malvaceae ranks as the 17<sup>th</sup> largest family with *Hermannia* making up the majority of these species.**

Rank	Family	Total sp.	Number endemic (% of total species)	Total genera (number endemic)	Species/genus
1.	Asteraceae	1036	655 (63)	121(33)	8.6
2.	Fabaceae	761	629 (83)	37(6)	20.6
3.	Iridaceae	677	540 (80)	28(6)	24.2
4.	Aizoaceae	659	524 (80)	76(18)	7.5
5.	Ericaceae	657	637 (97)	1(0)	657
6.	Scrophulariaceae	414	297 (72)	33(7)	12.5
7.	Proteaceae	329	319 (97)	14(9)	23.5
8.	Restionaceae	318	294 (93)	19(10)	16.7
9.	Rutaceae	273	257 (94)	15(6)	18.2
10.	Orchidaceae	227	138 (61)	25(2)	9.1
11.	Poaceae	207	80 (39)	61(3)	3.4
12.	Cyperaceae	206	101 (49)	29(4)	7.1
13.	Hyacinthaceae	191	83 (43)	14(0)	13.6
14.	Campanulaceae	183	140 (76)	13(6)	14.1
15.	Asphodelaceae	157	81 (51)	8(0)	19.6
16.	Geraniaceae	157	91 (58)	3(0)	52.3
17.	Polygalaceae	141	122 (86)	3(0)	47.0
18.	Rhamnaceae	137	127 (92)	5(1)	27.4
19.	Crassulaceae	134	35 (26)	5(0)	26.8
20.	Thymeleaceae	125	94 (75)	4(1)	31.3
<b>Existing</b>	<b>Malvaceae</b>	<b>91</b>	<b>56 (61)</b>	<b>9(0)</b>	<b>10.1</b>
<b>Updated</b>	<b>Malvaceae</b>	<b>147</b>	<b>105 (71.4)</b>	<b>9(0)</b>	<b>16.0</b>

**Table 10.2 Ranking of the largest genera in the Cape Flora “post” *Hermannia conspectus* (Goldblatt and Manning 2000). The % endemic refers to the proportion of species confined to the CFR. i.e. Of the top 20 largest genera, *Hermannia* has the 6<sup>th</sup> highest number of endemic species, with the 14<sup>th</sup> highest level of endemism.**

Rank	Genus	# Spp.	# Endemic	% Endemic	Rank	Genus	# Spp.	# Endemic	% Endemic
1	<i>Erica</i>	658	635	97	11	<i>Senecio</i>	110	58	53
2	<i>Aspalathus</i>	272	257	95	12	<i>Muraltia</i>	106	100	94
3	<i>Pelargonium</i>	148	79	53	13	<i>Gladiolus</i>	105	86	82
4	<i>Agathosma</i>	143	138	99	14	<i>Selago</i>	101	79	78
5	<i>Phylica</i>	133	126	95	15	<i>Crassula</i>	95	26	27
6	<i>Hermannia</i>	127	94	74	16	<i>Disa</i>	92	78	85
7	<i>Lampranthus</i>	124	118	95	17	<i>Ruschia</i>	88	79	90
8	<i>Oxalis</i>	118	94	80	18	<i>Restio</i>	85	82	97
9	<i>Moraea</i>	115	79	69	19	<i>Leucadendron</i>	82	79	96
10	<i>Cliffortia</i>	114	104	91	20	<i>Helichrysum</i>	81	35	43

**Table 10.3 Vernacular names.** As with most South African species in the literature, these are Afrikaans names. They allude to either their appearance (granny's bonnet, doll's rose), medicinal use (plaster bush, eight-day healing bush), their utility as drought fodder in grazing (opslag), or as a warning (prick bush, itchy bush). Names in enclosed in apostrophes are translated names. [1] (Bosman, van der Merwe et al. 1967); [2] (Adams 1976); [3] (Ross 1972); [4] (Curtis 1796); [5] (Verdoorn 1980); [6] (Thavs 1910); [7] (Letsie 2007); [8] (Thulin 1989); [9] (Appidi, Grierson et al. 2008); [10] (Ellery and Ellery 1997); [11] (Wild, Biegel et al. 1972); [12] (Cufodontis 1959).

<i>Hermannia</i> sp.	Vernacular name	English name or translation
spp	pleisterbos	_plaster bush'
spp	poprosies	_doll's roses'
spp (USA)		honeybells
<i>abrotanoides</i>	leeubekkie [3], voelbekkie [3]	_lion mouth', _bird mouth'
<i>alnifolia</i>		alder-leafed hermannia [4]
<i>althaeifolia</i>	pokkiesblom [3]	_pox flower', marsh-mallow leafed hermannia [4,5]
<i>althaeoides?</i>	mavulakuvaliwe (Sotho) [9]	_sweet yellow bells'
<i>amoena</i>	jeukbossie	_itch bush'
<i>angularis</i>	poprosie [3]	doll's rose
<i>betonicifolia</i>	asmabossie [3], seletjane-se-seholo (Zulu) [7]	_asthma bush', untranslated.
<i>boraginiflora</i>	gombossie [3]	_gum bush'
<i>boranensis</i>	rambi [8], salo-weni (Somali) [8,12]	untranslated
<i>coccocarpa</i>	ouma se kappie [3], moederkappie [2,3], opslag [3], seletjane (sesuto) [7], qena-e-ngenyane [7] (pg. 557)	_granny's bonnet', _mother's bonnet', _increase' (good for grazing), untranslated.
<i>comosa</i>	kapokkie [3], leeubekkie, swaelbossie	_fluffy ball', _lions mouth', _sulphur bush'
<i>cuneifolia</i>	pleisterbos	_plaster bush'
<i>var. cuneifolia</i>		
<i>cuneifolia var. glabrescens</i>	agtdaegeneesbossie [3], geneesbossie [3], geel pleisterbossie [5], gannabossie, motoo oa thaba (Zulu?)	_eight-day healing bush', _healing bush', _yellow plaster bush', _lye-bush' (ash-bush)
<i>depressa</i>	rooiopslag [3], seletjane (Zulu?) [7], phate-ea-ngaka (Zulu?) [7] (pg 534), moleko (Zulu?) [7] (pg 397), patengaka (Zulu?) [7] (pg 525)	_red flush' / _red increase', untranslated.
<i>desertorum</i>	pleisterbos	_plaster bush'
<i>disermifolia</i>	jeukbossie	_itchy bush'
<i>erodioides</i>	moederkappie [3], oumasekappie [3], opslag [3]	_mother's bonnet', _granny's bonnet', _increase' (good for grazing)
<i>filiifolia</i>	broodblom	_bread bush'
<i>flammea</i>	poprosie [3]	_doll's rose'
<i>flammula</i>	poprosie [3]	_doll's rose'
<i>gerrardii</i>	bitterblaar [3]	_bitter leaves'
<i>glanduligera</i>	masogomabe [10]	
<i>grandiflora</i>	heuningbossie [3]	_honey bush'
<i>grandifolia</i>	bitterblaar [3]	_bitter leaves'
<i>glabrata</i>	kopblaar pleisterbos	_head-leaf plasterbush'

<i>gracilis</i>	Jansenville pleisterbos	<u>Jansenville plasterbush</u>
<i>grandiflora</i>	ouma-se-kappie	<u>granny</u> 's bonnet
<i>hyssopifolia</i>	pokkiesblom [1,3], agtdaegeneesbossie [3]	<u>pox-flower</u> , <u>eight-day healing bush</u>
<i>incana</i>	escoba dura (Spanish)	<u>stiff broom</u>
<i>lavendulifolia</i>		lavender-leafed hermannia [4]
<i>linearifolia</i>	pleisterbos [5], rooipleisterbos [3,5]	<u>red plasterbush</u>
<i>linifolia</i>	rooiloot	<u>red shoot</u>
<i>macra</i>		meagre hermannia [5]
<i>minutiflora</i>	jeukbossie	<u>itchy bush</u>
<i>modesta</i>	ishitoni sha (Venda) [5]	
<i>multiflora</i>	geelpleisterbos, oumeidbos, geelbroodbos, gannabos [3]	<u>yellow plaster bush</u> , <u>old maid</u> 's bush, <u>yellow bread bush</u> ; <u>lye-bush</u> (for soap); chinese-lantern,
<i>paniculata</i>	Nagar (Somali: prob. Merehan) [12], reko (Somali) [12]	
<i>pauciflora</i>	Texas burstwort	
<i>paucifolia</i>	goewermentsbos, governmentsbossie [5], skitterybossie [5], purgurbossie [5], scholtzbossie [5]	<u>governments bush</u> , <u>diarrhoea bush</u>
<i>pulchella</i>	verfbossie, bergpleisterbossie [3], groenheuning [3]	<u>paint bush</u> , <u>mountain plaster bush</u> , <u>green honey</u>
<i>pulverata</i>	vaalpleister,	<u>grey plaster</u> , powdered hermannia [5]
<i>quartiniana</i>	granny's bonnet [11], ruwuti (Central Shona) [11]	
<i>saccifera</i>	komybossie [3]	<u>cumin bush</u>
<i>scordifolia</i>	geelkruipbroodbos	<u>yellow creeping bread bush</u>
<i>spinosa</i>	steekbossie [3]	<u>prick bush</u>
<i>stricta</i>	woestynroos, rooiopslag [3]	<u>desert rose</u> , <u>red increase</u>
<i>texana</i>		Santa-Catalina burstwort
<i>trifoliata</i>	tandebossie [3]	<u>tooth bush</u>
<i>trifurca</i>	broodkos, koerasie, vet-en-brood; koerhassie (Khoi) [5]	<u>breadfood</u> , <u>courage</u> , <u>fat and bread</u>
<i>tomentosa</i>	lusernbos	<u>lucerne bush</u>
<i>veronicifolia</i>	rooiopslag [3], setlhare-sa-diso-tsa- banyana (Zulu?) [7]	<u>red increase</u>
<i>vestita</i>	brandbossie [3], swawelossie, katte kruie [5]	<u>fire bush</u> , <u>sulphur bush</u> , <u>cat herbs</u>

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Table 10.4 Pollen characters derived from Coetzee & van der Schijff (1979). As many of the characters and states were not applicable to *Hermannia* (such as pollen spikes which are absent in *Hermannia*), this set corresponds to entry numbers in the publication (i.e. character 3-9 are not applicable). Square brackets surround two or more states that have been coded (i.e. [56] is state 5 and state 6). Character number: 1 - Polar diameter of colpate pollen and diameter of porate pollen; 2 - Equatorial diameter of colpate pollen and diameter of porate pollen; 9 - Colpi length; 10 - Thickness of exine; 11 - Apertural exine thickness; 12 - Polar thickness of exine; 13 - Length of lacunae; 14 - Width of lacunae; 15 - Muri width; 16 - Sexine texture; 17-LO pattern; 18 - Sexine thickness / nexine thickness; 19 - Colour of pollen (excluded from analysis); 20 - Number of apertures.

Acc.	Name	Character #														
		1	2	9	10	11	12	13	14	15	16	17	18	19	20	
2	<i>Corchorus asplenifolius</i>	9	7	4	7	[68]	6	8	9	[46]	4	2	2	3	3	
16	<i>Sparmannia africana</i>	9	8	4	7	9	8	9	[89]	[89]	4	0	1	3	3	
19	<i>Grewia bicolor</i>	9	8	4	9	9	8	9	9	[89]	4	3	1	3	3	
52	<i>Triumfetta welwitschii</i>	8	5	4	7	[78]	7	[79]	[89]	[49]	4	0	1	5	3	
58	<i>Dombeya rotundifolia</i>	7	7	4	[78]	0	0	0			2	0	4	3	3	
75	<i>abrotanoides</i>	[23]	[24]	[24]	[23]	[34]	3	[15]	[13]	[25]	5	0	1	3	3	
76	<i>affinis</i>	[12]	2	[13]	[24]	[23]	[24]	[27]	[25]	[25]	4	2	1	3	3	
77	<i>alnifolia</i>	[35]	[45]	[35]	[34]	[67]	[35]	[38]	[38]	[48]	5	2	1	4	4	
78	<i>althaeifolia</i>	[79]	[57]	[67]	[36]	[58]	[46]	[48]	[38]	[36]	5	2	2	3	3	
79	<i>althaeoides</i>	[46]	[45]	[46]	[14]	[47]	[35]	[26]	[27]	[48]	6	2	1	3	3	
80	<i>amabilis</i>	[24]	[23]	[34]	[13]	[12]	[13]	[15]	[16]	[25]	4	2	1	2	3	
81	<i>amoena</i>	[35]	[34]	[46]	[45]	[45]	5	[26]	[14]	[36]	6	2	2	3	3	
82	<i>angolensis</i>	[12]	[12]	[23]	[25]	2	[35]	[57]	[35]	[45]	4	2	1	2	3	
83	<i>angularis</i>	[59]	[46]	[24]	[24]	[89]	[15]	[38]	[39]	[47]	4	2	2	4	3	
84	<i>antonii</i>	[12]	2	[23]	[34]	[12]	[34]	[26]	[14]	[15]	5	2	1	3	3	
85	<i>argillicola</i>	2	2	[34]	[36]	[57]	[45]	[25]	[02]	[24]	6	0	1	3	3	
86	<i>aspera</i>	[47]	[46]	[45]	[25]	[45]	[35]	[36]	[27]	[36]	5	0	1	2	4	
87	<i>betonicifolia</i>	[12]	2	[34]	[24]	[23]	[34]	[16]	[03]	[24]	4	2	1	3	3	
88	<i>boraginiflora</i>	1	2	[12]	[23]	1	[23]	[67]	[36]	[13]	4	0	1	4	3	
89	<i>brachymalla</i>	2	2	[25]	[23]	[13]	[34]	[37]	[25]	[36]	5	2	1	3	3	
90	<i>bryoniifolia</i>	[35]	[34]	[45]	[34]	[46]	[35]	[25]	[03]	[26]	6	0	1	3	4	
91	<i>burchellii</i>	[12]	2	[12]	[26]	[35]	[15]	[14]	[03]	[39]	4	0	1	3	3	
92	<i>cernua</i>	2	[23]	[23]	[24]	[45]	[34]	[26]	[03]	[24]	4	0	1	2	3	
93	<i>coccocarpa</i>	[13]	[23]	[15]	[24]	[45]	[34]	[46]	[04]	[15]	4	2	2	2	3	
94	<i>comosa1</i>	[57]	[56]	[46]	7	6	[36]	[25]	[25]	[35]	6	2	2	3	3	
95	<i>comosa</i>	[89]	[57]	[57]	[56]	[89]	[56]	[47]	[37]	[37]	6	2	2	3	4	
96	<i>complicata</i>	[12]	2	[24]	[13]	[35]	[14]	[47]	[37]	[36]	6	2	1	3	3	
97	<i>concinifolia</i>	[36]	[45]	[24]	[34]	[34]	[34]	[28]	[16]	[38]	4	2	2	4	3	
98	<i>confusa</i>	[68]	[56]	[57]	[23]	[35]	[24]	[16]	[03]	[15]	6	2	1	3	4	

99	<i>conglomerata</i>	[45]	4	4	[34]	[46]	[45]	[67]	[68]	[45]	7	2	2	3	4
100	<i>cristata</i>	[12]	2	[23]	[34]	[23]	[34]	[38]	[17]	[36]	4	2	1	4	3
101	<i>cuneifolia</i> var. <i>c.</i>	[79]	[67]	[46]	[47]	[56]	[25]	[18]	[18]	[37]	5	2	2	3	3
102	<i>c. var. glabrescens</i>	[68]	[57]	[36]	[37]	[56]	[36]	[15]	[06]	[38]	5	2	1	3	4
103	<i>damarana</i>	2	[23]	[14]	[13]	[36]	[14]	[38]	[28]	[26]	5	2	1	2	3
104	<i>decipiens</i>	[57]	[45]	[45]	[24]	[237]	[24]	[25]	[25]	[58]	5	2	2	4	3
105	<i>decumbens</i>	[47]	[35]	6	[56]	[67]	5	[15]	[02]	[25]	6	2	1	4	3
106	<i>denudata</i>	[34]	[34]	[24]	[34]	4	[34]	[37]	[03]	[26]	7	2	2	4	4
107	<i>erecta</i>	[46]	5	[34]	[34]	4	[34]	[47]	[15]	[47]	4	2	1	4	4
108	<i>depressa</i>	[12]	2	[13]	[23]	[12]	[34]	[16]	[14]	[26]	4	2	2	3	3
109	<i>desertorum</i>	[57]	[45]	[56]	[35]	[67]	[45]	[16]	[19]	[36]	6	2	2	3	4
110	<i>diffusa</i>	1	[12]	[12]	[23]	[23]	[34]	[25]	[03]	[25]	5	2	1	3	3
111	<i>disermifolia</i>	[35]	[34]	[47]	[45]	[56]	[45]	[35]	[13]	[14]	5	2	2	4	3
112	<i>disticha</i>	[57]	5	[456]	[34]	[67]	[35]	[37]	[14]	[48]	5	2	1	3	4
113	<i>diversistipula</i> var. <i>d.</i>	[47]	[45]	3	[46]	[37]	[45]	[16]	[16]	[58]	5	2	1	5	3
114	<i>d. var. graciliflora</i>	[46]	[45]	4	[45]	[46]	[45]	[35]	[36]	[27]	4	2	3	3	3
115	<i>elliottiana</i>	[12]	2	[12]	[24]	[35]	[14]	[16]	[17]	[46]	5	2	1	3	3
116	<i>engleri</i>	[12]	2	[23]	[13]	[34]	[14]	[36]	[26]	[25]	5	2	2	3	3
117	<i>erodioides</i>	[12]	2	[23]	[24]	[35]	[34]	[38]	[15]	[25]	4	2	1	3	3
118	<i>exilis</i>	[12]	2	[12]	[34]	[45]	[35]	[25]	[05]	[13]	4	2	1	2	3
119	<i>filifolia</i> var. <i>f.</i>	[48]	[47]	4	[34]	4	3	[47]	[48]	[38]	4	2	2	4	3
120	<i>f. var. grandicalyx</i>	[45]	[45]	[456]	[34]	4	[34]	[47]	[48]	[46]	5	2	1	4	3
121	<i>flammea</i>	[38]	[47]	[356]	[13]	[36]	[15]	[78]	[38]	[57]	4	2	1	4	3
122	<i>flammula</i>	[89]	[68]	4	[34]	[46]	[15]	[58]	[69]	[36]	7	2	2	3	3
123	<i>fruticulosa</i>	1	2	[12]	[23]	[23]	[24]	[25]	[26]	[36]	5	2	1	4	3
124	<i>garipepina</i>	[24]	[23]	[456]	[23]	[46]	[14]	[27]	[27]	[36]	5	2	2	2	3
125	<i>geniculata</i>	[12]	2	[13]	3	[13]	3	[47]	[15]	[36]	5	2	1	3	3
126	<i>gerrardii</i>	1	2	[23]	3	[23]	[34]	[28]	[05]	[35]	5	2	1	3	3
127	<i>glabrata</i>	[12]	2	[23]	[24]	[12]	[45]	[26]	[15]	[37]	4	2	1	3	3
128	<i>glanduligera</i>	1	2	[12]	[12]	1	[13]	[46]	[47]	[36]	4	2	1	3	3
129	<i>glandulosissima</i>	1	[12]	[13]	[13]	[13]	[24]	[57]	[67]	[13]	5	2	1	4	3
130	<i>gracilis</i>	[57]	[56]	4	[36]	[56]	[46]	[27]	[28]	[46]	5	2	1	4	3
131	<i>grandiflora</i>	1	2	[12]	[23]	4	[24]	[27]	[28]	[46]	5	2	1	3	3
132	<i>grandifolia</i>	1	2	[23]	[23]	2	[34]	[28]	[25]	[37]	4	0	1	3	3
133	<i>grandistipula</i>	[12]	2	3	[23]	[23]	[34]	[18]	[05]	[26]	4	2	1	3	3
134	<i>grisea</i>	[12]	[12]	[12]	[13]	[13]	[13]	[47]	[47]	[26]	5	2	2	3	3
135	<i>guerkeana</i>	[24]	[23]	[24]	[13]	[35]	[14]	[47]	[37]	[35]	4	2	2	3	3
136	<i>helianthemum</i>	1	[12]	[12]	[13]	[13]	[13]	[37]	[24]	[34]	5	2	1	3	3
137	<i>helicoidea</i>	[34]	[34]	4	4	[45]	[45]	[24]	[14]	[35]	5	2	1	4	4
138	<i>heterophylla</i>	[12]	2	[13]	[23]	[23]	[34]	[37]	[15]	[35]	4	2	2	3	3
139	<i>hispidula</i>	[34]	[34]	[456]	[34]	[45]	4	[27]	[27]	[45]	5	2	1	4	4
140	<i>holosericia</i>	[47]	[45]	4	[45]	[46]	[45]	[17]	[18]	[46]	5	2	2	3	3



141	<i>hyssopifolia</i>	5	[46]	[23]	[47]	[56]	[46]	[48]	[48]	[69]	5	2	1	4	3
142	<i>incana</i>	4	[45]	[456]	[14]	[57]	[14]	[25]	[26]	[36]	5	2	2	3	4
143	<i>involutrata</i>	4	[45]	4	[34]	[45]	[34]	[16]	[26]	[25]	4	2	1	4	3
144	<i>jacobeifolia</i>	[12]	[23]	[23]	[34]	[56]	[35]	[18]	[04]	[15]	4	2	1	3	3
145	<i>johanssenii</i>	[46]	[35]	4	[45]	5	[45]	[17]	[05]	[25]	5	2	2	3	4
146	<i>joubertiana</i>	[78]	[57]	[356]	1	4	1	[58]	[68]	[67]	6	0	1	2	3
147	<i>lacera</i>	[12]	[12]	[23]	[24]	2	[34]	[17]	[04]	[17]	4	2	2	3	3
148	<i>lancifolia</i>	[12]	2	[23]	3	3	3	[37]	[24]	[25]	4	2	2	3	3
149	<i>lavandulifolia</i>	[46]	[45]	4	[35]	[56]	[35]	[28]	[29]	[57]	5	2	1	3	3
150	<i>leucantha</i>	1	[12]	[12]	[23]	2	3	[45]	[13]	[34]	4	2	1	4	3
151	<i>linearifolia</i>	[12]	2	[13]	3	[23]	3	[14]	[14]	[26]	4	2	1	3	3
152	<i>linifolia</i>	[25]	[34]	4	[34]	[34]	[34]	[14]	[03]	[25]	6	2	1	4	3
153	<i>linnaeoides</i>	1	2	[12]	[23]	[23]	[24]	[45]	[14]	[13]	4	2	2	3	3
154	<i>macowanii</i>	1	2	[23]	[23]	[23]	4	[26]	[24]	[36]	4	2	1	3	3
155	<i>macra</i>	[36]	[34]	4	[36]	[46]	[46]	[16]	[17]	[35]	6	2	1	3	4
156	<i>malvaefolia</i>	[36]	[35]	[56]	[34]	[67]	[45]	[35]	[23]	[15]	4	2	1	3	3
157	<i>marginata</i>	1	[12]	[12]	3	[12]	3	[27]	[15]	[36]	5	2	2	3	3
158	<i>micrantha</i>	[57]	[56]	[456]	[47]	[67]	4	[37]	[27]	[46]	5	2	2	4	4
159	<i>minimifolia</i>	1	2	[12]	[23]	2	3	[36]	[26]	[35]	4	2	2	3	3
160	<i>minutiflora</i>	[23]	[23]	4	4	4	4	[27]	[03]	[24]	6	2	1	3	3
161	<i>modesta</i>	1	2	[12]	[23]	[13]	[34]	[46]	[46]	[25]	4	2	2	4	3
162	<i>montana1</i>	1	2	2	2	[23]	3	[46]	[25]	[24]	5	2	1	3	3
163	<i>montana</i>	2	2	[34]	3	3	4	[48]	[26]	[45]	5	2	2	3	3
164	<i>mucronulata</i>	[47]	6	[456]	[47]	[57]	[46]	[37]	[38]	[49]	5	2	1	4	4
165	<i>muirii</i>	[45]	4	[24]	[35]	4	[34]	[27]	[15]	[37]	4	2	1	4	3
166	<i>multiflora</i>	[48]	[47]	6	[23]	[48]	[16]	[25]	[25]	[58]	5	2	2	3	4
167	<i>muricata</i>	3	[34]	4	4	6	[45]	[16]	[04]	[24]	6	2	1	4	4
168	<i>oblongifolia</i>	[12]	2	[23]	[23]	2	[34]	[27]	[16]	[25]	5	2	1	3	3
169	<i>odorata</i>	[57]	[45]	[56]	[35]	[46]	[35]	[38]	[29]	[38]	5	2	1	4	3
170	<i>oligosperma</i>	3	3	[24]	[23]	[34]	[23]	[48]	[16]	[27]	4	2	2	3	3
171	<i>parviflora</i>	[23]	[23]	4	[24]	[57]	[25]	[37]	[35]	[14]	4	2	1	2	3
172	<i>parvula</i>	1	[12]	1	2	1	[12]	[37]	[04]	[25]	5	2	1	4	3
173	<i>patellicalyx</i>	[35]	[35]	4	4	[67]	4	[46]	[02]	[26]	6	2	1	4	4
174	<i>paucifolia</i>	3	[34]	[24]	[34]	4	[34]	[27]	[13]	[24]	6	2	1	4	4
175	<i>pinnata</i>	1	2	1	3	2	3	[46]	[25]	[35]	4	2	1	3	3
176	<i>prismatocarpa</i>	[57]	[45]	4	[35]	[56]	[46]	[147]	[17]	[34]	6	2	1	3	4
177	<i>pulchella</i>	[12]	2	[24]	[24]	[23]	[14]	[37]	[15]	[26]	5	2	1	3	3
178	<i>pulverata</i>	[35]	[34]	[34]	3	[34]	3	[26]	[15]	[47]	5	2	1	4	3
179	<i>quartiniana</i>	[12]	[23]	[23]	[24]	[23]	[34]	[26]	[24]	[14]	4	2	2	3	3
180	<i>rautanenii</i>	1	2	[12]	[24]	[13]	[24]	[15]	[15]	[35]	4	2	1	3	3
181	<i>repetenda</i>	[57]	[45]	4	[46]	[89]	[45]	[18]	[18]	[46]	5	2	1	3	4
182	<i>resedifolia</i>	[12]	2	[13]	[34]	[24]	[45]	[36]	[15]	[15]	4	2	2	3	3
183	<i>rigida</i>	5	[34]	4	4	[46]	4	[17]	[04]	[26]	5	2	1	4	4

184	<i>rogersii</i>	1	2	2	3	2	3	[37]	[14]	[36]	5	2	1	4	3
185	<i>rudis</i>	[57]	[56]	7	[47]	[68]	[46]	[28]	[29]	[57]	7	2	1	3	4
186	<i>rugosa</i>	5	4	5	4	[45]	4	[14]	[13]	[37]	5	2	1	4	4
187	<i>saccifera</i>	1	[23]	[23]	[34]	[56]	[35]	[36]	[14]	[14]	4	2	2	3	3
188	<i>salvifolia</i> var. <i>s.</i>	[69]	[57]	[37]	[37]	[47]	[46]	[38]	[29]	[68]	4	2	2	4	3
189	<i>s. var. oblonga</i>	[59]	[57]	[47]	[25]	[57]	[35]	[27]	[27]	[69]	4	2	2	3	3
190	<i>sandersonii</i>	[58]	[46]	[46]	[56]	[57]	[56]	[28]	[13]	[24]	7	0	2	4	4
191	<i>scabra</i>	[36]	[35]	[35]	[34]	4	[34]	[25]	[12]	[35]	5	2	1	4	4
192	<i>scordifolia</i>	[34]	4	[56]	[24]	[56]	[24]	[47]	[02]	[24]	6	2	1	3	3
193	<i>scordifolia2</i>	[78]	[56]	[57]	[235]	[235]	[45]	[24]	[13]	[25]	5	0	2	2	3
194	<i>sisymbriifolia</i>	1	[23]	[24]	[24]	[34]	[24]	[16]	[17]	[46]	4	2	1	3	3
195	<i>solaniflora</i>	2	1	[24]	[23]	[13]	[13]	[27]	[27]	[26]	4	2	2	3	3
196	<i>spinosa</i>	[24]	[23]	[24]	[13]	2	[13]	[26]	[26]	[26]	4	2	2	3	3
197	<i>staurostemon</i>	1	2	[14]	[24]	[23]	3	[48]	[15]	[24]	5	2	1	3	3
198	<i>stellulata</i>	2	2	[34]	[34]	[45]	4	[28]	[04]	[24]	4	2	2	2	3
199	<i>stipulacea</i>	[57]	[45]	[36]	[26]	[17]	[15]	[25]	[25]	[47]	5	2	2	4	4
200	<i>stricta</i>	[12]	[23]	[13]	[24]	[24]	[24]	[28]	[29]	[58]	4	2	1	4	3
201	<i>suavis</i>	[89]	[78]	[67]	[24]	[78]	[14]	[26]	[27]	[46]	5	2	1	4	3
202	<i>sulcata</i>	[67]	[56]	[34]	[35]	[46]	[46]	[25]	[26]	[45]	4	2	1	4	4
203	<i>ternifolia</i>	[48]	[47]	4	[37]	[58]	[36]	[37]	[23]	[59]	4	2	2	3	4
204	<i>tigrensis</i>	[12]	2	[13]	[23]	[13]	[34]	[38]	[38]	[25]	4	2	1	4	3
205	<i>tomentosa</i>	[12]	[23]	[13]	[14]	[13]	[14]	[46]	[47]	[25]	4	2	2	2	3
206	<i>transvaalensis</i>	1	2	[12]	3	[23]	3	[36]	[26]	[34]	5	2	2	4	3
207	<i>trifoliata</i>	[68]	[47]	[57]	[36]	[78]	[45]	[58]	[57]	[68]	5	2	2	4	4
208	<i>umbratica</i>	[12]	[12]	[23]	[13]	[12]	[34]	[35]	[04]	[24]	5	2	1	2	3
209	<i>velutina</i>	[48]	[46]	[23]	[34]	[36]	[35]	[27]	[27]	[36]	5	2	2	2	3
210	<i>veronicifolia</i>	[12]	2	[23]	[23]	[23]	[34]	[26]	[13]	[45]	5	2	2	3	3
211	<i>vestita</i>	[24]	3	[45]	4	4	4	[27]	[04]	[23]	5	2	1	4	3
212	<i>viscosa</i>	1	2	[12]	[12]	[12]	[23]	[37]	[25]	[24]	4	2	1	3	3
213	<i>woodii</i>	[13]	[23]	[24]	[24]	[45]	[34]	[18]	[05]	[14]	4	2	2	3	3

**Table 10.5 Characters used in the parsimony analysis utilizing PAUP\*.**

<b>Analysis #</b>	<b>DELTA char #</b>	<b>Unit</b>	<b>Character</b>
1	5	cm	Height of mature plant
2	6	cm	Diameter of mature plant
3	58	mm	Mature stipule length
4	78	mm	Petiole length for mature leaves
5	91	mm	Leaf blade length in mature leaves
6	92	mm	Leaf blade width
7	134	mm	Peduncle length to base of bract
8	143	mm	Bracts length of longest bract
9	167	mm	Pedicel length of upper pedicels
10	183	mm	Calyx length from pedicel apex
11	185	mm	Calyx lobe width at sinus
12	206	mm	Petal length, including the claw
13	207	mm	Petal width
14	220	mm	Claw length, measured from base to broadening of petal blade
15	221	mm	Claw width, measured at the widest point
16	233	mm	Stamen length from point of attachment to receptacle to anther tip
17	234	mm	Filament length between the attachment of the receptacle and the anther
18	255	mm	Anther length
19	261	#	Anther, estimate of number of beard hairs
20	263	#	Anther, approximate number of total hairs excluding the beard
21	272	mm	Ovary length, excluding stipe
22	284	mm	Style length

Table 10.6 States of characters from Table 10.5 with units provided in Table 10.5.

<b>Char</b>	<b>State 1</b>	<b>State 2</b>	<b>State 3</b>	<b>State 4</b>	<b>Char</b>	<b>State 1</b>	<b>State 2</b>	<b>State 3</b>	<b>State 4</b>
<b>1</b>	-10	10-20	20-26.3	+36.3	<b>12</b>	-7	7-8.5	8.5-9.6	9.6+
<b>2</b>	-40	40-60	60-92.5	+92.5	<b>13</b>	-3	3-4	4-5.5	5.5+
<b>3</b>	-2.8	2.5-4.4	4-7	+6	<b>14</b>	-2.2	2.2-3	3-4	4+
<b>4</b>	-3	3-4.5	4.5-7	+7	<b>15</b>	-1.3	1.3-1.7	1.7-2.3	2.3+
<b>5</b>	-12.5	12.5-19	19-29	29+	<b>16</b>	-4.6	4.6-5.5	5.5-6.7	6.7+
<b>6</b>	-6	6-8 9.9-	8-13.5	13.5+	<b>17</b>	-2.8	2.8-3.3	3.3-4.2	4.2+
<b>7</b>	-9.9	16.8	16.8-25	25+	<b>18</b>	-2.5	2.5-3.4	3.4-4	4+
<b>8</b>	-2.5	2.5-3.6	3.6-5.6	5.6+	<b>19</b>	-5	5-12	12-19	19+
<b>9</b>	-5	5-9.5	9.5-12	12+	<b>20</b>	-25	25-60	60-100	100+
<b>10</b>	-4.5	4.5-5.3	5.3-6.3	6.3+	<b>21</b>	-1.9	1.9-2.3	2.3-2.7	2.7+
<b>11</b>	-2.5	2.5-3.3	3.3-3.8	3.8+	<b>22</b>	-2.9	2.9-4	4-5	5+

**Table 10.7 Character states from the input file. Brackets enclose more than one appropriate state for a character. „?” denotes a missing state. The collector number after the name is only shown where more than one exemplar of a species has been encoded, otherwise the collector number may be obtained from the DELTA dataset.**

Species	Character states
<i>acocksii</i>	(12)1(234)(12)(12)??(123)?(12)?(123)?1??(23)1??(23)?
<i>acocksii dge 1026</i>	21(23)?1(123)(23)31(12)1(12)(12)(23)(34)221??22
<i>adenotricha</i>	??????????2(12)(12)2(12)231231
<i>akkersdamensis</i>	1(23)(23)(34)(123)(34)(234)4(234)(123)1(12)(23)123(23)31(12)22
<i>albiflora</i>	(12)(12)(23)?(12)(123)1(12)1?1(12)1(12)2121??32
<i>albiflora_de_winter</i>	(12)1(234)?(123)?(12)(23)?(12)?2?(234)?(34)4(12)????
<i>angustibracteata</i>	(12)4(1234)(1234)1(12)(12)(12)3214323434443-34
<i>antonii</i>	2(23)(34)(34)4??(23)?(23)?(23)???(12)1(12)????
<i>antonii_dge</i>	4(12)4(234)(34)(34)1(1234)?41(34)24(12)443(23)(34)14
<i>argillicola</i>	(12)1111111?1111111111121
<i>auricoma</i>	(23)3(34)4111(34)3443(12)42333(23)442
<i>ballerinica</i>	(234)(1234)(23)(12)(23)(123)(12)(34)?1211??111??1?
<i>bicolor</i>	(23)(23)(12)(123)(1234)?2(12)?(23)?(12)????(34)??(12)?
<i>brachymalla</i>	??(34)(34)(34)??3?(12)?1???(123)(12)(12)?(12)?
<i>bredaensis</i>	???(12)(123)?(23)(34)?(12)?(12)?(23)?1?3??4?
<i>brittmannii</i>	??(23)(1234)(34)(123)(234)(123)13111(12)3213?421
<i>burchellii</i>	(34)(1234)111(23)(12)(12)(23)314311111?(23)11
<i>burkei</i>	44(34)4(34)(34)14(12)423(23)324441434
<i>sperata</i>	13(123)(123)(23)(234)(34)(12)(23)(12)(234)(12)(23)(34)4?43??4(23)
<i>cedarbergensis</i>	4(12)(12)1(123)(123)2(12)(12)1(12)(234)(34)(23)3141??2(34)
<i>cernua</i>	(23)1(23)(123)(23)(123)(23)(123)(34)2(234)2(23)(34)3?(23)(23)??(23)(23)
<i>fragrans</i>	334(123)(123)(123)(34)3(234)314424444?13(34)
<i>rocherpanensis</i>	(23)3(23)?11(12)(34)(34)411(23)11212?3??
<i>cordata</i>	13(234)(34)(234)4(23)4(34)443(12)43442??4(23)
<i>cristata bol</i>	31(34)(123)(234)(234)(234)(123)?4(23)44444441(34)44
<i>depressa</i>	14(123)(123)(234)(34)(234)(123)(234)(12)14323(23)(23)3(23)223
<i>diffusa</i>	???(1234)(1234)(34)(234)(123)?(123)?????(34)(12)????
<i>diffusa dge 1777</i>	(23)(23)(23)(123)3(23)(34)(123)(34)213321342?242
<i>dissectifolia</i>	(234)(12)(23)(1234)(123)?(34)(12)?(12)?(123)?(12)?2(23)????
<i>echinocapsulare</i>	(23)1(234)(12)(12)14(123)?(123)4112?114??4?
<i>elliottiana</i>	(23)(23)(234)1(12)1(34)(12)441444(12)34(12)(34)14(23)
<i>elliottiana – ADH</i>	43(234)1(123)(12)(34)(1234)1414444142414(23)
<i>erodioides</i>	1(123)(12)(234)(123)?4(123)?(12)?(12)?(23)??24??1?
<i>filipedunculata</i>	??(123)?1?4(12)?(12)?(23)?(234)?(23)3(12)??2?
<i>fruticulosa</i>	4(23)1(12)1(12)11?31(23)31(34)212?(12)21
<i>geniculata</i>	(12)4(34)(23)444444344444441443
<i>gerrardii</i>	(23)441441434342423421434

<i>Gilesia biniflora</i>	12(12)(123)22(23)1?11111111?111
<i>glabrata</i>	44(23)(123)3?(234)(34)?(23)?(34)?(34)?3(34)?(34)?
<i>glabripedicellata</i>	41(34)(123)(1234)1(34)(23)2(1234)1(34)(34)(23)(23)(12)(34)(234)(34)2(234)(34)
<i>ternifolia</i>	????????(12)1443332(34)443(34)
<i>grandiflora</i>	441111(123)13114412111?(23)11
<i>grandifolia</i>	?(1234)(234)4113(234)313232433(12)434
<i>grandistipula</i>	(23)1(34)(123)(34)(234)(1234)(34)(1234)42(23)(12)423322(34)32
<i>grossularifolia</i>	(123)1(234)(12)(123)?(23)(23)?(12)?(23)?(23)?1(12)?(23)?
<i>harveyi</i>	4(23)(23)(12)(123)(34)(23)3(23)424(34)(34)(34)(34)(34)(34)?(34)3(34)
<i>herpetiformis</i>	14(12)(34)2(123)(234)2(12)21111(12)131(23)121
<i>heterophylla</i>	4?(34)(1234)(123)(123)(23)4?(23)?(23)?(34)?33?4?
<i>heterophylla-dge 1888</i>	43(12)(12)(12)1(23)4221443444(34)????
<i>hoarensis</i>	????????213333221131(23)
<i>humifusa</i>	(23)34(34)(23)(123)(234)4(234)(23)(123)(23)4(23)421(234)?123
<i>humilis</i>	????(234)(123)2(12)??(34)?(23)?11??4?
<i>inflata</i>	????23??4423(34)13321(34)42
<i>jacobeifolia</i>	2(12)(12)(23)11(12)2?412(12)11424(23)133
<i>kammanassii</i>	(23)4(23)(12)(234)(234)(34)4?413312434?14(23)
<i>lancifolia</i>	22(234)(34)4(12)344444444444??44
<i>larustipularis</i>	3(23)(1234)(234)(234)(1234)44(234)2144133(34)2(34)144
<i>linearis</i>	4(23)12(34)1112?111123(23)414(12)3
<i>linnaeoides</i>	131(234)1(123)(23)1?111(12)11112(12)112
<i>litoralis</i>	1(23)(34)(1234)(12)1442(12)(12)4(34)(23)4342?244
<i>nessii</i>	14(34)(34)(34)(34)44(12)3344414431(34)24
<i>longipetala</i>	44(12)1(123)(123)1144144(234)3341?443
<i>malvifolia</i>	11(123)(1234)(1234)(34)1(12)?21(12)23(12)22(12)?311
<i>meyeriana</i>	(23)4(1234)(34)1(123)(12)(12)(12)24114432(34)?223
<i>microtesticulare</i>	13(23)(123)1(123)(123)(12)11111111113211
<i>middelburgensis</i>	(12)(123)?(34)4?4(34)?4?(34)?(34)?44(34)?4?
<i>nana</i>	(123)(12)(12)(34)(12)(23)4(12)?(12)?(234)????1(34)11(234)?
<i>oblongifolia</i>	21(23)(234)(34)(234)(12)(34)4(123)122(23)2(12)2(12)1(12)21
<i>oligosperma</i>	43(234)4(34)4?(12)?1111(12)1111??11
<i>onychotenax</i>	44(234)(123)(1234)(1234)11(12)11(12)(23)(34)4(23)32?12(23)
<i>palmeri</i>	(23)(23)1(123)(12)(123)(123)13412(23)(12)14241144
<i>parviflora</i>	43(34)(123)(234)(1234)(234)3211111111(12)211
<i>pauciflora</i>	42(12)(34)(23)(34)(12)122121221111121
<i>picta</i>	(123)1(12)(12)(123)(123)2(12)1211211111231
<i>pinnata</i>	(12)3(34)(12)(12)243(34)312(23)13223?233
<i>pinnata_de_w</i>	34????4????(34)?(34)?3(34)?4?
<i>pinnata_rse</i>	(12)3(23)2(34)(23)44(34)3(12)4434(23)31?241
<i>platycaulis</i>	(23)1(23)(12)(23)(12)(34)3(12)1(234)(12)(12)1(12)?11??1?
<i>presliana</i>	3(12)(123)2(12)(123)(12)(123)(12)11212211(12)4222

<i>myrrhifolium</i>	24??????22(23)4342234332
<i>orgasmiodorata</i>	14??????324433232433(23)
<i>pulchella</i>	(34)3(12)(123)(234)?1(123)?(34)?(34)?(34)?(34)?(34)?(34)?(34)?(34)?
<i>quartiniana</i>	(12)4(34)(234)(34)(234)(23)(23)4(234)132(123)4444?(34)24
<i>rautanenii</i>	32(34)(34)4(234)3(34)44(23)42(34)34(34)41(34)24
<i>resedifolia</i>	31(12)(234)(23)?22?2?1?1??(123)???(12)?
<i>rogersii</i>	3(23)(234)(12)4(34)12?3111?222413(12)2
<i>rubrarivularis</i>	41(12)(123)(123)(123)(12)1(12)(12)(234)(123)(23)23?3(34)?(34)?
<i>saccifera</i>	41(12)(12)(234)(23)32(12)42333333(34)4(234)1-34
<i>saccifera</i>	(23)4(23)(23)(234)(23)4(34)(34)444434443?(23)24
<i>scabricaulis</i>	14(23)(34)(234)?4(34)?(12)?(234)?(34)?(34)?(23)????
<i>simulans</i>	(23)3(23)(123)(1234)?(34)(123)?(234)?(23)?(23)?????4?4?
<i>sisymbriifolia</i>	32(123)1(12)(123)(123)1(123)1(1234)1122111??11
<i>sneubergensis</i>	1(123)3(123)(123)(123)??(12)(123)21(12)12114??1?
<i>odoratissima</i>	42(234)1(123)(12)(12)(34)3?13(34)23334(23)433
<i>staurostemon</i>	114?4????(34)?(234)????(34)?(34)?
<i>stellulata</i>	13(34)(34)4(123)(34)(23)2112121(23)23(12)232
<i>stipitata</i>	??(234)(1234)(123)(123)(23)(12)?(34)?(234)?(23)??42????
<i>stricta</i>	42111111?314(34)42442?12(23)
<i>texana</i>	(34)(12)(123)4(34)4(23)1132(34)(34)322211(34)?1
<i>traansvaalensis</i>	14(234)(1234)4414(234)4(234)434(34)4444344
<i>trisecta</i>	14(123)(12)1(23)(34)(34)(12)31(12)21132(34)(34)2(12)2
<i>triumfettifolia</i>	(23)1(34)(34)4(234)14121(23)(12)(23)(23)332(12)313
<i>upright muricata</i>	44(234)1(123)(123)(1234)(123)(12)4(12)333423?1(34)23
<i>verdoorniae</i>	23(34)44?1(34)?(34)?(1234)?(34)?(34)?(234)?(34)?
<i>violacea</i>	(23)3(12)(123)(12)(1234)(23)2(23)11111111(23)(12)11
<i>woodii</i>	1(1234)4(34)443(34)4(123)1(12)(23)2(34)(23)2(34)?(1234)1

**Table 10.8 Molecular samples used and associated herbarium specimens. Sample name refers to the name utilized in analysis. Collecting number acronyms are provided at the bottom of the table. Where no acronym is given, this refers to my collecting number that is formatted as DDMMYY/collection number for the day. Codes: ADH - A. Harrower; DGE - D. Gwynne-Evans; DTW - D. Wilson; PW - P. Winter; TT-S - T. Trinder-Smith. Collecting numbers preceded by an asterisk refer to GENBANK codes. All specimens or representative duplicates are lodged in the Bolus Herbarium except where stated in brackets after the collecting number.**

<b>Sample Name</b>	<b>Species</b>	<b>Collecting Number</b>
2083Walthe	<i>Waltheria indica</i>	DGE 2083
1930pinnat	<i>pinnata</i>	DGE 1930
HMSITS4001	<i>meyeriana-sandy</i>	260905/19
1664pinnat	<i>pinnata</i>	DGE 1664
2037resedi	<i>resedifolia</i>	DGE 2037
1995con	<i>meyeriana</i>	DGE 1995
2020coccoc	<i>coccocarpa</i>	DGE 2020
HLNITS4002	<i>namaquensis</i>	181005/27
2145con	<i>grandiflora</i>	DGE 2145
HBUIITS4001	<i>burchellii</i>	110306/17
1943vertic	<i>verticillata</i>	DGE 1943
1000cuneif	<i>pinnata</i>	DGE 1000
HCIITS4001	<i>ciliaris</i>	161005/1a
HLIITS4001	<i>litoralis</i>	DGE 1951
1777diffus	<i>diffusa</i>	DGE 1777
H1777diffu	<i>diffusa</i>	DGE 1777
1881confus	<i>confusa</i>	DGE 1881
GBITS4glab	<i>glabrata</i>	260905/s.n.
HGVITS4003	<i>glabrata</i> (oorlogskloof)	150905/s.n.
PIITS4pict	<i>picta</i>	26.09.05/6
2141pulche	<i>pulchella</i>	DGE 2141
1994stipit	<i>stipitata</i>	DGE 1994
HSCAITS500	<i>candiflora</i>	ADH1236
meyeriana	<i>meyeriana</i>	100905/6
elephantul	<i>coriolis</i>	301008/1
lacerakamm	<i>kammanasii</i>	ADH1691
esperantii	<i>esperantii</i>	081005/20
spnovaffgl	sp. aff. <i>glabrata</i>	21.08.06/4
oxalidiflo	<i>oxalidiflora</i>	
trifurcasp	<i>trifurcoides</i>	100905/17
hondekliips	cf. <i>psammophila</i>	18.10.05/16
spnovvanrh	<i>supplicans</i>	17.10.05/26
1883con	sp.	DGE 1883
1941bredae	<i>bredaensis</i>	DGE 1941
2045linnae	<i>linnaeooides</i>	DGE 2045
A945CON	<i>malvifolia</i>	ADH 945
Contigl	<i>malvifolia</i>	DGE
oligosperm	<i>oligosperma</i>	050106/5
Gilesiabin	<i>biniflora</i>	Bates 47
cernua	<i>cernua</i>	28.01.06/15
coccocarpa	<i>coccocarpa</i>	DGE 2144
campanifor	<i>campaniformis</i>	150106/20
0coccocarp	<i>coccocarpa</i>	ADH 1236
dissectifo	<i>dissectifolia</i>	PW6781
1coccocarp	<i>coccocarpa</i>	DGE 2020



2coccocarp	<i>coccocarpa</i>	ADH 1855
3coccocarp	<i>coccocarpa</i>	28.01.06/13
spnovaffvi	<i>sneeubergensis</i>	04.0106/5
1569con	<i>coccocarpa</i>	DGE 1569
VIITS4spno	<i>sp nov aff violacea</i>	020206/11
2021coccoc	<i>coccocarpa</i>	DGE 2021
A1855con	<i>coccocarpa (lesotho)</i>	ADH 1855
A850CON	<i>coccocarpa</i>	ADH 850
A1892con	<i>coccocarpa</i>	ADH 1892
EHITS4erod	<i>erodioides</i>	DGE 2142
1914cernua	<i>cernua</i>	DGE 1914
491nanacon	<i>nana</i>	DGE 491
ERITS4erod	<i>erodioides</i>	DGE 2379
2062depres	<i>depressa</i>	DGE 2062
depressa	<i>depressa</i>	10.03.03/2
auricoma	<i>auricoma</i>	PW 27.02.06
geniculata	<i>geniculata</i>	SPB 6516
traansvaal	<i>traansvaalensis</i>	DGE 2130
cordata	<i>cordata</i>	20.08.05/1
antonii	<i>antonii</i>	DGE 2127
antonii 1	<i>antonii</i>	Seagrief 3101
oblongifol	<i>oblongifolia</i>	10.03.03/15
stellulata	<i>stellulata</i>	100303/15
harveyi	<i>harveyi</i>	280106/25
parvula	<i>parvula</i>	050106/6
PCITS4pauc	<i>paucifolia</i>	100905/18
HWOITS4002	<i>woodii</i>	030106/1
GDITS4gerr	<i>gerrardii</i>	020106/1
2100traans	<i>traansvaalensis</i>	DGE 2100
GEITS4geni	<i>geniculata</i>	SPB 6516
HGRITS4004	<i>grandistipula</i>	PW6769
HBKITS5mbu	<i>burkei</i>	DGE 2398
2101lancif	<i>lancifolia</i>	DGE 2101
HLAITS4001	<i>lancifolia</i>	SPB 6599
2129montan	<i>montana</i>	DGE 2129
2297CON	sp.	
HQUITS4001	<i>quartiniana</i>	100306/9
H2198	sp.	DGE 2198
HGSITS4003	<i>lanterna</i>	27.10.05/44
ZGSITS4gro	<i>lanterna</i>	27.10.05/44
1937cedarb	<i>cedarbergensis</i>	DGE 1937
1322grossu	<i>grossularifolia</i>	DGE 1322
acocksii	<i>acocksii</i>	11.04.2006/1
1982albifl	<i>albiflora</i>	DGE 1982
ballerinic	<i>ballerinica</i>	18.09.2005
0ballerini	<i>ballerinica</i>	18.09.2005
cedarberge	<i>cedarbergensis</i>	DGE 2167
HN4ITS5mti	<i>tigrensis</i>	MNB 34
tigrensis	<i>tigrensis</i>	MNB 33
MOITS4mode	<i>modesta</i>	DGE 1374
1665spinos	<i>spinoso</i>	DGE 1665
spinoso	<i>spinoso</i>	DGE 1665
1361spinos	<i>spinoso</i>	DGE 1361
2040linear	<i>linearis</i>	DGE 2040

linearifol	<i>linearifolia</i>	140106/21
1374modest	<i>modesta</i>	DGE 1374
1383affini	<i>affinis</i>	DGE 1383
1362con	<i>fruticulosa</i>	DGE 1362
1367frutic	<i>fruticulosa</i>	DGE 1367
2017strict	<i>stricta</i>	DGE 2017
1369frutic	<i>fruticulosa</i>	DGE 1369
1372con	<i>fruticulosa</i>	DGE 1372
1379con	<i>eenii</i>	DGE 1379
2024toment	<i>tomentosa</i>	DGE 2024
1373engler	<i>engleriana</i>	DGE 1373
BOITS4bora	<i>boraginiflora</i>	DGE 2394
2078glandu	<i>glanduligera</i>	DGE 2078
glandulige	<i>glanduligera</i>	DGE 2085
1377gariiep	<i>gariepensis</i>	DGE 1377
1376gariiep	<i>gariepensis</i>	DGE 1376
2009trifur	<i>trifurca</i>	DGE 2009
TPITS4spno	<i>trifurcoides</i>	100905/17
1387amabil	<i>amabilis</i>	DGE 1387
		Greenway, P.J. & Kanuri 11832
UHITS5uhli	<i>uhligii</i>	(PRE)
palmeri	<i>palmeri</i>	TJA 1780
tex3	<i>texana</i>	Saunders 3415
2128crista	<i>cristata</i>	DGE 2128
2001pfeili	<i>pfeilii</i>	DGE 2001
1350con	<i>onychotenax</i>	DGE 1350
conglomera	<i>conglomerata</i>	280106/3
wcnp	<i>aff. scabra</i>	DGE s.n.
desertorum	<i>desertorum</i>	DGE 2146
confusa	<i>confusa</i>	DGE 1062
2150exleip	<i>exleipoldtii</i>	DGE 1250
1087murica	<i>muricata</i>	DGE 1087
1910incana	<i>incana</i>	DGE 1910
ZEITS4Echi	<i>echinocapsulare</i>	170905/s.n.
1770prisma	<i>prismatocarpus</i>	DGE 1770
1776rugosa	<i>rugosa</i>	DGE 1776
1075distic	<i>disticha</i>	DGE 1075
1771multif	<i>multiflora</i>	DGE 1771
1767con	sp.	DGE 1767
1884linifo	<i>linifolia</i>	DGE 1884
2151aspera	<i>aspera</i>	DGE 2151
1779hispid	<i>hispidula</i>	DGE 1779
HKCCcon	<i>cuneifolia</i>	DGE 1000
HKDcon	sp.	
linifolia	<i>linifolia</i>	141006/2
MIITS4micr	<i>micrantha</i>	D. Basich 1
1947procum	<i>procumbens</i>	DGE 1947
1101procum	<i>procumbens</i>	DGE 1101
1886scordi	<i>scordifolia</i>	DGE 1886
HCMITS4003	<i>comosa</i>	110306/10
1902.1asper	<i>aspera</i>	DGE 1902
368con	<i>minutiflora</i>	DGE 1368
1368minuti	<i>minutiflora</i>	DGE 1368
VSITS4vest	<i>vestita</i>	150106/11

1891johans	<i>johanssenii</i>	DGE 1891
decumbens	<i>decumbens</i>	DGE 1079
Dan10Hlive	<i>bolusii</i>	DTW 10
pulverata	<i>pulverata</i>	DGE 1893
HRAcon	<i>decumbens</i>	DGE s.n.
1774althae	<i>althaeoides</i>	DGE 1774
1966spnovd	<i>nessyii</i>	DGE 1966
1945con	<i>althaeifolia</i>	DGE 1945
1948con	<i>althaeifolia</i>	DGE 1948 ex. R. Turner
althaeoide	<i>althaeoides</i>	190106/10
muricata	<i>muricata</i>	DGE 1902
1355con	sp.	DGE 1355
1378comosa	<i>comosa</i>	DGE 1378
vampirica	<i>macra</i>	181005/s.n.
vampiricam	<i>macra</i>	181005/s.n.
2007macrac	<i>macra</i>	DGE 2007
MAITS5mmac	<i>macra</i>	DGE 2007
ISITS4skyf	<i>skyfii</i>	DGE 1105
2025bryoni	<i>bryoniifolia</i>	DGE 2025
filiifolia	<i>filiifolia</i>	DGE 1903
flammea	<i>flammea</i>	DGE 1913
ternifolia	<i>ternifolia</i>	DGE 1950
HCCITS4002	<i>concinifolia</i>	08.10.05/19
1913flamme	<i>flammea</i>	DGE 1913
HK960nrpag	<i>diversistipula</i>	DGE 960
1926filiif	<i>filiifolia</i>	DGE 1926
1717rudisC	<i>rudis</i>	DGE 1717
1979hyssop	<i>hyssopifolia</i>	DGE 1979
1310ternif	<i>ternifolia</i>	DGE 1310
1903filiif	<i>filiifolia</i>	DGE 1903
gracilis1	<i>gracilis</i>	081005/7
salviifoli	<i>salviifolia</i>	DGE 1973
1915decipi	<i>decipiens</i>	DGE 1915
1933CON	<i>cf. odorata</i>	DGE 1933
t389con	sp.	TT-S 389
HSUITS4004	<i>suavis</i>	210106/23
HVEITS4001	<i>velutina</i>	210106/10
1702sulcat	<i>sulcata</i>	DGE 1702
1932decipi	<i>decipiens</i>	DGE 1932
Waltherias	<i>Waltheria maritima</i>	J. Saunders 3195
2121Dombey	<i>Dombeya rotundifolia</i>	DGE 2121
1381Dombey	<i>Dombeya rotundifolia</i>	DGE 1381
DAN13melha	<i>Melhania sp.</i>	DTW 13
Brachychit	<i>Brachychiton populneus</i>	*AJ277463
fuertesima	<i>Fuertisimalva chilensis</i>	*DQ156318
Anisodonte	<i>Anisodonte malvastroides</i>	*EF419547
1904modiol	<i>Modiola caroliniana</i>	DGE 1904
tarasaoper	<i>Tarasa operculata</i>	*AY172225
Hibiscusco	<i>Hibiscus diversifolius</i>	DGE 1968
2053Corcho	<i>Corchorus asplenifolius</i>	DGE 2053
Corchorusa	<i>Corchorus aestuans</i>	*DQ311676
2124Triumf;	<i>Triumfetta welwitschii</i>	DGE 2124

#### Exemplars used in the chloroplast study

HJL	<i>serpens</i>	DGE 2097
HAK	<i>akkersdamensis</i>	DGE s.n.
HLG	<i>longipetala</i> (Stinkfontein)	DGE s.n.
DHCL	<i>coccocarpa</i> (Lesotho)	ADH 1855
HGF	<i>grandiflora</i>	DGE 2145
HAP	<i>leucantha</i>	300406/2
HMY	<i>mysteriosa</i>	DGE 1315
HNG	<i>pinnata</i> (riviersonderend)	11.05.06/1
HFA	<i>tutui</i>	DGE 1315
HCS	<i>cristata</i>	Steyn, H.M. 291
HLV	<i>linifolia</i> (Federicas commonage)	141006/2
HFO	<i>floribunda</i>	DGE 2027
HMC	<i>mucronulata</i>	DGE 1965
HDV	<i>diversistipula</i>	DGE 1957

**Table 10.9 Inflorescence morphology extracted from Verdoorn (1980). Column one is the species number in Verdoorn (1980). Column 3 is the number of flowers on a peduncle. The number of peduncles per axil is not recorded here. The last column is the summary of the description of inflorescence morphology per species.**

Verdoorn			
No.	Species	No. of flowers	Description
1	<i>cristata</i>	1	?
2	<i>merxmulleri</i>	1 to few	cyme
3	<i>sandersonii</i>	1	cyme
4	<i>seineri</i>	1	cyme
5	<i>tomentosa</i>	1	cyme
6	<i>eenii</i>	1	cyme
7	<i>boraginiflora</i>	1	cymes appearing racemose
9	<i>glanduligera</i>	1	cyme
8	<i>viscosa</i>	1	cyme
10	<i>glandulosissima</i>	1	cyme
11	<i>grisea</i>	1	appearing racemose
12	<i>solaniflora</i>	1	cymes appearing racemose
13	<i>minimiflora</i>	1	?
14	<i>engleri</i>	1	axillary cymes
15	<i>guerkeana</i>	1	cyme
16	<i>micropetala</i>	1	cyme
17	<i>amabilis</i>	1	cymes appearing racemose
18	<i>modesta</i>	1	cyme
19	<i>tigrens</i>	1	?
20	<i>linearifolia</i>	1	Pseudoraceme [racemose]
21	<i>helianthemum</i>	1	cymes appearing racemose
22	<i>damarana</i>	1	cyme
23	<i>garijepina</i>	1	cymes appearing racemose
24	<i>complicata</i>	1	cyme
25	<i>trifurca</i>	1	(pseudo) raceme
26	<i>affinis</i>	1	cyme

27	<i>fruticulosa</i>	1	cyme
28	<i>spinosa</i>	1	cyme
29	<i>linifolia</i>	1	cymes in terminal racemose cyme
30	<i>decumbens</i>	?	terminal in pseudocymose racemes or panicles
31	<i>prismatocarpa</i>	?	racemose or paniculate cymes
32	<i>scordifolia</i>	?	terminal forming paniculate or racemous cymes
33	<i>ternifolia</i>	usually 1	upper axils
34	<i>trifoliata</i>	?	cymes in terminal heads
35	<i>concinifolia</i>	1 to 2	upper axils
36	<i>muirii</i>	1 to 2	cymes in upper axils
		1 to several	
37	<i>floribunda</i>	(mostly 3)	cymes in upper axils axillary on ultimate dichotomous branches that appear to be racemose or paniculate cymes
38	<i>bryoniifolia</i>	1-3 (usually 2) compound axillary, terminal 2- fld	
39	<i>cordifolia</i>	?	compound, axillary cymes
40	<i>hispidula</i>	?	racemose cyme
41	<i>rugosa</i>	1 to 3	racemose cymes
42	<i>althaeoides</i>	1 to several	cymes
43	<i>minutiflora</i>	1 to 3	cymes in upper axils
44	<i>althaeifolia</i>	2 or 3	pseudopanicles
45	<i>johanssenii</i>	1 to 2 (rarely 3)	racemose cymes
46	<i>comosa</i>	usually 2 1 to several	cymes in upper axils
47	<i>incana</i>	(usually 2)	paniculate cymes
48	<i>vestita</i>	1 to 3	racemose cymes
49	<i>amoena</i>	2 to 3	racemose or paniculate cymes
50	<i>disermifolia</i>	1 to 3	pseudoracemose cyme
51	<i>mucronulata</i>	few-flowered	upper axils
52	<i>suavis</i>	?	cymes in upper axils
53	<i>hyssopifolia</i>	?	apical bracteate cymes
54	<i>salviifolia</i>	1 to 2	cymes in upper axils forming dense clusters
55	<i>holoserica</i>	?	compound cymes
56	<i>lavandulifolia</i>	1 to 3	leaf-opposed cymes
57	<i>odorata</i>	few-flowered	pseudoracemose cyme
58	<i>sulcata</i>	?	racemose cymes
59	<i>velutina</i>	?	paniculate cymes
60	<i>gracilis</i>	few-flowered	racemose cymes
61	<i>diversistipula</i>	usually 2	axillary cyme
62	<i>cuneifolia</i>	1 to 2	raceme of secund cymes
63	<i>desertorum</i>	few-flowered	racemose cymes
64	<i>pfeilii</i>	few-flowered	racemose cymes
65	<i>multiflora</i>	1 to 2	racemose cymes
66	<i>alnifolia</i>	2 to 3	racemose or paniculate cymes
67	<i>muricata</i>	?	paniculate cymes
68	<i>repetenda</i>	?	paniculate cymes
69	<i>rigida</i>	1 to 3	cymes
70	<i>helicoidea</i>	?	scorpioid cymes
71	<i>aspera</i>	?	simple or paniculate cymes
72	<i>conglomerata</i>	?	sessile cymes

73	<i>micrantha</i>	1 to 2	racemose cymes
74	<i>disticha</i>	few-flowered	racemose or paniculate cymes
75	<i>decipiens</i>	few-flowered	simple or branched cyme
76	<i>involutrata</i>	few-flowered	branched cyme
77	<i>pillansii</i>	1 to 2	cymes
78	<i>stipulacea</i>	1 to 2	cymes
79	<i>filiifolia</i> var. <i>f.</i>	1 or more	racemose cymes
80	<i>denudata</i>	1 to 3	cymes
81	<i>flammea</i>	1 to 2	racemose cymes
82	<i>flammula</i>	1 to 2	cymes
83	<i>joubertiana</i>	2 to 3	cymes
84	<i>scabra</i>	1 to 2	racemose or paniculate cymes
85	<i>angularis</i>	2	cymes
86	<i>rudis</i>	1 to 2	cymes
87	<i>abrotanoides</i>	1 to 2	racemose cymes
88	<i>pulverata</i>	1 to 2	racemose cymes
89	<i>procumbens</i>	few-flowered	racemose cymes
90	<i>confusa</i>	1 to 2	racemose cymes
91	<i>macra</i>	1 to 2	racemose or paniculate cymes
92	<i>juttae</i>	1 to 2	racemose cymes
93	<i>paucifolia</i>	1 to 2	racemose or paniculate cymes

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**Table 11.0.11 Character list utilized in the DELTA package. The character number is preceded by a „#“ sign, the states are in the lines below, with the state number followed by a „,“, and no number indicates a continuous character with the units given. The start of sections of major organs are highlighted with bold font.**

- 
- |   |   |
|---|---|
| <p>#1. Synonyms/<br/> #2. &lt;Longevity of plants&gt;/<br/>     1. Perennial/<br/>     2. Annual/<br/> #3. &lt;Habit, whether compact or loose&gt;/<br/>     1. compact/<br/>     2. cushion-shaped/<br/>     3. loosely branched/<br/> #4. &lt;Habit&gt;/<br/>     1. herb/<br/>     2. dwarf shrub/<br/>     3. shrub/<br/>     4. suffrutex/<br/> #5. Height &lt;plant&gt;/<br/>     cm/<br/> #6. Diameter &lt;plant&gt;/<br/>     cm/<br/> #7. <b>Stems</b> &lt;firmness&gt;/<br/>     1. herbaceous/<br/>     2. sub-herbaceous/<br/>     3. sub-woody/<br/>     4. woody/<br/> #8. Stems &lt;taproot&gt;/<br/>     1. from a central taproot &lt;lying flat&gt;/<br/>     2. arising annually from a perennial<br/>     rootstock/<br/> #9. Stems &lt;direction&gt;/<br/>     1. straggling/<br/>     2. sprawling/<br/>     3. decumbent/<br/>     4. procumbent/<br/>     5. ascending/<br/>     6. erect/<br/>     7. virgate/<br/>     8. divaricate &lt;wide-angled branching&gt;/<br/> #10. Stems &lt;whether slender or robust&gt;/<br/>     1. slender/<br/>     2. robust/<br/> #11. Stems &lt;density&gt;/<br/>     1. sparsely branched/<br/>     2. densely branched/</p> | <p>#12. Stems &lt;branching position&gt;/<br/>     1. branched from the base/<br/>     2. branched in the upper part/<br/> #13. Young stems &lt;colour&gt;/<br/>     1. green/<br/>     2. brown/<br/>     3. reddish brown/<br/>     4. dark brown/<br/>     5. grey/<br/> #14. Young stems &lt;sculpturing&gt;/<br/>     1. smooth/<br/>     2. longitudinally finely grooved/<br/> #15. Mature stems &lt;stems condition&gt;/<br/>     1. waxy/<br/>     2. older bark peeling in grey silvery strips/<br/> #16. Mature stems &lt;colour&gt;/<br/>     1. green/<br/>     2. brown/<br/>     3. reddish brown/<br/>     4. blackish/<br/>     5. blackish grey/<br/>     6. grey/<br/>     7. silvery/<br/> #17. Underground part/<br/>     1. a woody taproot/<br/>     2. an erect woody root-stock/<br/>     3. a branched system of roots/<br/>     4. a branched system of rhizomes/<br/>     5. a number of fusiform swollen roots/<br/>     6. not known/<br/> #18. Young growth &lt;whether glabrous,<br/>     glandular or with an indumentum&gt;/<br/>     1. glabrous/<br/>     2. glandular/<br/>     3. becoming 'varnished' due to glands<br/>     deliquescing/<br/>     4. viscous/<br/>     5. with an indumentum &lt;eg. stellate<br/>     hairs&gt;/<br/> #19. Mature growth &lt;indumentum&gt;/<br/>     1. glabrescent/</p> |
|---|---|



2. with indumentum sparser/  
3. retaining the indumentum/  
#20. **Indumentum** <general description>  
<whether inconspicuous or only visible under a lens>/  
1. inconspicuous <not detectable with the naked eye>/  
2. detectable with the naked eye <conspicuous>/
- #21. Indumentum <whether dense, sparse etc>/  
1. very sparse/  
2. sparse/  
3. moderately dense/  
4. dense/  
5. very dense/
- #22. Indumentum <whether pubescent, tomentose, etc.>/  
1. puberulous <sparsely hairy>/  
2. pubescent <softly shortly hairy>/  
3. tomentose <dense, fine erect hairs>/  
4. villous <long weak, crisped? hairs>/  
5. hispid <stiff bristly hairs>/  
6. felted <like felt, dense intertwined hairs>/  
7. lepidote <with flat appressed, scalelike hairs>/
- #23. Indumentum <additional description>/  
#24. Indumentum <whether white, brown etc.>/  
1. white/  
2. silvery white/  
3. silvery green/  
4. silvery yellow/  
5. grey/  
6. yellowish/  
7. brownish/  
8. pale brown/  
9. golden brown/  
10. yellowish green/
- #25. Indumentum consisting of/  
1. glandular hairs/  
2. stellate hairs/  
3. unicellular bristles/  
4. unicellular crisped hairs/  
5. multicellular crisped hairs/
- #26. <Description of plant part indumentum>/  
#27. Glandular hairs <whether conspicuous or inconspicuous>/  
1. inconspicuous/
2. easily overlooked when mixed with stellate hairs/  
3. conspicuous even when mixed with stellate hairs/  
4. with glands immersed in the epidermal surface/
- #28. Glandular hairs consisting of/  
1. sessile globose hairs/  
2. sub-sessile globose hairs/  
3. stalked hairs/
- #29. Glandular hairs sessile or sub-sessile, globose <whether minute - clearly visible with a 25x lens; medium sized - clearly visible with a 15x lens; or large - clearly visible with a 10x lens>/  
1. minute/  
2. medium sized/  
3. large/  
4. variable in size/
- #30. Glandular hairs sessile or sub-sessile, globose, <whether sparse, dense etc.>/  
1. very sparse/  
2. sparse/  
3. moderately dense/  
4. dense/  
5. very dense/
- #31. Stalked glandular hairs <whether minute - clearly visible with a 25x lens; medium sized - clearly visible with a 15x lens; or large - clearly visible with a 10x lens>/  
1. minute/  
2. medium sized/  
3. large/  
4. variable in size/
- #32. Stalked glandular hairs <whether dense, sparse etc>/  
1. very sparse/  
2. sparse/  
3. moderately dense/  
4. dense/  
5. very dense/
- #33. Stalked glandular hairs <shape>/  
1. globoid/  
2. pin-shaped/  
3. club-shaped/  
4. cone-shaped/  
5. strap-shaped/  
6. shortly stalked/

7. disc-shaped/
- #34. Stalked glandular hairs <whether stalk is longer, shorter etc. than the apical gland>/
1. stalk shorter than the apical gland/
  2. stalk as long as apical gland/
  3. stalk 2 to 4 times as long the apical gland/
  4. stalk 5 to many times as long as the apical gland/
- #35. Stalked glandular hairs <whether stalk terete, flattened etc.>/
1. terete/
  2. conical/
  3. flattened/
  4. with alternate cells laterally flattened/
- #36. Apical cell of stalked glandular hair <whether pale or dark>/
1. pale/
  2. dark/
  3. purple/
  4. amber/
- #37. Stellate hairs <whether present, dense, sparse etc>/
1. absent/
  2. very sparse/
  3. sparse/
  4. moderately dense/
  5. dense/
  6. very dense/
- #38. Stellate hairs <whether minute - clearly visible with a 25x lens; medium sized - clearly visible with a 15x lens; or large - clearly visible with a 10x lens>/
1. minute/
  2. medium sized/
  3. large/
  4. variable in size/
- #39. Stellate hairs <whether coarse or fine>/
1. very fine/
  2. fine/
  3. coarse/
  4. <not so (implicit)>/
- #40. Stellate hairs <whether uniform or variable in size on the same organ>/
1. more or less uniform in size/
  2. variable in size/
- #41. Stellate hairs <Whether different in size on the different organs, small on the...; larger on the...; small and large on the...>/
- #42. Stellate hairs <whether tufted, with a central disc or peltate>/
1. tufted/
  2. spreading/
  3. apressed/
  4. strongly apressed/
  5. with a central disc/
  6. with a strongly developed central disc/
  7. peltate/
  8. scalelike/
  9. scalelike, strongly apressed/
  10. some reduced to a single bristle/
- #43. Stellate hairs <whether sessile or stalked etc.>/
1. sessile/
  2. sub-sessile/
  3. stalk up to 1/3 the length of the arms/
  4. stalk up to 1/2 the length of the arms/
  5. stalk more than 1/2 the length of the arms/
- #44. Stellate hairs <whether bulbous based or not>/
1. bulbous based/
  2. not bulbous based (explicit)/
- #45. Stellate hairs <hair colour>/
1. silvery white/
  2. yellowish/
- #46. Stellate hair branches <whether bristly, etc.>/
1. slender/
  2. soft/
  3. crisped/
  4. shaggy/
  5. woolly/
  6. bristly/
- #47. Stellate hair branches <whether few (2-5), several (6-10), numerous (11 or more)>/
1. sometimes reduced to a single bristle/
  2. few (2-6)/
  3. several (7-10)/
  4. numerous (11 or more)/
- #48. Multicellular hairs <whether elongate soft etc.>/
1. some hairs gland tipped/

- 2. elongate/
  - 3. crisped/
  - 4. woolly and soft/
  - 5. somewhat bristly/
- #49. Unicellular simple hairs <whether bristly, soft etc.>/
- 1. fine/
  - 2. soft/
  - 3. woolly/
  - 4. long and slender/
  - 5. crisped/
  - 6. bristly/
- #50. **Stipules** <size relative to leaves>/
- 1. smaller than the leaves/
  - 2. foliaceous/
  - 3. indistinguishable from the leaves/
- #51. Stipules <division>/
- 1. one on each side of the petiole/
  - 2. divided into a number of separate elements and together with the leaves, forming a leafy whorl at each node/
- #52. Stipules <shape>/
- 1. linear/
  - 2. narrowly oblong/
  - 3. oblong/
  - 4. broadly oblong/
  - 5. narrowly ovate/
  - 6. ovate/
  - 7. broadly ovate/
  - 8. narrowly obovate/
  - 9. obovate/
  - 10. broadly obovate/
  - 11. orbicular/
  - 12. narrowly triangular/
  - 13. triangular/
  - 14. broadly triangular/
  - 15. antler shaped/
  - 16. elliptic/
  - 17. lanceate-elliptic/
- #53. Stipules <whether entire or lobed>/
- 1. entire <usually>/
  - 2. serrate/
  - 3. toothed at apex/
  - 4. shallowly lobed/
  - 5. deeply lobed/
  - 6. consisting of one large and one small lobe/
  - 7. lacerate/
- #54. Stipules <clasping stem etc.>/
- 1. base narrowed/
  - 2. base as wide as stipule/
  - 3. base wide clasping the stem/
  - 4. connate, clasping the stem/
  - 5. leaving a node-like ring after dehiscing/
- #55. Stipules <whether larger in the upper part of the plant>/
- 1. larger in the upper part of the plant/
  - 2. not larger <(implicit)>/
- #56. Stipules <colour>/
- 1. green/
  - 2. brown/
  - 3. dark rusty brown/
- #57. Stipules <length>/
- mm long/
- #58. Stipules <whether glabrous or covered with an indumentum>/
- 1. glabrous/
  - 2. subglabrous/
  - 3. <with an indumentum (explicit)>/
- #59. Stipules <whether sparsely or densely covered with hairs, glands>/
- 1. very sparsely/
  - 2. sparsely/
  - 3. moderately densely/
  - 4. densely/
  - 5. very densely/
- #60. Stipules <whether glabrous or covered with an indumentum>/
- 1. covered with/
  - 2. covered with a mixture of/
- #61. Stipules <whether with glands stellate hairs etc.>/
- 1. globose sessile glands/
  - 2. globose sub-sessile glands/
  - 3. pin-shaped glands/
  - 4. cone-shaped glands/
  - 5. club-shaped glands/
  - 6. strap-shaped glands/
  - 7. stellate hairs/
  - 8. coarse stellate hairs/
  - 9. fine stellate hairs/
  - 10. multicellular crisped hairs/
  - 11. unicellular bristles/
  - 12. unicellular crisped hairs/
  - 13. unicellular soft hairs/
  - 14. bristly hairs/

- #62. Stipules <whether with glands, stellate hairs etc., adaxially, abaxially or on both surfaces>/
1. adaxially/
  2. abaxially/
- #63. Leaves <arrangement>/
1. alternate/
  2. in spirals/
  3. forming pseudo-whorls together with stipules/
  4. densely clustered on abbreviated shoots/
  5. clustered towards the end of branches/
- #64. Leaves <texture>/
1. herbaceous/
  2. succulent/
  3. sub-succulent/
  4. leathery/
  5. papery/
  6. membranous/
- #65. Leaves <sessile or petiolate>/
1. sessile/
  2. sub-sessile/
  3. shortly petiolate/
  4. petiolate/
- #66. Petioles <length>/
- mm long/
- #67. Petioles <diameter>/
- mm/
- #68. Petioles <whether grooved or not>/
1. grooved/
  2. shallowly grooved/
  3. terete <cylindrical>/
  4. flattened/
- #69. Petioles <whether glabrous or covered with an indumentum>/
1. glabrous/
  2. <with indumentum (implicit)>/
- #70. Petioles <whether sparsely or densely covered with hairs, glands>/
1. very sparsely/
  2. sparsely/
  3. moderately densely/
  4. densely/
  5. very densely/
- #71. Petioles <whether covered with one or more types of hairs>/
1. covered with/
  2. covered with a mixture of/
- #72. Petioles <whether with glands, stellate hairs etc.>/
1. globose sessile glands/
  2. globose sub-sessile glands/
  3. pin-shaped glands/
  4. cone-shaped glands/
  5. strap-shaped glands/
  6. stellate hairs/
  7. coarse stellate hairs/
  8. fine stellate hairs/
  9. multicellular crisped hairs/
  10. unicellular bristles/
  11. unicellular soft hairs/
- #73. Leaf blade <uniformity of shape>/
1. fairly uniform in shape/
  2. variable in shape/
  3. very variable in shape/
- #74. Leaf blade <uniformity of size>/
1. fairly uniform in size/
  2. variable in size/
  3. very variable in size/
- #75. Leaf blade <whether flat>/
1. flat/
  2. plicate <folded/pleated like a fan>/
  3. conduplicate <folded together lengthwise>/
- #76. Leaf blade <lobing, pinnate/bipinnate>/
1. pinnately lobed/
  2. bipinnately lobed/
  3. pinnately lacerate/
  4. bipinnately lacerate/
- #77. Leaf blade <lobes, shape>/
1. filiform/
  2. linear/
  3. elliptic/
  4. elliptic-ovate/
  5. ovate/
  6. ovate-oblong/
  7. elliptic-oblong/
  8. narrowly-oblong/
  9. oblong/
  10. obovate/
  11. obovate-oblong/
  12. cuneate/
  13. obovate-cuneate/
  14. orbicular/
  15. sub-orbicular/
  16. in outline <in dissected leaves>/

#78. Leaf blade <whether narrow broad etc.>/

1. narrowly/
2. broadly/
3. narrowly to broadly/

#79. Leaf blade <shape>/

1. filiform/
2. linear/
3. lanceate/
4. lanceate-elliptic/
5. elliptic/
6. elliptic-ovate/
7. ovate/
8. ovate-oblong/
9. elliptic-oblong/
10. oblong/
11. oblanceate/
12. obovate/
13. obovate-oblong/
14. cuneate/
15. obovate-cuneate/
16. orbicular/
17. sub-orbicular/
18. in outline <in dissected leaves>/

#80. Leaf blade <length>/  
mm long/

#81. Leaf blade <width>/  
mm/

#82. Adaxial surface <of leaf blade, whether  
glabrous or covered with an  
indumentum>/

1. glabrous/
2. subglabrous/
3. with the nerves glabrous/
4. with the indumentum concentrated on  
the nerves/
5. with the indumentum concentrated in  
the areoles <the spaces between the  
veins>/
6. with indumentum spread evenly  
<(implicit)>/

#83. Adaxial surface <of leaf blade whether  
sparsely, densely covered with hairs,  
glands>/

1. very sparsely/
2. sparsely/
3. moderately densely/
4. densely/
5. very densely/

#84. Adaxial surface <of leaf blade whether  
covered with one or more types of hairs  
or glands>/

1. covered with/
2. covered with a mixture of/

#85. Adaxial surface <of leaf blade whether with  
glands, stellate hairs etc.>/

1. globose sessile glands/
2. globose sub-sessile glands/
3. pin-shaped glands/
4. cone-shaped glands/
5. strap-shaped glands/
6. stellate hairs/
7. coarse stellate hairs/
8. fine stellate hairs/
9. multicellular crisped hairs/
10. unicellular bristles/
11. unicellular soft hairs/

#86. Abaxial surface <of leaf blade whether  
glabrous or covered with an  
indumentum>/

1. glabrous/
2. subglabrous/
3. with the nerves glabrous/
4. with the indumentum concentrated on  
the nerves/
5. with the indumentum concentrated in  
the areoles/
6. <with indumentum spread evenly  
(explicit)>/

#87. Abaxial surface <of leaf blade whether  
sparsely, densely covered with hairs,  
glands>/

1. very sparsely/
2. sparsely/
3. moderately densely/
4. densely/
5. very densely/

#88. Abaxial surface <of leaf blade whether  
covered with one or more types of  
hairs>/

1. covered with/
2. covered with a mixture of/

#89. Abaxial surface <of leaf blade whether with  
glands, stellate hairs etc.>/

1. globose sessile glands/
2. globose subsessile glands/
3. pin-shaped glands/

- 4. cone-shaped glands/
- 5. strap-shaped glands/
- 6. stellate hairs/
- 7. coarse stellate hairs/
- 8. fine stellate hairs/
- 9. multicellular crisped hairs/
- 10. unicellular bristles/
- 11. unicellular soft hairs/
- 12. globose sub-sessile glands/
- 13. glandular/
- #90. Apex <of leaf blade>/
  - 1. acuminate/
  - 2. acute/
  - 3. obtuse/
  - 4. rounded/
  - 5. truncate/
- #91. Apex <of leaf blade, lobing>/
  - 1. lobed/
  - 2. 3-lobed/
  - 3. crenate/
  - 4. entire/
  - 5. coarsely toothed/
- #92. Base <of leaf>/
  - 1. acuminate/
  - 2. cuneate/
  - 3. rounded/
  - 4. cordate/
  - 5. flattened/
- #93. **Margin** <of leaf>/
  - 1. entire/
  - 2. <not entire, explicit>/
- #94. **Margin** <of leaf>/
  - 1. coarsely/
  - 2. finely/
  - 3. distinctly/
  - 4. obscurely/
  - 5. deeply/
  - 6. shallowly/
  - 7. unevenly/
- #95. **Margin** <serration>/
  - 1. dentate/
  - 2. serrate/
  - 3. serrate-crenate/
  - 4. dentate-serrate/
  - 5. lacerate/
  - 6. crenate/
  - 7. crenate-dentate/
  - 8. crenate-undulate/
  - 9. corrugated/
  - 10. lobate-crenate/
  - 11. sinuate/
  - 12. lobate, with lobes obtuse to acute/
  - 13. lobate-serrate/
- #96. **Margin** <whether dentate etc. in the upper 1/3, 1/2>/
  - 1. in upper third/
  - 2. in upper half/
  - 3. in the upper 1/3 to 1/2/
  - 4. in upper 2/3/
  - 5. <whole margin (implicit)>/
- #97. **Margin** <whether involute or flat>/
  - 1. involute/
  - 2. flat/
  - 3. undulate/
  - 4. crinkled/
- #98. **Margin** <additional description>/
- #99. **Margin** <indumentum density>/
  - 1. sparsely/
  - 2. densely/
  - 3. not sparsely or densely/
- #100. **Margin** <indumentum>/
  - 1. ciliate with stiff hairs/
  - 2. ciliate with stalked glands/
  - 3. sparsely glandular/
  - 4. stellate hairy/
  - 5. sparsely stellate/
  - 6. stellate scaly/
  - 7. glabrous/
  - 8. with a narrow red-brown rim/
  - 9. glandular/
- #101. **Venation** adaxially <type>/
  - 1. obscure/
  - 2. only midrib visible/
  - 3. only midrib and secondary veins visible/
  - 4. reticulate/
- #102. **Venation** adaxially <whether level, etc.>/
  - 1. level with leaf surface/
  - 2. slightly raised above the leaf surface/
  - 3. strongly raised above leaf surface/
  - 4. slightly sunken into the leaf surface/
  - 5. deeply sunken into the leaf surface/
- #103. **Venation** abaxially <type>/
  - 1. obscure/
  - 2. only midrib visible/
  - 3. only midrib and secondary veins visible/
  - 4. reticulate/

- #104. Venation abaxially <whether level etc>/  
 1. level with leaf surface/  
 2. slightly raised above the leaf surface/  
 3. strongly raised above leaf surface/  
 #105. Venation abaxially <where raised>/  
 1. only midrib raised/  
 2. midrib and secondary veins raised/  
 3. slightly sunken into the leaf surface/  
 4. deeply sunken into the leaf surface/  
 #106. Secondary veins <number>/  
 <to> on each side of midvein/  
 #107. Secondary veins <spacing>/  
 1. spaced more or less evenly/  
 2. 2 basal veins approximate/  
 3. 3 or more basal veins approximate/  
 4. obscure/  
 #108. Secondary veins <angle that secondary  
 veins make with midvein>/  
 1. almost parallel to midrib/  
 2. with acuminate angle with midvein <0–  
 44>/  
 3. with acute angle with midvein <45–64>/  
 4. with blunt angle with midvein <65–90>/  
 #109. **Inflorescence** <consisting of>/  
 1. one-flowered/  
 2. two-flowered (geminate)/  
 3. three-flowered/  
 4. several-flowered/  
 5. many-flowered/  
 6. many-flowered, compound/  
 7. many-flowered clusters of cymes  
 arranged in/  
 #110. Inflorescence <appearance>/  
 1. dense/  
 2. somewhat contracted/  
 3. lax/  
 4. very lax and open/  
 #111. Inflorescence <whether secund or not>/  
 1. secund/  
 2. not secund, (implicit)/  
 #112. Inflorescence <position>/  
 1. axillary/  
 2. pseudoterminal/  
 3. leaf-opposed/  
 #113. Inflorescence <type>/  
 1. cymes/  
 2. cymose racemes/  
 3. cymose panicles/  
 4. compound cyme/  
 5. <additional description>/  
 #114. Inflorescence <where borne>/  
 1. borne towards the ends of branches/  
 2. borne towards the ends of branches with  
 the supporting leaves diminishing in  
 size towards the apex of the branch/  
 3. borne erect on decumbent stems/  
 4. borne on erect sidebranches of  
 decumbent stems/  
 5. consisting of geminate cymes at ends of  
 branches with the leaves completely  
 reduced/  
 6. borne spread along young branches/  
 #115. Inflorescence <length>/  
 mm long/  
 #116. Inflorescence <width, for compound  
 inflorescences only>/  
 mm wide/  
 #117. **Peduncle** <length>/  
 mm long/  
 #118. Peduncle of ultimate cymes <length, for  
 compound inflorescences only>/  
 mm long/  
 #119. Peduncle of geminate cymes <length>/  
 mm long/  
 #120. Peduncle <whether glabrous or covered  
 with an indumentum>/  
 1. glabrous/  
 2. <with indumentum (implicit)>/  
 #121. Peduncle <whether sparsely or densely  
 covered with hairs, glands>/  
 1. very sparsely/  
 2. sparsely/  
 3. moderately densely/  
 4. densely/  
 5. very densely/  
 #122. Peduncle <indumentum covering>/  
 1. covered with <an indumentum>/  
 2. covered with a mixture of <hair or gland  
 types>/  
 #123. Peduncle <indumentum type>/  
 1. globose sessile glands/  
 2. globose sub-sessile glands/  
 3. pin-shaped glands/  
 4. cone-shaped glands/  
 5. strap-shaped glands/  
 6. stellate hairs/

7. coarse stellate hairs/  
 8. fine stellate hairs/  
 9. multicellular crisped hairs/  
 10. unicellular bristles/  
 11. unicellular soft hairs/  
 12. obscure glands/  
 13. glandular - not valid char/  
 #124. **Bracts** <whether present(number) or absent>/  
 1. absent/  
 2. minute/  
 3. one/  
 4. two/  
 5. three/  
 6. <present (implicit)>/  
 #125. Bracts <whether joined>/  
 1. connate/  
 2. connate at base/  
 3. free/  
 #126. Bracts <peduncle piercing; when bract envelopes peduncle>/  
 1. asymmetrically pierced by the peduncle/  
 2. more or less symmetrically pierced by the peduncle/  
 3. <not pierced (implicit)>/  
 #127. Bracts <whether narrow or broad>/  
 1. narrowly/  
 2. broadly/  
 3. very broadly/  
 4. <not narrow nor broad (implicit)>/  
 #128. Bracts <shape>/  
 1. linear/  
 2. oblong/  
 3. elliptic/  
 4. ovate/  
 5. obovate/  
 6. orbicular/  
 7. sub-orbicular/  
 8. <other shapes>/  
 9. linear-lanceate/  
 #129. Bracts <shape 2 eg. hooded>/  
 1. hooded/  
 2. boat-shaped/  
 3. salver-shaped/  
 4. asymmetrically saucer-shaped <in perforated leaves only>/  
 #130. Lobes of bracts <whether lobed>/  
 1. entire/  
 2. lobed/  
 #131. Lobes <of bracts>/  
 1. lobes very shallow/  
 2. lobes up to half the length of the bract/  
 3. lobes more than half the length of the bract/  
 4. lobed to near the base/  
 5. bilobed, lobes entire or shallowly lobed at apex/  
 6. antler-shaped/  
 7. lacerate/  
 #132. Lobes <of bracts, describe>/  
 #133. Bracts <size>/  
 mm. long/  
 #134. Bracts <indumentum glabrosity>/  
 1. glabrous/  
 2. sub-glabrous/  
 3. <with indumentum (explicit)>/  
 #135. Bracts <indumentum density>/  
 1. very sparsely/  
 2. sparsely/  
 3. moderately densely/  
 4. densely/  
 5. very densely/  
 #136. Bracts <covering>/  
 1. covered with/  
 2. covered with a mixture of/  
 #137. Bracts <indumentum types>/  
 1. globose sessile glands/  
 2. globose sub-sessile glands/  
 3. pin-shaped glands/  
 4. cone-shaped glands/  
 5. strap-shaped glands/  
 6. stellate hairs/  
 7. coarse stellate hairs/  
 8. fine stellate hairs/  
 9. unicellular crisped hairs/  
 10. multicellular crisped hairs/  
 11. unicellular bristles/  
 12. unicellular soft hairs/  
 13. glandular <older forms>/  
 14. hairy <older forms>/  
 #138. **Pedicels** <thickness>/  
 1. filiform/  
 2. slender/  
 3. stout/  
 #139. Pedicels <length in non-geminate cymes>/  
 mm long in non-geminate cymes/



- #140. Pedicels upper <pedicel length in geminate-cymes>/  
mm long in geminate-cymes/
- #141. Pedicels upper <pedicels exertion from bract>/  
1. well exerted from the bract/  
2. shortly exerted from the bract/  
3. included in the bract/
- #142. Pedicels lower <pedicels length in geminate-cymes>/  
mm long/
- #143. Pedicels lower <pedicel exertion from bract in geminate-cyme>/  
1. included in the bract/  
2. as long as the bract <possibly redundant as equals included>/  
3. shortly exerted from the bract/  
4. well exerted from the bract/
- #144. Pedicels <whether sparsely or densely covered with hairs, glands>/  
1. very sparsely/  
2. sparsely/  
3. moderately densely/  
4. densely/  
5. very densely/
- #145. Pedicels <whether glabrous or covered with an indumentum>/  
1. glabrous/  
2. <with indumentum (explicit)>/
- #146. Pedicels <whether covered with an indumentum of one or more types of hair>/  
1. covered with/  
2. covered with a mixture of/
- #147. Pedicels <whether with glands stellate hairs etc.>/  
1. globose sessile glands/  
2. globose sub-sessile glands/  
3. pin-shaped glands/  
4. cone-shaped glands/  
5. strap-shaped glands/  
6. stellate hairs/  
7. coarse stellate hairs/  
8. shaggy stellate hairy/  
9. fine stellate hairs/  
10. multicellular crisped hairs/  
11. unicellular bristles/  
12. unicellular soft hairs/
13. glandular/
- #148. Pedicels <additional description of indumentum>/
- #149. **Flowers** <bearing>/  
1. cernuous/  
2. erect/  
3. pendulous/
- #150. Flowers <shape>/  
1. urceolate/  
2. campanulate/  
3. mouth constricted, petals contorted/  
4. cup-shaped/
- #151. Flowers <with petals flared or not>/  
1. the limb of the petals flared/  
2. not flared (explicit)/
- #152. Flowers <colour>/  
1. white/  
2. cream/  
3. pale yellow/  
4. yellow/  
5. dark yellow/  
6. orange/  
7. orange-red/  
8. red/  
9. scarlet/  
10. brick red/  
11. salmon/  
12. pink/  
13. mauve/  
14. purple/  
15. blue/  
16. petals tipped with red/  
17. one margin of petal red/  
18. liver coloured/
- #153. Flowers <whether scented or not>/  
1. strongly scented/  
2. scented/  
3. <not scented (implicit)>/  
4. <additional description>/
- #154. Flowers <diameter of flower from petal tip to petal tip>/  
mm diameter/
- #155. Flowers <width of throat>/  
mm/
- #156. **Calyx** <shape>/  
1. urceolate/  
2. campanulate/  
3. patelliform <pan or dish shaped>/

- 4. inflated/
- 5. bladder-shaped/
- 6. angled/
- 7. cup-shaped/
- #157. Calyx <texture>/
  - 1. firm/
  - 2. membranous/
  - 3. chartaceous <papery>/
  - 4. leathery/
- #158. Calyx <whether accrescent or not>/
  - 1. slightly accrescent in fruit/
  - 2. accrescent <increasing in size> in fruit/
  - 3. strongly accrescent in fruit/
  - 4. not accrescent in fruit <implied>/
- #159. Calyx <length>/
  - mm long/
- #160. Calyx <width>/
  - mm wide/
- #161. Abaxial surface <outside of calyx, whether glabrous or covered with an indumentum>/
  - 1. glabrous/
  - 2. <with indumentum (implicit)>/
- #162. Abaxial surface <of calyx, whether sparsely or densely covered with hairs, glands>/
  - 1. very sparsely/
  - 2. sparsely/
  - 3. moderately densely/
  - 4. densely/
  - 5. very densely/
- #163. Abaxial surface <of calyx, whether covered with an indumentum of one or more types of hair>/
  - 1. covered with/
  - 2. covered with a mixture of/
- #164. Abaxial surface <of calyx, whether with glands stellate hairs etc.>/
  - 1. globose sessile glands/
  - 2. globose subsessile glands/
  - 3. pin-shaped glands/
  - 4. cone-shaped glands/
  - 5. strap-shaped glands/
  - 6. papillate glandular hairs/
  - 7. stellate hairs/
  - 8. coarse stellate hairs/
  - 9. fine stellate hairs/
  - 10. multicellular crisped hairs/
- 11. unicellular bristles/
- 12. unicellular soft hairs/
- #165. Adaxial surface <inside of calyx, whether glabrous or with an indumentum>/
  - 1. glabrous/
  - 2. with an indumentum (implicit)/
- #166. Adaxial surface <hair density of calyx>/
  - 1. very sparsely/
  - 2. sparsely/
  - 3. moderately densely/
  - 4. densely/
  - 5. very densely/
- #167. Adaxial surface <of calyx, whether covered with an indumentum of one or more types of hair>/
  - 1. covered with/
  - 2. covered with a mixture of/
- #168. Adaxial surface <of calyx, whether with indumentum>/
  - 1. globose sessile glands/
  - 2. globose subsessile glands/
  - 3. pin-shaped glands/
  - 4. cone-shaped glands/
  - 5. strap-shaped glands/
  - 6. papillate glandular hairs/
  - 7. stellate hairs/
  - 8. coarse stellate hairs/
  - 9. fine stellate hairs/
  - 10. multicellular crisped hairs/
  - 11. unicellular bristles/
  - 12. unicellular soft hairs/
  - 13. club-shaped glands/
- #169. Calyx lobes with veins <vein visibility>/
  - 1. indistinct/
  - 2. distinct <clearly visible>/
  - 3. not raised/
  - 4. slightly raised/
  - 5. strongly raised/
  - 6. reticulate/
- #170. Calyx lobes with veins <how much raised>/
  - 1. not raised/
  - 2. slightly raised/
  - 3. strongly raised/
  - 4. reticulate/
- #171. Calyx lobes <length>/
  - 1. shorter than the tube/
  - 2. as long as the tube/

3. longer than the tube/  
#172. Calyx lobes <whether narrow or reduced>/  
1. abruptly narrowed from the rim of the tube/  
2. reduced to a mucro on the rim of the tube/  
3. lobes well developed/  
#173. Calyx lobes <shape>/  
1. linear/  
2. narrowly triangular/  
3. triangular/  
4. broadly triangular/  
5. narrowly ovate/  
6. ovate/  
7. broadly ovate/  
8. obovate/  
9. broadly obovate/  
#174. Apex <of lobes>/  
1. obtuse/  
2. acute/  
3. acuminate/  
#175. Margin <of lobes>/  
1. glabrous/  
2. fimbriate/  
3. glandular/  
4. fringed with fine crisped simple hairs/  
5. fringed with bristles/  
6. stellate/  
7. indumentum as on tube/  
8. entire/  
#176. **Petals** <whether convolute etc.>/  
1. convolute/  
2. <not convolute(implicit)>/  
#177. Petals <length w.r.t calyx>/  
1. longer than the calyx/  
2. as long as the calyx/  
3. shorter than the calyx/  
#178. Petals <length>/  
mm long/  
#179. Petals <width>/  
mm wide/  
#180. Petals <shape>/  
1. narrowly oblong/  
2. oblong/  
3. broadly oblong/  
4. narrowly ovate/  
5. ovate/  
6. broadly ovate/  
7. narrowly obovate/  
8. narrowly obovate cuneate/  
9. narrowly obovate attenuate/  
10. obovate/  
11. spathulate/  
12. broadly obovate/  
13. obovate cuneate/  
14. broadly obovate cuneate/  
15. suborbicular/  
16. cuneate/  
17. elliptic oblong/  
#181. Petals <whether gradually or abruptly narrowed into>/  
1. gradually narrowed into/  
2. abruptly narrowed into/  
#182. Petals <limb(base) of petals narrowed into>/  
1. an obscure claw/  
2. a short claw/  
3. a well developed claw/  
#183. Petals <whether glabrous or with an indumentum>/  
1. glabrous adaxially/  
2. glabrous abaxially/  
3. with an indumentum/  
#184. Adaxial petal indumentum <whether sparsely or densely covered with hairs, glands>/  
1. very sparsely/  
2. sparsely/  
3. moderately densely/  
4. densely/  
5. very densely/  
#185. Adaxial petal indumentum <Petals, whether covered with an indumentum of one or more types of hair, adaxially>/  
1. covered with/  
2. covered with a mixture of/  
#186. Adaxial petal indumentum <Petals, whether with glands stellate hairs etc.adaxially>/  
1. globose sessile glands/  
2. globose subsessile glands/  
3. pin-shaped glands/  
4. cone-shaped glands/  
5. strap-shaped glands/  
6. stellate hairs/  
7. coarse stellate hairs/

8. fine stellate hairs/
  9. retrorse stellate hairs/
  10. multicellular crisped hairs/
  11. unicellular bristles/
  12. retrorse unicellular bristles/
  13. unicellular soft hairs/
- #187. Adaxial petal indumentum <Petals, whether indumentum is in lower or upper half adaxially>/
1. on the lower part of the claw/
  2. in lower half/
  3. in lower 3/4/
  4. on the upper part of the claw/
  5. in upper half/
  6. on claw only/
  7. in the throat of the claw/
  8. on the infolded part of the claw/
  9. all over/
- #188. Abaxially <Petals, whether sparsely or densely covered with hairs, glands abaxially>/
1. very sparsely/
  2. sparsely/
  3. moderately densely/
  4. densely/
  5. very densely/
- #189. Abaxially <Petals, whether covered with an indumentum of one or more types of hair abaxially>/
1. glabrous/
  2. covered with/
  3. covered with a mixture of/
- #190. Abaxially <Petals, whether indumentum white or silvery>/
1. silvery white/
  2. white/
  3. not silvery or white (implicit)/
- #191. Abaxially <Petals, whether with glands stellate hairs etc. abaxially>/
1. globose sessile glands/
  2. pin-shaped glands/
  3. cone-shaped glands/
  4. strap-shaped glands/
  5. stellate hairs/
  6. coarse stellate hairs/
  7. coarse, retrorse stellate hairs/
  8. fine stellate hairs/
  9. fine retrorse, stellate hairs/
10. multicellular crisped hairs/
  11. unicellular bristles/
  12. unicellular soft hairs/
- #192. Abaxially <Petals, whether indumentum is in lower or upper half etc. abaxially>/
1. in the lower half/
  2. in the lower 3/4/
  3. in the upper half/
  4. on the claw only/
  5. on the upper part of the claw/
  6. on the lower part of the claw/
  7. all over/
- #193. Claw <length>/  
mm long/
- #194. Claw <width>/  
mm wide/
- #195. Claw <whether straight or curved>/
1. straight/
  2. curved/
  3. bent at (nearly) a right angle to the limb/
- #196. Claw <lenght w.r.t limb>/
1. shorter than the limb/
  2. as long as the limb/
  3. longer than the limb/
- #197. Claw <indumentum>/
1. glabrous/
  2. glandular with sessile glands/
  3. glandular with stalked glands/
  4. stellate hairy/
  5. retrorsely stellate hairy/
  6. retrorsely bristly/
  7. bristly/
- #198. Claw <whether hairy adaxially or abaxially>/
1. in the mouth/
  2. on the keel/
  3. on the infolded part/
  4. abaxially/
  5. adaxially/
- #199. Claw <margin>/
1. an adaxial infolded margin/
  2. an adaxially strongly infolded margin/
  3. flat/
- #200. Stamens 5 <length>/  
mm long, opposite the carpels/
- #201. **Filaments** <length>/  
mm long/
- #202. Filaments <free or joined>/

1. free/
  2. joined at the base/
  3. joined to the base of the ovary to form a short stipe/
  4. joined to form a staminal tube/
- #203. Filaments <dilation>/
1. cruciform, widened abruptly below the apex into two arms which do not overlap the base of the anther/
  2. abruptly widened just below the apex but not cruciform the dilated part not overlapping the base of the anther/
  3. widened at the apex, the widened part overlapping the base of the anther/
  4. widened towards the middle the widened part not overlapping the base of the anther/
  5. hardly widened upwards but abruptly narrowed just below the apex/
  6. gradually widened upward and abruptly narrowed just below the base of the anther/
  7. (*Hermannia*) Gradually rounded and overlapping the base of the anther/
- #204. Filaments <texture>/
1. membranous and hyaline/
  2. submembranous/
  3. chartaceous <=papery>/
  4. firm/
  5. fleshy/
  6. leathery/
- #205. Filaments <narrow or broad>/
1. narrowly/
  2. broadly/
  3. <not narrow nor broad (implicit)>/
- #206. Filaments <shape>/
1. linear/
  2. strap-shaped/
  3. elliptic/
  4. oblong/
  5. ovate/
  6. obovate/
  7. obtrullate/
  8. triangular/
- #207. Filaments <whether glabrous or with an indumentum>/
1. glabrous/
  2. <not glabrous (implicit)>/
- #208. Filaments <whether sparsely or densely covered with hairs, glands>/
1. very sparsely/
  2. sparsely/
  3. moderately densely/
  4. densely/
  5. very densely/
- #209. Filaments <whether covered with an indumentum of one or more types of hair>/
1. covered with/
  2. covered with a mixture of/
- #210. Filaments <whether with glands stellate hairs etc.>/
1. globose sessile glands/
  2. globose sub-sessile glands/
  3. pin-shaped glands/
  4. cone-shaped glands/
  5. strap-shaped glands/
  6. stellate hairs/
  7. coarse stellate hairs/
  8. coarse, retrorse stellate hairs/
  9. fine stellate hairs/
  10. fine retrorse, stellate hairs/
  11. multicellular crisped hairs/
  12. unicellular bristles/
  13. unicellular soft hairs/
- #211. Filaments <whether indumentum in upper or lower half etc.>/
1. in the upper half/
  2. in the upper two thirds/
  3. in the lower half/
  4. all over (implicit)/
- #212. Apex <of filaments>/
1. obtuse/
  2. truncate/
  3. rounded/
  4. narrowed and attenuate/
  5. filiform/
- #213. Arms <of filaments>/
1. transversely oblong/
  2. crescent-shaped/
  3. transversely reniform/
  4. truncate-triangular/
  5. kite-shaped/
  6. ob-triangular/
  7. gradually merging into the filament/
  8. poorly developed/

9. absent/
- #214. Arms <of filaments, in relation to base>/
1. approximate to base of anther/
  2. somewhat removed from the base of the anther/
  3. remote from base of anther/
  4. (*Hermannia*) Overlapping base of anther/
- #215. Arms <of filaments, flanges>/
1. without a raised flange/
  2. with a weakly developed flange/
  3. with an abaxial thickened flange/
  4. with a strongly developed abaxial flange/
- #216. Arms <of filaments, whether sparsely or densely hairy or not>/
1. sparsely hairy/
  2. fairly densely hairy/
  3. densely hairy/
- #217. Arms <of filaments, whether stellate hairy or bristly>/
1. glandular/
  2. with sessile glands/
  3. with sub-sessile glands/
  4. with stalked glands/
  5. stellate hairy/
  6. stellate bristly/
  7. bristly/
- #218. Arms <of filaments, where hairy>/
1. on the arms/
  2. on the thickened flange/
  3. on the extremities of the arms/
  4. all over (implicit)/
- #219. **Anther** <shape>/
1. lanceate/
  2. narrowly lanceate/
  3. narrowly lanceate-acuminate/
  4. lanceate-acuminate/
  5. narrowly oblong-lanceate/
  6. lanceate-oblong/
  7. base saccate/
- #220. Anther <length>/  
mm long/
- #221. Anther <width>/  
mm wide/
- #222. Anther <length w.r.t. filament>/
1. shorter than the part of the filament below it/
  2. as long as the part of the filament below it/
  3. longer than the part of the filament below it/
- #223. Anther <indumentum>/
1. glabrous/
  2. base of the anther thecae glabrous/
  3. base of the anther thecae with an upturned beard/
  4. base of anther thecae bearded/
  5. bristly on the sutures/
- #224. Anther <suture indumentum>/
1. bristly on the sutures/
  2. glabrous on the sutures/
- #225. **Ovary** five locular, placentation axillary <shape>/
1. depressed globoid/
  2. obloid/truncate/
  3. ovoid/
  4. narrowly obovoid/
  5. obovoid/
  6. broadly obovoid/
  7. oblong/
  8. broadly oblong/
  9. sub-globose/
- #226. Ovary <lobing>/
1. smooth/
  2. angled/
  3. lobed/
  4. ribbed/
  5. longitudinally grooved/
  6. <not angled, lobed (implicit)>/
- #227. Ovary <length>/  
mm long/
- #228. Ovary <width>/  
mm wide/
- #229. Ovary <whether sparsely or densely covered with hairs, glands>/
1. very sparsely/
  2. sparsely/
  3. moderately densely/
  4. densely/
  5. very densely/
- #230. Ovary <whether covered with an indumentum of one or more types of hair>/
1. covered with/
  2. covered with a mixture of/

- #231. Ovary <whether with glands stellate hairs etc.>/
1. globose sessile glands/
  2. globose sub-sessile glands/
  3. pin-shaped glands/
  4. cone-shaped glands/
  5. strap-shaped glands/
  6. stellate hairs/
  7. coarse stellate hairs/
  8. coarse, retrorse stellate hairs/
  9. fine stellate hairs/
  10. fine retrorse, stellate hairs/
  11. unicellular soft hairs/
  12. unicellular bristles/
  13. multicellular crisped hairs/
- #232. Ovary with indumentum <on angles & ribs only>/
1. on angles only/
  2. on ribs only/
  3. mainly on ribs/
  4. on apex of capsule/
- #233. Ovary <whether sessile, stipitate etc.>/
1. sessile/
  2. subsessile/
  3. shortly stipitate/
  4. conspicuously stipitate/
- #234. Styles 5, cohering <thickness>/
1. slender/
  2. stout/
  3. base somewhat swollen/
- #235. Styles <whether hairy or glabrous etc.>/
1. glabrous/
  2. glandular/
  3. stellate hairy/
  4. bristly/
- #236. Styles <length w.r.t. ovary>/
1. shorter than the ovary/
  2. as long as the ovary/
  3. longer than the ovary/
  4. much longer than the ovary/
- #237. Locules <of ovary>/
1. five/
- #238. Placenta <of ovary>/
1. axillary/
- #239. Ovules <ovules, whether few or many>/
1. numerous in each locule/
  2. few in each locule/
- #240. Capsule <shape>/
1. globose/
  2. sub-globose/
  3. obloid/
  4. obloid/truncate/
  5. ovoid/
  6. cylindric/
  7. ellipsoid/
  8. obovoid/
- #241. Capsule <length>/
- mm long/
- #242. Capsule <width>/
- mm wide/
- #243. Capsule <sessile or stipitate>/
1. sessile/
  2. subsessile/
  3. stipitate/
- #244. Capsule <dehiscence>/
1. tardily dehiscent/
  2. dehiscent/
- #245. Capsule <whether glabrous , sparsely or densely covered with hairs, glands>/
1. glabrous/
  2. very sparsely/
  3. sparsely/
  4. moderately densely/
  5. densely/
  6. very densely/
- #246. Capsule <indumentum covered?>/
1. covered with/
  2. covered with a mixture of/
- #247. Capsule <hair types>/
1. globose sessile glands/
  2. globose subsessile glands/
  3. stalked glands/
  4. pin-shaped glands/
  5. cone-shaped glands/
  6. strap-shaped glands/
  7. stellate hairs/
  8. fine stellate hairs/
  9. fine retrorse, stellate hairs/
  10. coarse stellate hairs/
  11. coarse, retrorse stellate hairs/
  12. unicellular soft hairs/
  13. unicellular bristles/
  14. multicellular crisped hairs/
- #248. Capsule <surface>/
1. smooth/
  2. bumpy/

- 3. angled/
  - 4. strongly angled/
  - 5. ribbed/
  - 6. shallowly grooved/
  - #249. Capsule angles or ribs <fringing of angles or ribs>/
    - 1. with sessile glands/
    - 2. with subsessile glands/
    - 3. with stalked glands/
    - 4. with pin-shaped glands/
    - 5. with stellate hairs/
    - 6. fringed with fine hairs/
    - 7. fringed with bristles/
  - #250. Capsule wall <whether firm, membranous, etc.>/
    - 1. membranous/
    - 2. chartaceous/
    - 3. firm in texture/
    - 4. leathery/
  - #251. Capsule wall <nerves, whether prominent or not>/
    - 1. nerves not raised/
    - 2. nerves slightly raised/
    - 3. nerves prominent/
  - #252. Carpels <apices & appendages>/
    - 1. with rounded apices/
    - 2. with short horn-like appendages/
    - 3. with long curved horn-like appendages/
  - #253. Seeds <shape>/
    - 1. reniform/
    - 2. sub-reniform/
    - 3. comma-shaped/
    - 4. angled/
  - #254. Seeds <surface texture>/
    - 1. smooth/
    - 2. finely rugose/
    - 3. tubercled/
    - 4. ribbed/
    - 5. corrugated/
  - #255. Seeds <colour>/
    - 1. brown/
    - 2. grey/
    - 3. black/
  - #256. Seeds <presence of white hilum>/
    - 1. with a white hilum/
    - 2. without a white hilum/
  - #257. Seeds <length>/
    - mm long/
  - #258. Seeds <width>/
    - mm wide/
  - #259. Chromosome number/
  - #260. Flowering <month>/
    - 1. January/
    - 2. February/
    - 3. March/
    - 4. April/
    - 5. May/
    - 6. June/
    - 7. July/
    - 8. August/
    - 9. September/
    - 10. October/
    - 11. November/
    - 12. December/
  - #261. Fruiting <month>/
    - 1. January/
    - 2. February/
    - 3. March/
    - 4. April/
    - 5. May/
    - 6. June/
    - 7. July/
    - 8. August/
    - 9. September/
    - 10. October/
    - 11. November/
    - 12. December/
  - #262. <Descriptive comment on flowering and fruiting>/
  - #263. **Habitat**/
  - #264. **Abundance**/
  - #265. **Affinities** with other species/
  - #266. **Distribution**/
  - #267. Notes/
  - #268. **Diagnostic characteristics**/
-



## 10.4 Guide to the summer-rainfall *Hermannia* species published in Plantlife, 2005.

### Discovering Doll's Roses

*A quick guide to identifying Hermannias of the Summer Rainfall areas of South Africa*

*Hermannia* "the doll's roses or poprosies" is a delightful and easily recognizable genus despite having a fantastic diversity of forms. It is worth recognizing as it is found in nearly every habitat in South Africa, and is often flowering when not much else is. It is easily recognized by the pendulous flowers with overlapping petals. They are sprawling herbs to woody shrubs. Around 200 species exist, with only five occurring outside Africa. Most species can be found in Southern Africa, with a concentration of endemics in the Cape, Namibia and the summer rainfall regions of South Africa. These 200 species are split almost in half into two subgenera. Subgenus *Hermannia* is typically Namibian (pink flowered) or Cape (yellow or orange flowered) and has the filament expanded above the base of the anther (See Fig 1, LHS). The Subgenus *Mahernia* contains a kaleidoscope of colours (red to blue to yellow to white), with petals ranging from closed (*H. pulchella*) to bell-shaped (*H. depressa*) to flaring (*H. saccifera*). Around half occur in the summer rainfall regions of South Africa, with the filament expanded below the base of the anther forming a cruciform (cross-like) filament (See fig 1, RHS).

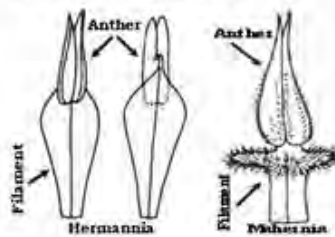


Fig 1



Fig 2

**Using this guide:** This article is designed to allow you to easily identify a specimen based on the leaf shape, the flower structure, and then the distribution. The leaves and flowers are depicted at life size, and are based on mature herbarium specimens. The key is useful in confirming your species. At this stage, many of the *Mahernia* are currently unpublished, and reliable identification can only be done at Pretoria herbarium, however publication will come soon and the names can be regarded as the most correct at this stage.

***Hermannia* collecting and atlasing:** Most *Hermannias* can readily be identified by photo, so if you see a *Hermannia* and have a GPS or camera with you please pass the information to me at [capebio@gmail.com](mailto:capebio@gmail.com).

species	voucher #	#*	alt (m)				
<i>antonii</i>	Codd, L.E. 2700	27	c. 1000	<i>montana</i>	Strey, R.G. 3215	c. 30	1000-1400
<i>auricoma</i>	Compton, R.H. 2966	17	750-1500	<i>oblongifolia</i>	Retief, E. 917	48	1200-1700
<i>Bicolor</i>	Leistner, O.A. 898	56	840-1700	<i>oligosperma</i>	Esterhuysen, 15496	16	1600-2300
<i>Brachymalla</i>	de Villiers, M. 103	15	1100-2500	<i>parviflora</i>	Flanagan, H.G. 2530	81	650-2000
<i>Burkei</i>	Hansen, O.J. 3157	104	1200-1500	<i>parvula</i>	Codd, L.E. 1137	23	1500-1600
<i>Coccocarpa</i>	Gemishuizen, G. 8738	350	400-3200		Retief & Gemishuizen 149	130	600-1300
<i>Cordata</i>	Smith, C.A. 1100	144	1440-1900	<i>pulchella</i>			
<i>Depressa</i>	van der Meulen, F. 106	196	660-1700	<i>quartiniiana</i>	Venter, F. 1907	126	700-2250
<i>Erodioides</i>	Herman, P. 1168	95	400-1700	<i>resedifolia</i>	Badenhorst, P.J. 48		900
<i>Geniculata</i>	Jenkins, T.J. 10245	107	600-2300	<i>rogersii</i>	Gemishuizen, G. 204		c. 1700
<i>gerrardii</i>	Pentz, J.A. 304	31	1000-2000	<i>saccifera</i>	Mauve, A.A. 4682	129	10-1500
<i>Grandifolia</i>	Bayliss, R.D.A. 7352	61	850-1600	<i>schlechteriana</i>	Ngwenya, A.M. 954	5	c. 1400
<i>Grandistipula</i>	Meyer, J.J. 184	156	500-1700	<i>staurostemon</i>	Jordean, M. 2938	41	1900-2100
<i>Lacera</i>	Olivier, M.C. 1695	66	20-700	<i>stellulata</i>	Acoccks, J.P.H. 1480	107	1200-1800
<i>Lanceifolia</i>	Thode 397A	110	500-2100	<i>transvaalensis</i>	Bruce, E.A. 473	56	1500-2300
<i>Linsaris</i>	Muller, P. 679	30	600-1500	<i>umbatica</i>	Van der Meulen, 274	10	1050-1600
<i>livinoides</i>	Acoccks, J.P.H. 215	30	1100-1400	<i>veronicifolia</i>	Archibald, EEA 5600	10	100-200
<i>mauiifolia</i>	Killick 29653	27	1800-2300	<i>woodii</i>	Ngwenya, A.M. 1697	8	250-2000
<i>middelburgensis</i>	Rogers, F.A. 24179	17	1400-1650	<i>violacea</i>	Phillipson, P.B. 914	3	1000-1300

\* refers to the number of specimens examined.

## Key to the species.

### Group 1: Leaves deeply incised to lacerate

- Deeply incised leaves; creeping stems; large upright pink or orange flower, S. coast..... *lacera*  
Characteristically lobed leaves; short erect to sprawling shrub; flowers pink to mauve, Kimberley region..... *resedifolia*  
Finely dissected leaves; upright shrub; red flowers, Gauteng & Transvaal..... *dissectifolia*

### Group 2: Leaves glabrous with a shiny appearance due to sessile glands

- Characteristically lobed leaf, flowers typically pink & white striped, mostly Western & Northern Cape..... *bicolor*  
Linear to slightly toothed margin, flowers pink to deep red, flowers bell-shaped..... *linearis*  
Densely leafy shrub with shiny leaves, flowers broadest in the middle, bright yellow fading to white..... *pulchella*

### Group 3: Leaves incised to lobed

- Species with many forms, plants upright, leaves serrate, flowers mauve to blue or pink, bell shaped..... *coccocarpa*  
Flat, spreading plant with characteristic broad incised leaves, flowers upright on very slender pedicels..... *erodioides*

### Group 4: Leaves entire or finely serrate, narrow to broad, flowers small

- Leaves small and narrow, flowers yellow, Gauteng..... *parvula*  
Leaves like *parvula*, to broad and oblong, flowers like *parvula* or in clusters, Natal and E Cape..... *parviflora*  
Neatly egg-shaped leaf, mauve flower, E. Cape..... *violacea*

### Group 5: Leaves broad, obovate, almost hairless

- Upright woody plant; leaves very coarsely toothed; all parts including petals stellate hairy; petals mauve to purple..... *schlechteriana*  
Plant semi-upright; leaves finely toothed; flowers flaring, yellow turning orange; petals hairless, calyx visibly hairy..... *veronicifolia*  
Sprawling plant with large flared yellow flowers; leaves coarsely toothed; all parts including petals and calyx glabrous..... *saccifera*

### Group 6: Leaves obovate, flat on ground; plants prostrate or from underground stems. Flowers orange, pink or yellow

- Glossy leaves mostly flat on ground, often purple coloured. Flowers orange to pink, occ. yellow. Grassland..... *depressa*  
Leaves tiny, against the ground in calcrete limestone pavements. Orange flowers small on upright pedicel..... *linnaeoides*

### Group 7: Leaves serrate, oblanceolata

- Plants scrambling to shrub forming, flowers typically yellow or cream, calyx reflexed..... *quartiniana*  
Leaves sprawling and ground hugging, flowers pink..... *stellulata*

### Group 8: Very erect plants with alternate, acute-angled ascending branches. Dense white stellate hairs on vegetative parts

- Flowers small in axillary clusters..... *antonii*  
Flowers larger with large calyx; flowers mostly terminal..... *staurostemon*

### Group 9: Leaves oblanceolate-linear, grey tomentosa, on thin stems

- Stems short and mostly unbranched. Leaves grey, dense on stem. Large yellow flowers..... *lanceifolia*  
Stems longer, more branched, with trailing stems. Flowers pink..... *oblongifolia*

### Group 10: Dull green leaves, grayish below; sprawling to weakly erect stemmed resprouters; Eastern Transvaal

- Leaves mostly small; plants with weak descending stems, forming densely leafy bushes..... *montana*  
Leaves larger, with distinctly raised midrib on leaf underside..... *brachymalla*  
Sprawling, densely leafy plant. Leaf venation obscure above but very visible below. Pilgrim's Rest area..... *rogersii*

### Group 11: Leaves discolorous with white woolly hairs on leaf underside and on inflorescences and stems; plants prostrate

- Leaves strongly discolorous, heart shaped; upper leaf sandpapery; Flowers in a woolly compound inflorescence..... *cordata*  
Leaves strongly discolorous, flowers biggest in gems on upright stalks from prostrate branches..... *geniculata*

### Group 12: Leaves large with stellate hairs, large flowers

- Plants with characteristic leaf, sparsely hairy. Flowers pink or red, petals exerted. Stellate hairs on veins on leaf underside..... *woodii*  
Leaf characteristically shaped, coarse stellate hairs..... *auricoma*  
Small multistemmed plants; radially spreading conspicuous stipules; petals barely protruding from calyx..... *grandis tipula*  
Leaves coarsely hairy; Amber coloured stellate hairs between veins above, but on veins below..... *transvaalensis*  
Amber coloured stellate hairs between veins above and below leaf..... *middelburgensis*

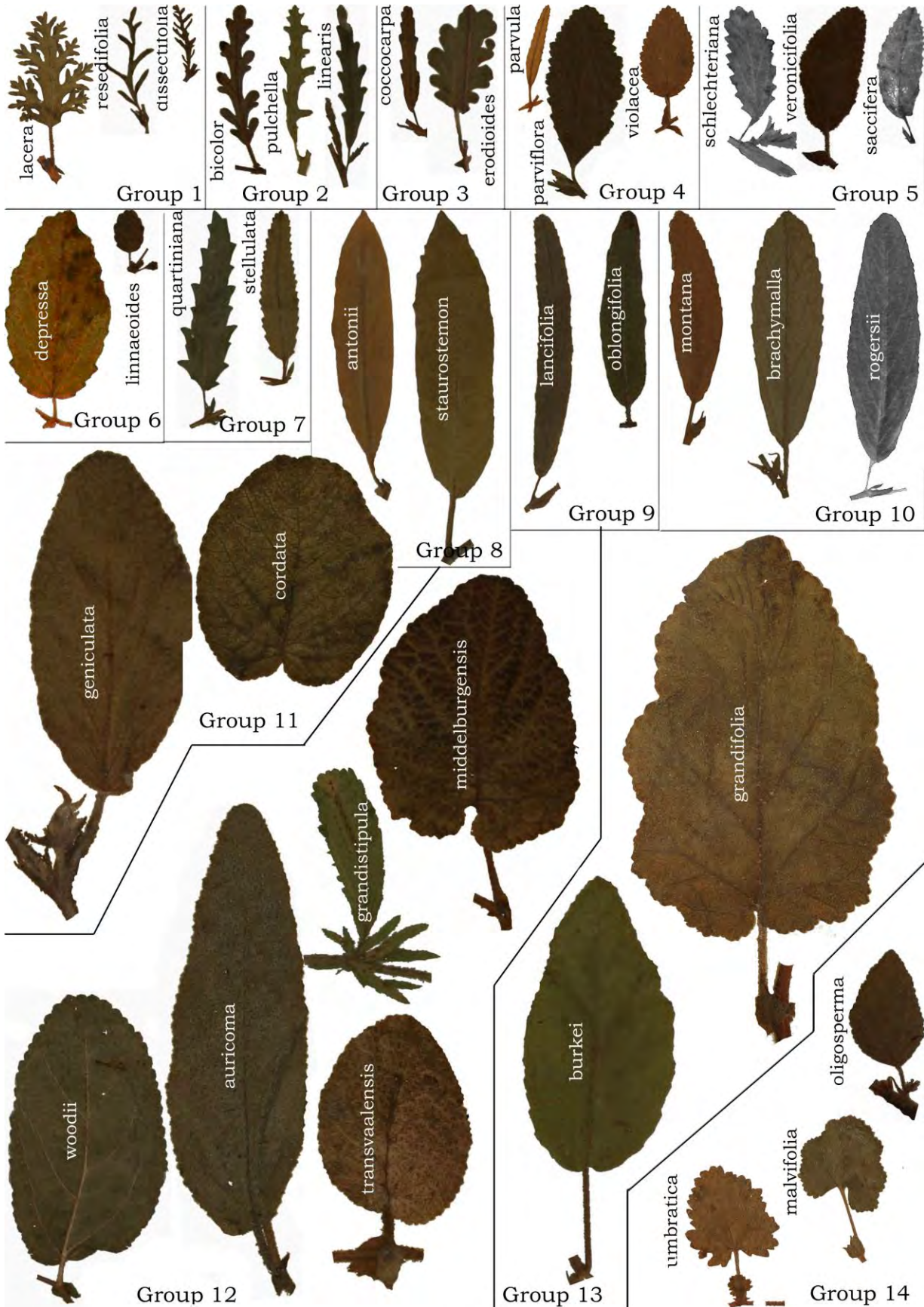
### Group 13: Leaves medium sized to massive; Inflorescences compound, petals well exerted from petals

- Largest leaves in genus, slightly discolorous with grey below; flowers in a compound inflorescence, stipules entire..... *grandifolia*  
Leaves resembling *geniculata* but with broader, cordate base, varying from *cordata* sized to bigger than *grandifolia*; Flowers in compound inflorescence. Large stipules lacerate..... *ferrardii*  
Sticky yellowish shrub with calyx becoming much larger in fruit. Leaves typically sparse forming untidy bush..... *burkei*

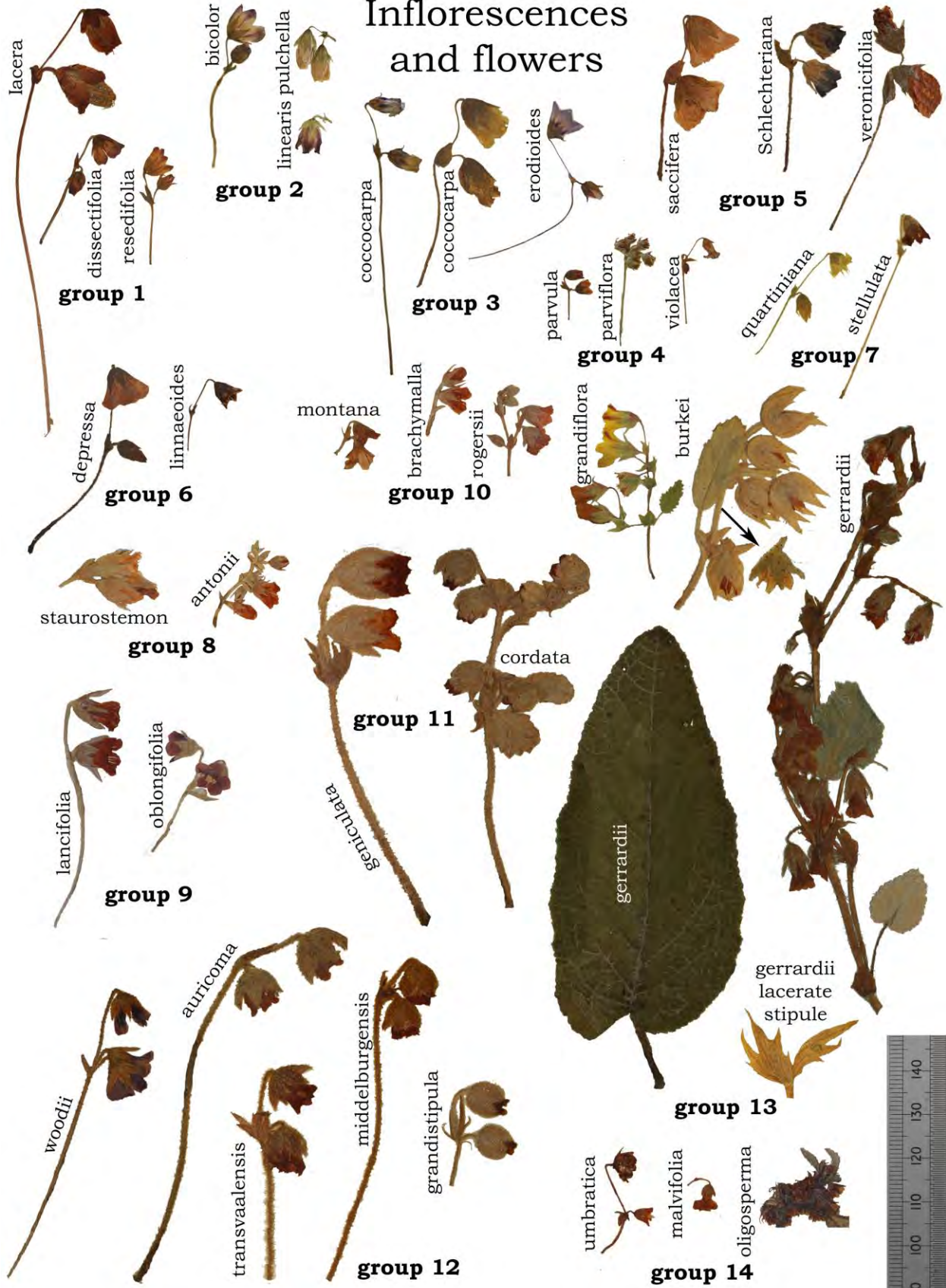
### Group 14: Small cordate or egg-shaped leaves, Drakensberg or Gauteng

- Plants sprawling with characteristic heart-shaped leaves; small yellow to white flowers, Gauteng..... *umbatica*  
Plants like *umbatica* but finer toothed and Drakensberg region, sprawling over rocks..... *mahifolia*  
Woody, upright plant with flowers small but in large dense clusters. Drakensberg mountains..... *oligosperma*

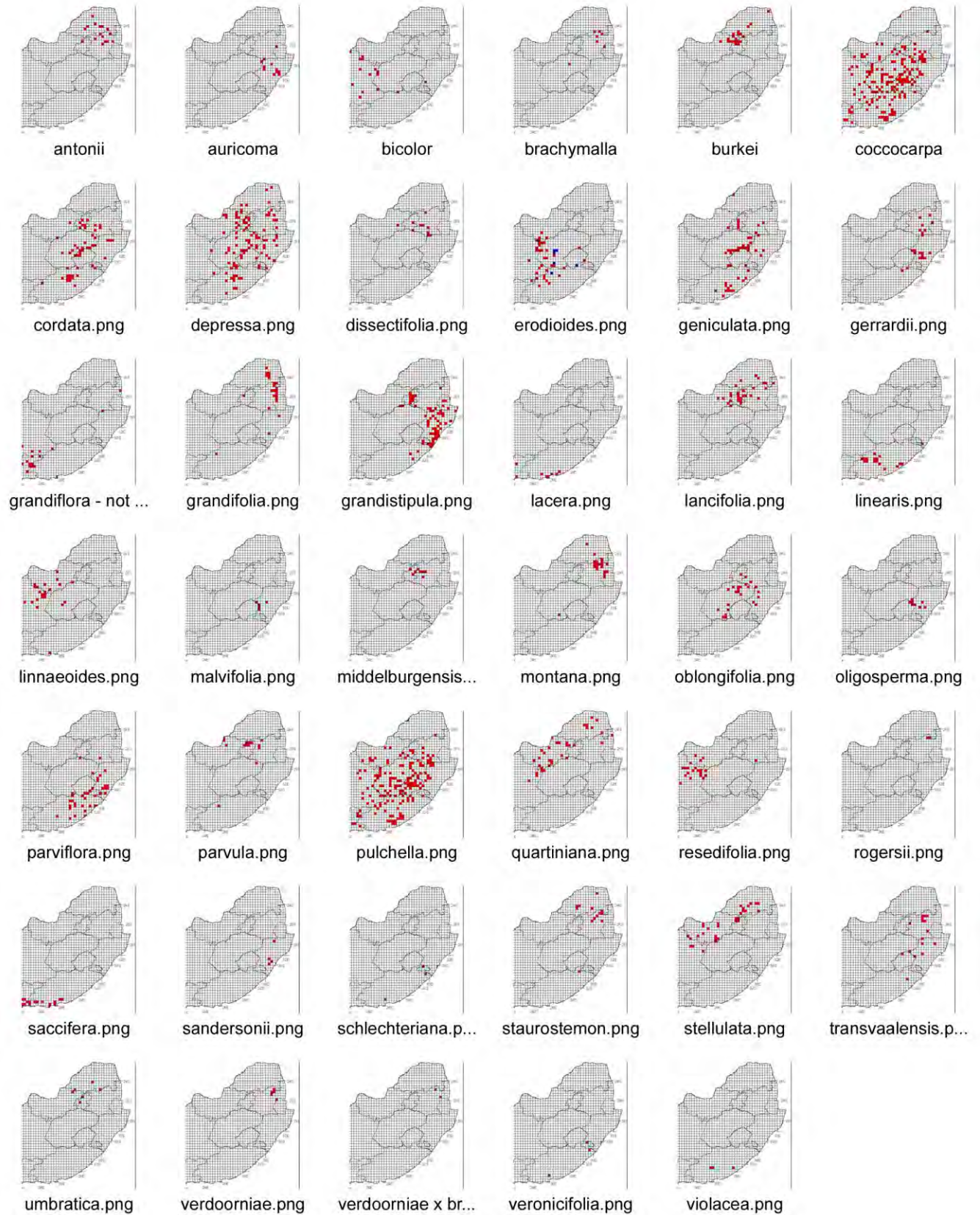




# Inflorescences and flowers







## 10.5 Screenshots incorporating *Hermannia* in the new online database and atlas, CASABIO.

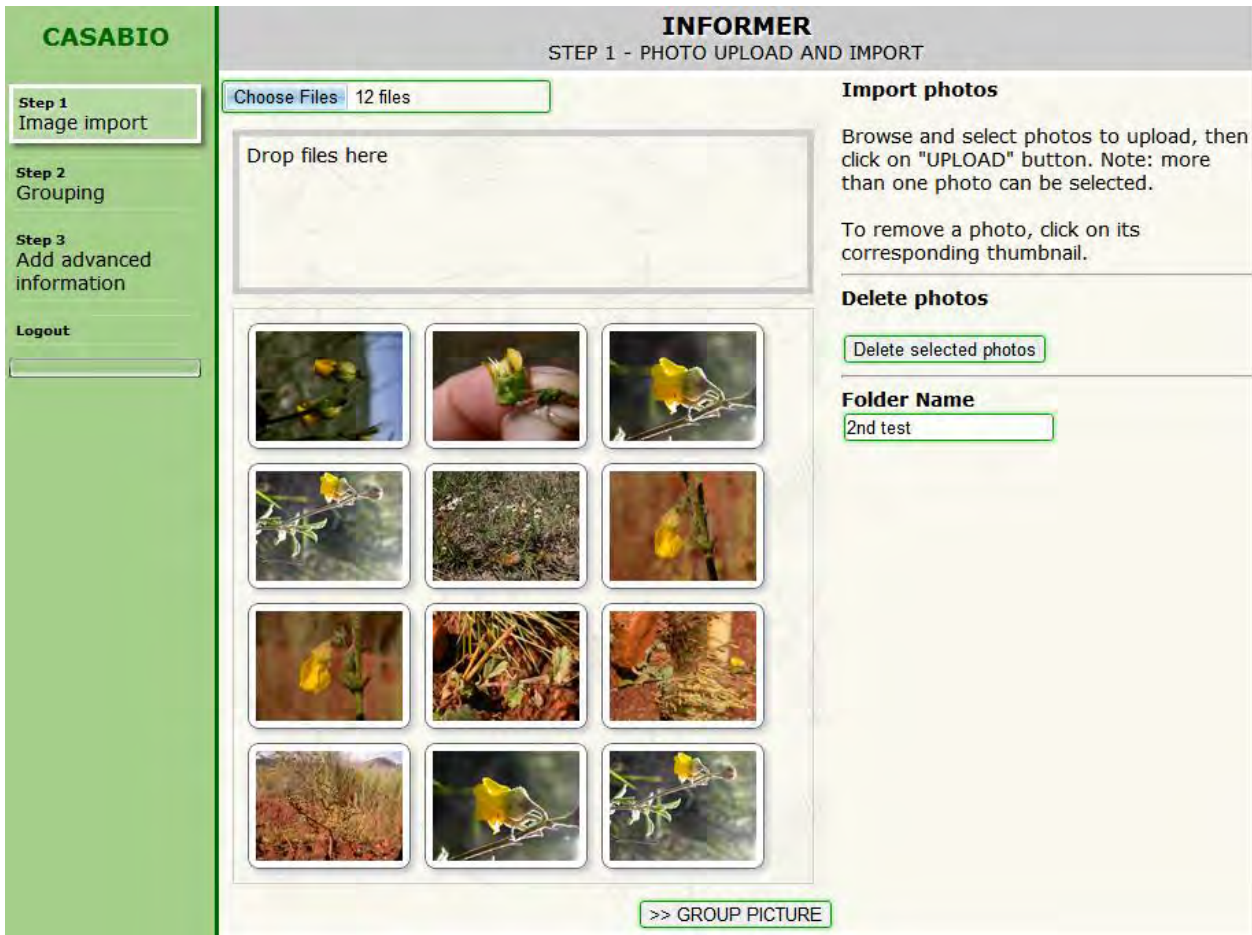


Fig. 11.0.1 Step 1: The following images portray the workflow associated with the CASABIO software currently in development. This software will form the basis for a *Hermannia* atlas. A folder or group of photos are selected to be worked with, either by choosing the files, or dragging and dropping onto the interface.



**CASABIO**

**INFORMER**  
STEP 2 - GROUPING

Step 1  
Image import

Step 2  
Grouping

Step 3  
Add advanced information

Logout

Group photos ⓘ of the same species together by using the sliders.

time interval  
Auto Group 60 sec

Exclude photos ⓘ

Exclude selected photos

Re-include selected photos

Image category

unusable  bad

duplicate  Inappropriate Subject

Image Subject

flower  leaf

fruit/capsule  pollinator

dissection  whole plant

population  landscape

herbarium specimen  distinguishing

<< BACK >> ADD INFORMATION

**Fig. 11.0.2 Step 2: Images are placed into units of a species at a place. The green and yellow groups represent separate units. They can also be tagged with attributes such as whether the photo is of a flower or whole plant.**

www.casabio.org/casabio/maps.php#

Lat  Long  Alt

ADD MODIFY

PATH PLOT

1) Path name

2) Add/Modify points  
 - Click on the maps to add new points  
 - To modify point, click on [this link](#)

3) [Link points to photos](#)

4) [Link points to Habitat Info](#)

No habita info linked

5) [Delete all the paths](#)

**Fig. 11.0.3 Step 3:** A route can be created (red line), and photos linked to one or more points. Habitat information can also be linked to particular points.



**CASABIO**

**INFORMER**  
STEP 3 - ADD BASIC INFORMATION

Step 1  
Image import

Step 2  
Grouping

**Step 3  
Add advanced information**

Logout

Name Basic Info Image Info Population Data Habitat Threats

**NAME**

Division

Family

Genus

Species

How sure are you about the classification

A guess

Fairly sure

Very sure

Verified

Locked

Common Name

Memory Box

<< BACK FINISH

**Fig. 11.0.4 Step 4:** Selected units (in blue) may be annotated with properties such as a species name, or population data, habitat information or threats. Clicking finish allows one to upload the pictures for identification by the user-community.

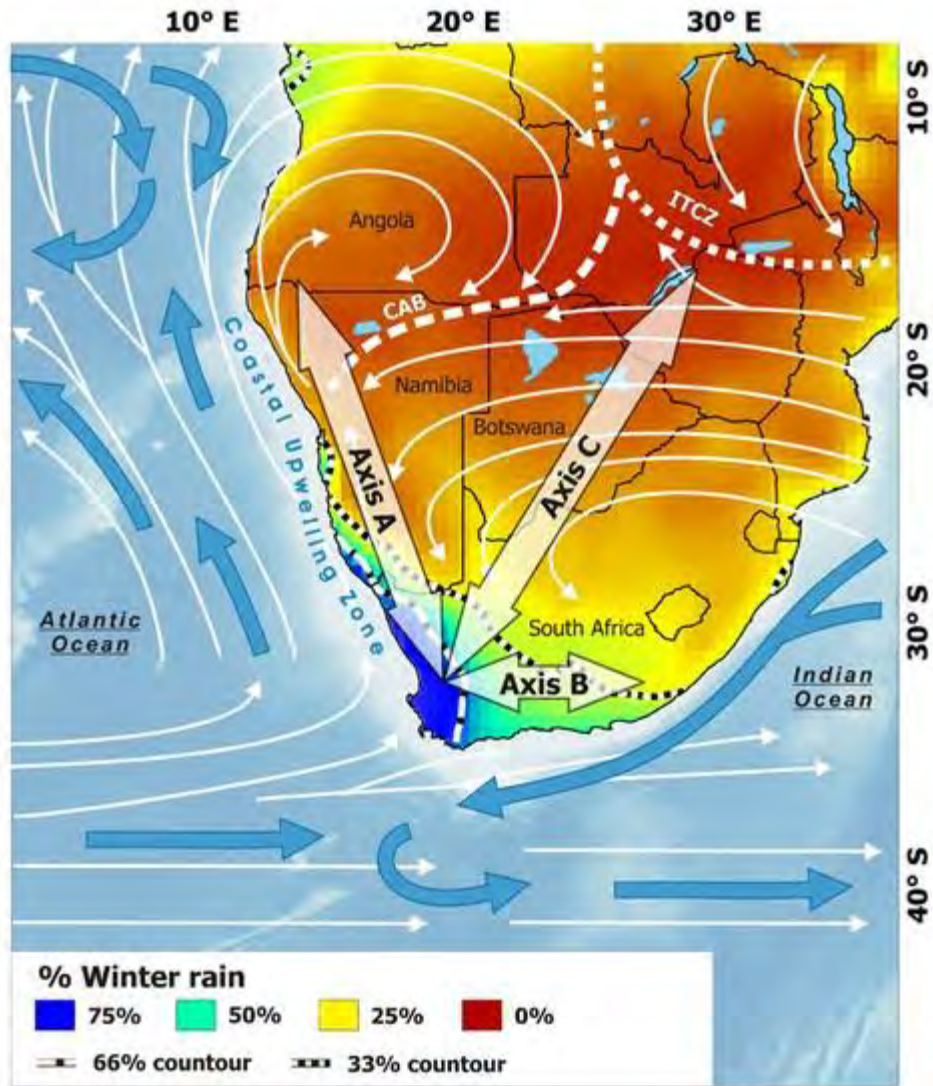


Fig. 11.0.5 A map showing rainfall seasonality. The contours show the contours of 33% and 66% summer rainfall. Axis A, B and C are not relevant for this study, but depict the regions primary climatic gradients. Map retrieved from [http://www.hyrax.univ-montp2.fr/project\\_location.html](http://www.hyrax.univ-montp2.fr/project_location.html).