

**A TAXONOMIC REVISION OF THE GENUS *PENTATRICHIA*
(ASTERACEAE)**

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

OF

THE UNIVERSITY OF NAMIBIA

AND

THE HUMBOLDT-UNIVERSITÄT ZU BERLIN

BY

ESMERIALDA SUZETTA KLAASSEN

April 2007

SUPERVISOR: DR. EZEKEIL KWEMBEYA

CO-SUPERVISOR: DR. ERIKA MAASS

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AT
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ESMERIALDA SUZETTA KLAASSEN

Supervisor: Dr. Ezekeil Kwembeya (National Botanical Research Institute)

Co-supervisor: Dr. Erika Maass (University of Namibia)

April 2007

DECLARATION

I, Esmerialda Klaassen, declare hereby that this study is a true reflection of my own research, and that this work, or part thereof has not been submitted for a degree in any other institution of higher education.

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ABSTRACT

A new revision of the genus *Pentatrichia* Klatt is presented here. Morphological data from previously described taxa: *P. alata* S.Moore, *P. avasmontana* Merxm., *P. petrosa* Klatt and *P. rehmi* (Merxm.) Merxm. were subjected to both univariate and multivariate statistical methods. Both herbarium material and voucher specimens collected during fieldwork were examined. Morphological character data were analysed by Unweighted Pair-group Method Arithmetic Average (UPGMA) clustering algorithms as to obtain groupings as objectively as possible. Cluster analyses revealed the existence of three species in the genus namely *P. alata*, *P. petrosa* and *P. rehmi*. *Pentatrichia avasmontana* Merxm. is reduced to subspecific level under *P. rehmi* (Merxm.) Merxm.; *P. rehmi* subsp. *avasmontana* (Merxm.) Klaassen & Kwembeya *comb.nov.* Two ordination methods Principal Coordinate Analysis (PCO) and Principal Component Analysis (PCA) were employed and confirmed the results obtained from the cluster analyses.

The results revealed that *P. avasmontana* does not warrant specific status as it came out nested within *P. rehmi*. *Pentatrichia avasmontana* is accordingly reduced to subspecific level under *P. rehmi*. Leaf characters and presence/absence of ray florets proved to be the most important characters in diagnosing species in the genus. Photographs of some of the morphological characters are provided. This revision includes a new key for the species, descriptions and distribution maps at the quarter degree level.

Field assessments of Namibian species facilitated comprehensive Red List assessments of the genus in Namibia. Two taxa emerged as “Least Concern” with *P. rehmii* subsp. *rehmii* falling in the “Vulnerable” (VUD1) category.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

The genus *Pentatrichia* was first described by Klatt (1895). It is known to consist of four species occurring in Namibia and South Africa and is considered monophyletic (Merxmüller, 1950; Merxmüller, 1954; Merxmüller, 1967; Anderberg, 1991; Anderberg, 1994; Herman *et al.*, 2000; Germishuizen and Meyer, 2003). Three of the species described namely: *P. avasmontana* Merxm., *P. petrosa* Klatt, and *P. rehmi* (Merxm.) Merxm. have been reported to occur in Namibia with *P. avasmontana* and *P. rehmi* being endemic to Namibia (Merxmüller, 1967; Craven, 1999; Germishuizen and Meyer, 2003; Loots, 2005). Unfortunately, no record of *P. rehmi* is housed in the National Herbarium of Namibia (WIND) or the National Herbarium (PRE), Pretoria, which houses a vast number of southern African plant specimens. The only existing specimen of *P. rehmi* is the type specimen, which is kept in the München Herbarium (M), Botanischen Staatssammlung, Germany. According to data from WIND (2005), *P. avasmontana* has a predominantly central distribution while *P. petrosa* is a more widespread species in Namibia. The fourth species *P. alata* S.Moore is listed as endemic to the Limpopo and Mpumalanga provinces in South Africa (Retief and Herman, 1997; Victor, 2002; Germishuizen and Meyer, 2003). Victor (2002) lists *P. alata* as LR-lc (Lower Risk-Least Concern).

Loots (2005) lists *P. avasmontana* as LC (Least Concern) and *P. rehmi* as DD (Data Deficient) for Namibia. Due to limited information available on *P. rehmi*, it has only been listed as Data Deficient.

1.2 Literature Review

The Asteraceae (sunflower) family is the largest of the flowering plant families, comprising about 23 000 species worldwide (Bremer *et al.*, 2003). The family is divided into several tribes, which are often arranged into three subfamilies namely, Barnadesioideae (a small South American group), Cichorioideae (with ligulate flowers) and Asteroideae (with disc and ray florets). The genus *Pentatrichia* belongs to the subfamily Asteroideae and tribe Gnaphalieae. Phylogenetic studies revealed that the Asteroideae is monophyletic (Bayer *et al.*, 2000). Bohm and Stuessy (2001) note that there are three basic modes of speciation in the Asteraceae, namely geographic (allopatric), catastrophic (peripheral isolates) and allopolyploidy with the geographic speciation being one of the most common.

The capitulum in Asteraceae consists of two kinds of florets namely actinomorphic, commonly referred to as disc florets, and zygomorphic or ray florets. Five basic kinds of zygomorphic florets are recognised: bilabiate florets, pseudobilabiate florets, true ray florets, 4-lobed rays and ligulate ray florets. True ray florets have been described as having a 3-lobed lamina and no adaxial lobes, which is common in the Asteroideae, the Liabeae and the Arctoteae-Arctotinae (Bremer, 1994).

In the Asteraceae, the capitulum functions as an alluring showpiece for pollinators and the disc florets usually form a flat surface consisting of many protruding reproductive organs over which insect visitors crawl, thus quickly fertilizing many florets (Turner, 1977b). The anthers form a hollow cylinder and dehisce inward, filling the cylinder with pollen before the flower opens. The pollen is brushed out of the anther cylinder by the growing style by means of hairs on the surface. Pollination in the Asteraceae takes place in two stages. During the first stage of pollination, the pollen is exposed to the visitors while the second stage is characterised by the separation of the stigmas to expose their papillar surface for the catching of incoming pollen (Turner, 1977b).

Sunflower heads represent a substantial reservoir of food resources concentrated in one place on the plant increasing predation pressure by insects (Bohm and Stuessy, 2001). A wide range of visitors and pollinators has been reported for the Asteraceae, ranging from insect groups such as Coleoptera, Diptera and Hymenoptera to hummingbirds (Turner, 1977a, 1977b; Grombone-Guaritini *et al.*, 2004). Studies on seasonal abundance and species composition of flower-visiting flies conducted by Souza-Silva *et al.* (2001) concluded that plant species receiving frequent visits from Diptera usually have many flowers and that Asteraceae showed a high insect visitor abundance.

The tribe Gnaphalieae is one of the largest in the family with more than 180 genera and 2 000 species with the two largest genera being *Helichrysum* (everlastings) and *Gnaphalium*. Furthermore the tribe Gnaphalieae has the following major

synapomorphies: pollen grains with a thick basal layer regularly perforated (gnaphaloid) and chromosome number $n=7$. The tribe has a worldwide distribution, and is particularly well represented in South Africa and Australia, while some of the species are grown as ornamentals (Anderberg, 1994). According to Koekemoer (1996) the Gnaphalieae has mainly an African distribution, which is reflected by the 24% occurring in southern Africa compared to 9% in the rest of the world. Koekemoer (1996) further notes that the largest proportion of endemic genera in the Asteraceae falls within the tribe Gnaphalieae and that the species endemism is about 90%. Molecular studies of the genera of Gnaphalieae from the basal African genera, *Anisothrix*, *Athrixia*, *Arrowsmithia*, *Callilepis*, *Pentatrichia* and *Printzia* in order to reconstruct the phylogeny of the Gnaphalieae worldwide revealed that *Pentatrichia* and *Anisothrix* are sister taxa (Bayer *et al.*, 2000).

The genus *Pentatrichia* consists of shrublets or shrubs, with branches glandular pilose to glabrescent (Merxmüller, 1954; Anderberg, 1991; Herman *et al.*, 2000). Leaves are alternate, cordate or lanceolate or ovate, petiolate or rarely sessile, incised with obtuse lobes, glandular pubescent and often reticulate (Anderberg, 1991; Herman *et al.*, 2000). Capitula are heterogamous or homogamous, solitary or subcorymbose and pedunculate (Klatt, 1895; Merxmüller, 1967; Anderberg, 1991). Ray florets when present are female and white (Herman *et al.*, 2000). Disc florets are bisexual and fertile (Anderberg, 1991; Herman *et al.*, 2000). Achenes are sparsely hairy (Anderberg, 1991). Pappus consists of free barbelate bristles in 1 row interspersed with an outer row of short, triangular scales (Merxmüller, 1954; Merxmüller, 1967; Anderberg, 1991; Herman *et al.*, 2000).

Pentatrichia formed the centre of a debate whether to retain it as a valid genus or to sink some of its species under other genera. At the heart of the sinking of the species was *P. alata*. Some authors placed it in the genus *Pulicaria* (Phillips, 1951; Merxmüller, 1954) as they perceived it to have a distinct two rowed pappus while Burt Davy sunk it under *Philyrophyllum* (Merxmüller, 1954). Moore considered sinking *Pentatrichia* under *Inula* on the basis of the one rowed pappus (Merxmüller, 1950). However, the pappus of *Pentatrichia* is unusual in that it has one row of bristles with scales arranged in one plane alternating each other. This type of pappus is absent from other Inulae and *Inula* is not found in southern Africa, being a tropical African species, therefore it is unlikely to have evolved from the same ancestor as *Pentatrichia* (Merxmüller, 1954). Due to the presence of one row of pappus bristles and the scales, *Pentatrichia* can thus also not be placed under *Pulicaria*, which has a distinct two rowed pappus. However, the pappus in *Pentatrichia* is not a constant character, especially in *P. petrosa* where up to 8 bristles were found (Merxmüller, 1950). This was confirmed by field studies where some of the specimens had more bristles than the normal of five bristles per achene recorded in the literature. *Pentatrichia* has thus been retained as stated by Moore (1904) on the basis of the pappus characters. According to Klatt (1895), *Pentatrichia* is morphologically similar to *Athrixia*.

1.3 Problem Statement and Justification

The Global Strategy for Plant Conservation (GSPC) promotes research in taxonomy so that plant diversity, both in the wild and in the context of human activities, can be well understood and utilized to support conservation action. Taxonomy is the starting point for many studies such as basic and applied research, Environmental Impact Assessments (EIA's), and conservation, underpinning the importance of taxonomy. This was emphasised by the outcome of the Biosystematics End-User Workshop held in 2002 which indicated that access to updated descriptions and keys to the plants that occur in Namibia was a top priority for most customers, *inter alia* extension officers, conservation officials, students and lecturers and researchers (Irish, 2003).

Conservation of endemic species is of utmost importance in the conservation of Namibia's floral heritage. For this purpose Namibia has entered into international agreements such as the Important Plant Areas (IPA) Project which look at areas with potential conservation value (e.g. high occurrence of endemics, plants with restricted distribution ranges) that might be affected by altered landuse practices (e.g. water extraction activities, commercial farming practices). The type locality for *P. rehmi* falls within one of the areas identified for Namibia (north-east Namibia including the Waterberg escarpment and Otavi Mountains within the Karstveld (Hofmeyr, 2004)) which could potentially lead to the genetic erosion of the species necessitating the generation of taxonomic information needed for risk assessment of important plant species. Furthermore Namibia is involved with international organisations such as the Council for Scientific and Industrial Research (CSIR), which is focusing on the

bioprospecting of endemics in particular, screening for economical important properties such as medicinal properties.

The genus *Pentatrichia* was last revised in 1954 by Merxmüller and is in need of revision due to the following reasons:

- 1) The existing keys are not only outdated, but in German and Latin making them unavailable to the wider scientific community.
- 2) The genus contains largely Namibian endemics, which might be threatened by extinction due to our ignorance of its alpha taxonomy and its limited distribution.
- 3) There is a need for more field studies to give a comprehensive assessment of the conservation status of *P. rehmi* as no drawings, no pictures and no specimens exist for some of the species, especially *P. rehmi*, which makes positive identification of this species difficult.
- 4) The genus is known to occur in one of the potential IPA's, which might be affected by altered land use practices, necessitating the generation of taxonomic information needed for risk assessment.
- 5) No ethnobotanical data has been collected due to the unfamiliarity of the genus and its habitat preference.
- 6) The genus has horticultural potential as it forms attractive displays against rock faces in its natural habitat.

1.4 Key Questions

- 1) How many morphological/phenetic species exist within the genus *Pentatrichia*?
- 2) What are the most useful characters delimiting species within this genus?
- 3) What is the taxonomic status of *P. rehmi*?
- 4) What is the conservation status of the taxa?

1.5 Aim and Objectives

The overall aim of the current study is to produce a taxonomic revision of the genus *Pentatrichia*. This work differs from previous studies in that it employs statistical treatment of character data in order to obtain a classification that is both operational and objective. Specific objectives associated with this aim are as follows.

- 1) To investigate the taxonomic usefulness of morphological characters in the genus.
- 2) To determine diagnostic characters delimiting the different species and develop an updated English identification key for the genus.
- 3) To provide distribution maps for all the species.
- 4) To assess the conservation status of Namibian species belonging to the genus *Pentatrichia*.

CHAPTER 2: STUDY AREA

2.1 Flora of southern Africa Region

This study was aimed at contributing to the knowledge and understanding of the Flora of southern Africa (FSA). The Flora of southern Africa region generally covers the area south of the Kunene, Limpopo and Okavango Rivers including Namibia, Botswana, South Africa, Lesotho and Swaziland (Huntley, 1994; Golding, 2002). The FSA region is predominantly a warm-temperate and arid to semi-arid region with a mean annual rainfall of about 400 mm which varies greatly over the region (Van Wyk and Smith, 2001; UWC, 2006). This region has a rich biodiversity, which is attributed to its position with respect to subtropical summer rainfall and temperate rainfall regions combined with complex topography and the heterogeneity of geology and soils (UWC, 2006). Much of the region is characterized by savanna, woodland and montane grasslands. The FSA region consists of more than 10% of the world's flora, which is concentrated on 2.5% of the earth's land surface with about 60% of the species being endemic to the region (Van Wyk and Smith, 2001). As a result of the high rate of endemism in southern Africa, seven centres of plant diversity have been identified including the Wolkberg Centre of Endemism in South Africa, which covers an area of 13.3%, as well as the Kaokoveld in Namibia, covering 7% of the region (UWC, 2006).

The study was carried out within the boundaries of Namibia although one of the species, *P. alata*, occurs in the Wolkberg Centre of Endemism of South Africa,

which includes part of the Limpopo and Mpumalanga Provinces. A general background overview of this area is provided in section 2.3.

2.2 Namibia

Namibia covers an area of 823 680 km² with a coastline of 1 570 km and is classified by two geological zones: western Namibia which is typified by a variety of rock formations exposed in rugged valleys, escarpments, mountains and open plains, and eastern Namibia which is more uniform and defined by sands. These rock formations and mountains proved to play an integral part in the establishment of the taxa under revision. Soils are of various types but mainly include Leptosols, Arenosols, Cambisols and Regosols (Mendelsohn *et al.*, 2002).

Namibia is a very arid country with a harsh and variable climate characterized by predominantly greatly variable summer rainfall (Figure 1), high summer and low winter temperatures. High rainfall occurs around the Otavi Triangle and Waterberg as a result of moist air being forced upward by the hills causing the rising air to cool and condense resulting in rain (Mendelsohn *et al.*, 2002). The only perennial rivers form the northern and southern borders of the country. These include the Orange River in the south, the Kunene and Okavango rivers in the north, the Zambezi-Chobe and Kwando-Linyanti rivers in the north-east (Mendelsohn, *et al.*, 2002). As figure 2 indicates, the greatest part of Namibia is dominated by Tree & Shrub Savanna, which is subdivided into the Acacia Tree & Shrub Savanna and the Broadleaved Tree & Shrub Savanna.

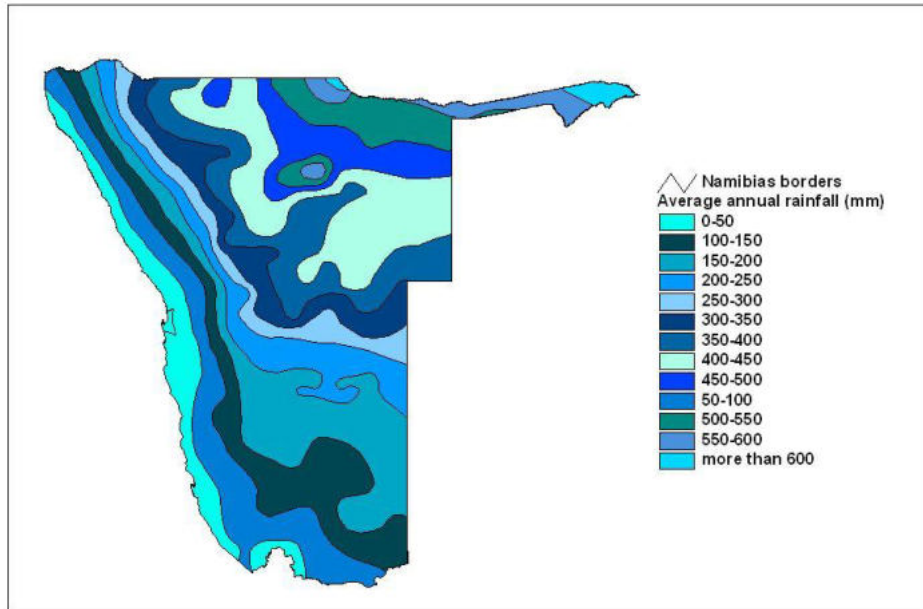


Figure 1: Average rainfall in Namibia (Mendelsohn *et al.*, 2002).

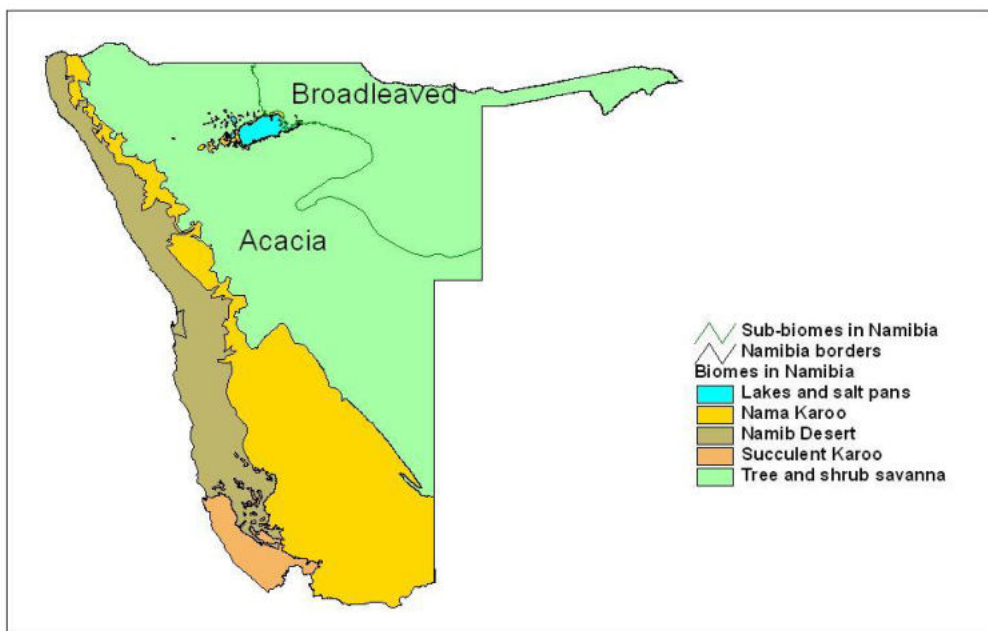


Figure 2: Biomes of Namibia (Mendelsohn *et al.*, 2002).

2.3 Wolkberg Centre of Endemism

The Wolkberg Centre of Endemism is named after Wolkberg situated 25 km southwest of Tzaneen, a mountain forming part of the Drakensberg Escarpment (Figure 3), with prominent vertical cliffs and steep mountain slopes, covering an area of 5 980 km² (UWC, 2006; Van Wyk and Smith, 2001). This Centre includes parts of the Limpopo and Mpumalanga Provinces of South Africa. According to Van Wyk and Smith (2001) the geology of the area is characterised by quartzite with conglomerate, escarpmental edge, while dolomite covered with shale and mudstone is also present. The area receives summer rainfall with the mean annual rainfall ranging between 1 000 mm and 2 000 mm (UWC, 2006; Van Wyk and Smith, 2001). According to Van Wyk and Smith (2001) the dolomitic outcrops are more arid than the quartzitic outcrops due to the fact that it falls in the mist shadow of the escarpment crests.



Figure 3: Wolkberg Centre of Endemism (map: H. Steyn, PRE).

The vegetation is classified as temperate and subtropical grassland characterised by montane grassland with pockets of Afromontane Forest confined to the slopes of the main escarpment and savanna (Van Wyk and Smith, 2001; UWC, 2006). According to Van Wyk and Smith (2001) about 90 species are endemic or near endemic to the quartz and shale substrates compared to about 40 species favouring dolomitic substrates. The families Asteraceae, Iridaceae and Liliaceae are considered to have the largest number of endemic taxa on quartzitic rock types while Acanthaceae, Euphorbiaceae and Lamiaceae are the largest for the dolomitic substrates. Van Wyk

and Smith (2001) further noted that most of the non-succulent endemics are small perennial plants including *Pentatrichia alata*.

CHAPTER 3: MATERIAL AND METHODS

3.1 Material

Herbarium specimens were obtained from the National Herbarium of Namibia (WIND); Pretoria National Herbarium (PRE), Compton Herbarium (NBG) and South African Museum Herbarium (SAM), South African National Biodiversity Institute, South Africa; München Herbarium (M), Botanischen Staatssammlung, Germany and Zürich Herbarium (Z), Institut für Systematische Botanik, Universität Zürich, Switzerland. Plants were also studied in the field and all the associated information was collected.

3.2 Methods

Thirty-nine herbarium specimens of *P. alata*, *P. avasmontana*, *P. petrosa* and *P. rehmi* were subjected to morphometric analyses. Each herbarium specimen was regarded as an Operational Taxonomic Unit (OTU) (Appendix 3). A list of fifty-three characters was prepared and measurements of selected characters were taken. These characters included both quantitative and qualitative characters (Appendix 2). Continuous characters were measured with a digital calliper in mm with an average of three measurements taken per character to increase accuracy (Appendix 4). Binary and qualitative characters were scored as absent [0] or present [1] and no [0] or yes [1] respectively (Appendix 2). A data matrix of all characters (Appendix 6) was compiled using NTSYS data editor (Rolf, 2004). A data matrix was compiled for

quantitative characters using STATISTICA (Statsoft, 2004). Approximate flowering time was determined using herbarium specimens (Table 4). Incomplete specimens were excluded from this study.

Field studies were conducted in the central part of Namibia (Daan Viljoen Game Reserve and Aredareigas Nature Estate) and the north-eastern part of Namibia (Waterberg Plateau Park, Otavi-Grootfontein area). One field trip was carried out in Central Namibia during July 2006. Two trips were undertaken to north-eastern Namibia, during July and September 2006 to Waterberg Plateau Park as well as during January and September 2006 to the Otavi-Grootfontein area. Voucher specimens were collected according to standard herbarium techniques. Photographs of plants and associated notes were taken in the field. In addition, Red List assessments of individual species were also undertaken and analysed with the help of RAMAS software (Akçakaya and Ferson, 2001), which is based on the IUCN Red List classification system (IUCN, 2001). Leaf material was collected and dried rapidly in silica gel for DNA analyses and sent to Dr. R. Bayer of the Commonwealth Scientific and Industrial Research Organization (CSIRO) (Canberra, Australia) who is currently doing molecular studies on this group. Species distribution maps were generated using MAPPIT Geographical Mapping System software version 2.0 (NBI, 1996).

Translations of Latin diagnosis were done according to Gledhill (2002) and Stearn (2004). Author abbreviations follow Brummit and Powell (1992), whilst acronyms of lending institutions follow Holmgren *et al.*, (1990).

3.2.1 Field Studies

Fieldwork was undertaken in central Namibia in the Daan Viljoen Game Reserve and the Aredareigas Nature Estate and north-eastern Namibia specifically Waterberg Plateau Park and Guchab Mountain near Grootfontein.

Central Namibia:

The Daan Viljoen Game Reserve is situated 30 km west of Windhoek. The area is dominated by schist, the common rock formation in the Khomas Hochland, which is evident by the visible banding in the rocks consisting of dark and light layers (Figure 4) caused by varying amounts of different minerals (Grünert, 2003).



Photo: E. Klaassen

Figure 4: Schist rock formation, Daan Viljoen Game Reserve.

The Grossherzog-Friedrich Mountain situated in the Aredareigas Nature Estate about 15 km south of Windhoek is characterised by schist, sandstone and quartzite. According to Mendelsohn *et al.* (2002) the vegetation of this region is classified as Highland Shrubland which consist of shrubs and low trees and Lithic (very shallow soils) Leptosols as well as Eutric (fertile soils with high base saturation) Regosols.

North-east Namibia:

The Waterberg is situated 60 km east of Otjiwarongo and forms a table mountain with a prominent plateau of about 40 000 hectares with its highest point at 1 930 m above sea level. This mountain is a popular tourism attraction and is conserved within the Waterberg Plateau Park. The mountain is surrounded by steep cliffs except in the north-eastern direction where it gradually merges with the Kalahari Sandveld to the east (Schneider, 2004). The Waterberg Plateau Park is characterised by predominantly Etjo Sandstone (Grünert, 2003), as can be observed from the steep rock cliffs (Figure 5), rock formations on the plateau and along the walking trails at the Okatjikona Environmental Education Centre, whereas the rock formations at Onjoka Conservation Station is dominated by dolerite and the Omingonde Formation which is represented by conglomerate, sandstone and shale. Vegetation is classified as Thornbush Shrubland and dominated by *Acacia* shrubland (Mendelsohn *et al.*, 2002).



Photo: E. Klaassen

Figure 5: Steep sandstone rock cliffs, Fig Tree Walk, Waterberg Plateau Park.

The Otavi Mountain land, specifically the area within which the Guchab Mountain is situated, is generally characterised by limestone and dolomite, quartzite and conglomerate (Grünert, 2003), (Figure 6). Vegetation is classified as the Karstveld and represented by mixed woodland (Figure 7) and Mollic (soil with good surface structure) Leptosols (Mendelsohn *et al.*, 2002).



Photo: S. Rügheimer



Photo: S. Rügheimer

Figure 6: Different rock formations, Guchab Mountain.

Figure 7: Karstveld vegetation, Guchab Mountain.

3.2.2 Multivariate Methods

3.2.2.1 Cluster Method

A rectangular matrix with thirty-nine rows (OTUs) and fifty-three columns (characters) was constructed. The data were log-transformed to normalize and then

standardized by subtracting the mean of each column of variables and dividing the remainder by the standard deviation to remove the effect of size variation. A similarity distance matrix using Manhattan distances was computed for the OTUs from the standardized data. The SAHN (Sequential Agglomerative Hierarchical Nested Clustering) method was used based on the similarity matrix, and grouping algorithms single linkage, complete linkage and UPGMA (Unweighted Pair-group Method Arithmetic Average) were used to generate phenograms. The cophenetic values for each of the grouping algorithms were computed to compare the similarity matrix and the cophenetic value matrix to test the goodness of fit of the phenograms.

3.2.2.2 Ordination Methods

Ordination methods were employed to check the repeatability of the groupings obtained by the cluster analyses. Two ordination methods, Principal Coordinate Analysis (PCO) and Principal Component Analysis (PCA) were used in this study.

The PCO used the same data matrix that was used for the cluster analyses. As for the cluster analyses the data was first log transformed, standardized and a similarity matrix computed. Data was log transformed by the rows to normalize it and standardized to remove the effect of size variation. Standardization was done by subtracting the mean from the value of each object and then dividing it by the standard deviation. A similarity distance matrix using Manhattan distances was computed for the OTUs from the standardized data. The data was then double-centred using squared distances. The double-centred matrix was then used to extract the eigen vectors. The eigen vectors were plotted directly.

For the PCA, a data matrix of seven quantitative characters namely; leaf length, leaf width, petiole length, capitula length, capitula width, peduncle length and achene length was constructed. The data was then log transformed by the columns and standardized by the columns by subtracting the mean from the value of each object and then dividing it by the standard deviation. A similarity matrix was computed using the standardized data based on the coefficient correlation. The eigen vectors were extracted and projected onto the objects to produce the PCA plot.

3.2.3 Univariate Methods

Box-and-whisker plots were generated using STATISTICA (Statsoft, 2004) to determine the variability of each character as well as the extent of overlap. These were graphed to explore the variability of seven quantitative characters used in the cluster and ordination analyses. The characters examined are leaf length, leaf width, petiole length, capitula length, capitula width, peduncle length and achene length.

CHAPTER 4: RESULTS

4.1 Cluster Analyses

Table 1: Cophenetic correlation coefficients for the different clustering algorithms computed using Manhattan distance.

Data set	Clustering method	Cophenetic correlation coefficient
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Multivariate data	Single linkage	0.72413
	Complete linkage	0.76544
	UPGMA	0.78221

UPGMA clustering obtained the highest cophenetic correlation coefficient.

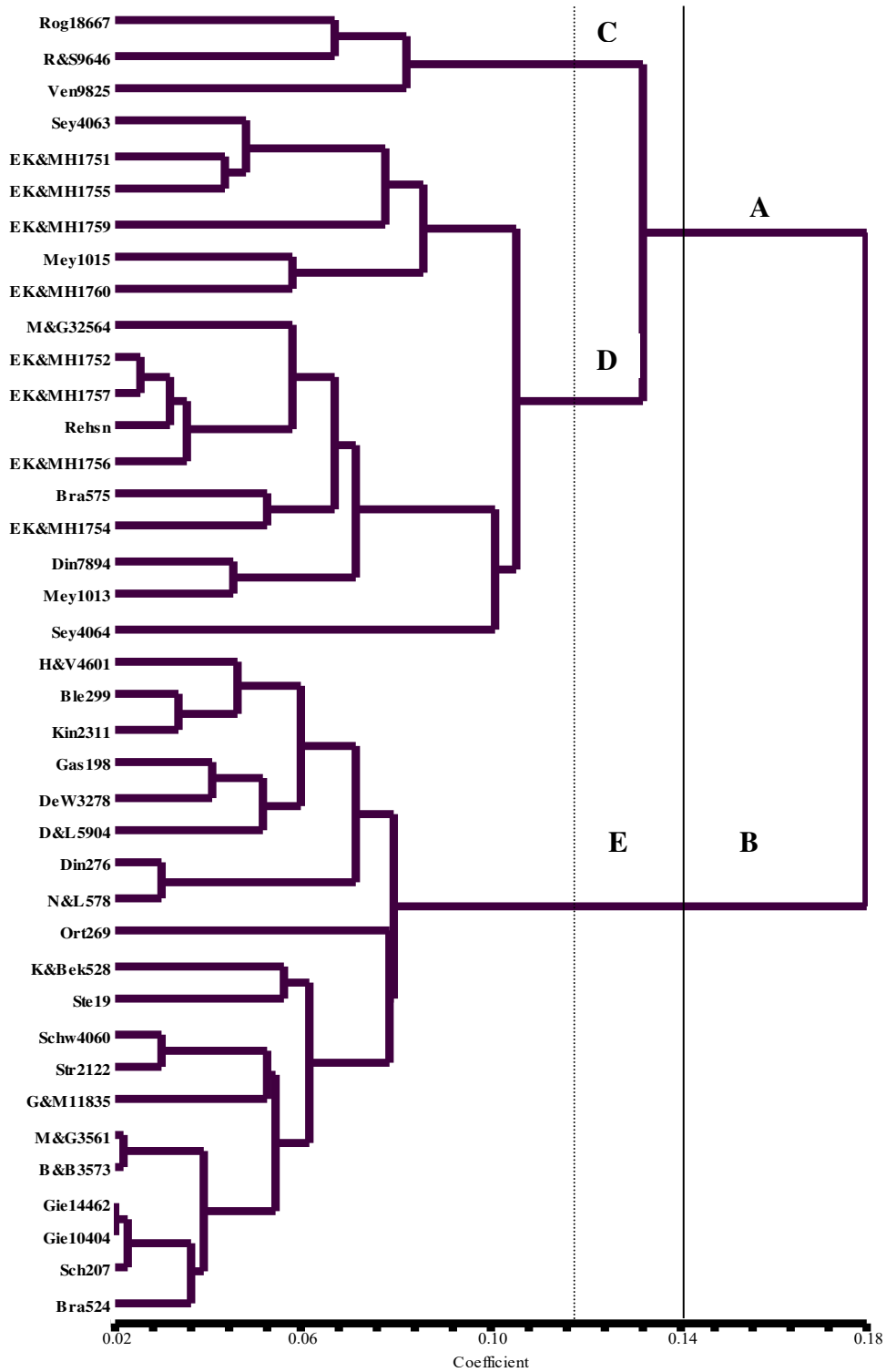


Figure 8: UPGMA generated phenogram. Two discrete clusters (A & B) are revealed with a phenon line drawn at $r = 0.14$. Three discrete clusters (C, D & E) are revealed when $r = 0.116$.

4.2 Ordination Analyses

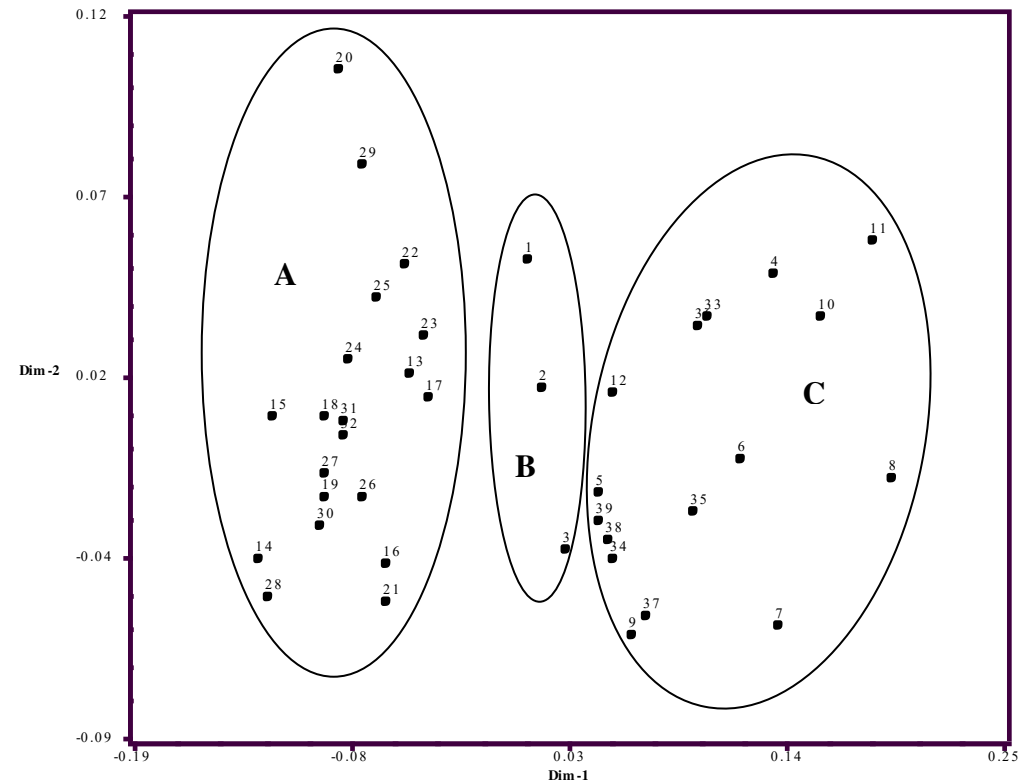


Figure 9: Principal Coordinate Analysis (PCO) plot based on mixed characters using dimensions 1 and 2. Three distinct groupings (A, B & C) are revealed. A: *P. petrosa*, B: *P. alata* and C: *P. avasmontana* and *P. rehmi*. Clusters are given names according to the type specimens nested within them. OTU labels are according to Appendix 3.

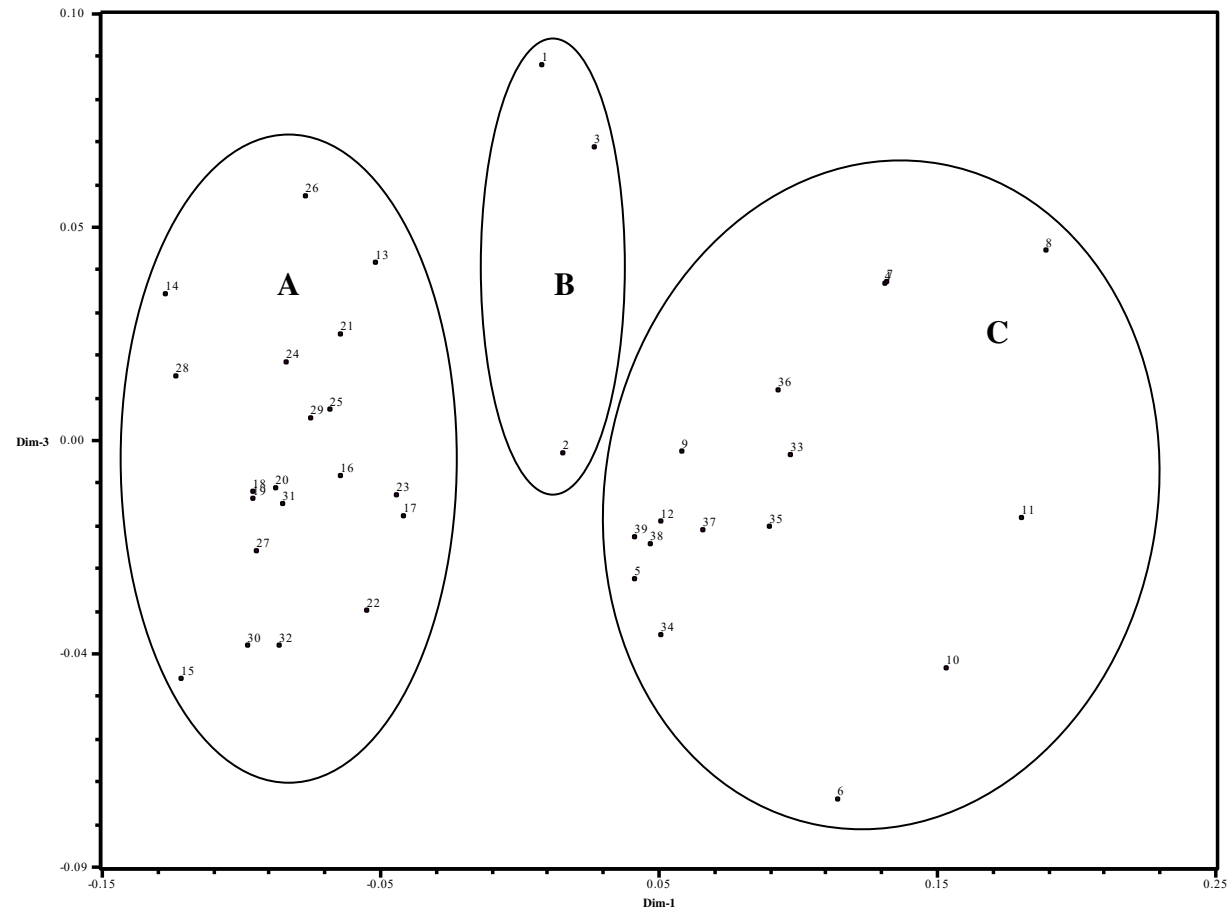


Figure 10: Principal Coordinate Analysis (PCO) plot based on mixed characters using dimensions 1 and 3. Three distinct groupings (A, B & C) are revealed. A: *P. petrosa*, B: *P. alata* and C: *P. avasmontana* and *P. rehmi*. Clusters are given names according to type specimens nested within them. OTU labels are according to Appendix 3.

Table 2: Contributions of the characters to the total variation in the PCO plot.

OTU	Eigen value	Percent	Cumulative
1	0.33851424	80.6933	80.6933
2	0.05776549	13.7698	94.4631
3	0.04698523	11.2001	> 100%
4	0.01977907	4.7148	> 100%
5	0.01604802	3.8254	> 100%
6	0.01200888	2.8626	> 100%
7	0.00780186	1.8598	> 100%
8	0.00606329	1.4453	> 100%
9	0.00493405	1.1762	> 100%
10	0.00481429	1.1476	> 100%
11	0.00408546	0.9739	> 100%
12	0.00350628	0.8358	> 100%
13	0.00293948	0.7007	> 100%
14	0.00159856	0.3811	> 100%
15	0.00131835	0.3143	> 100%
16	0.00072758	0.1734	> 100%
17	0.00050029	0.1193	> 100%
18	0.00005892	0.0140	>100%
19	0.00001484	-0.0035	>100%
20	0.00000000	-0.0000	>100%
21	-0.00011291	-0.0269	>100%
22	-0.00031301	-0.0746	>100%

23	-0.00040702	-0.0970	>100%
24	-0.00050859	-0.1212	>100%
25	-0.00062198	-0.1483	>100%
26	-0.00090914	-0.2167	>100%
27	-0.00124078	-0.2958	>100%
28	-0.00185241	-0.4416	>100%
29	-0.00223492	-0.5327	>100%
30	-0.00274682	-0.6548	>100%
31	-0.00321189	-0.7656	>100%
32	-0.00413046	-0.9846	>100%
33	-0.00464134	-1.1064	>100%
34	-0.00641940	-1.5302	>100%
35	-0.00892730	-2.1280	>100%
36	-0.00939903	-2.2405	>100%
37	-0.01473456	-3.5124	>100%
38	-0.02031975	-4.8437	>100%
39	-0.02722566	-6.4899	>100%

Sum of eigen values = 0.419507

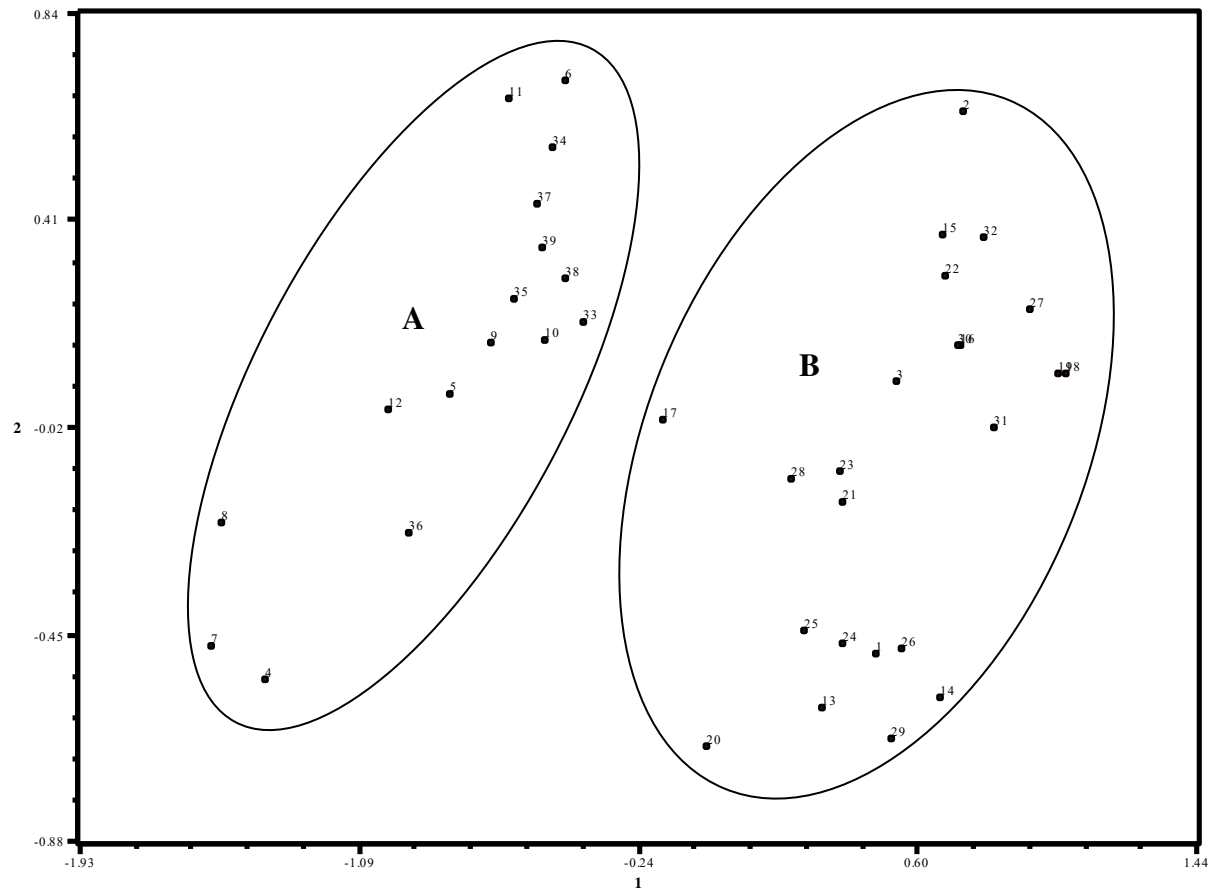


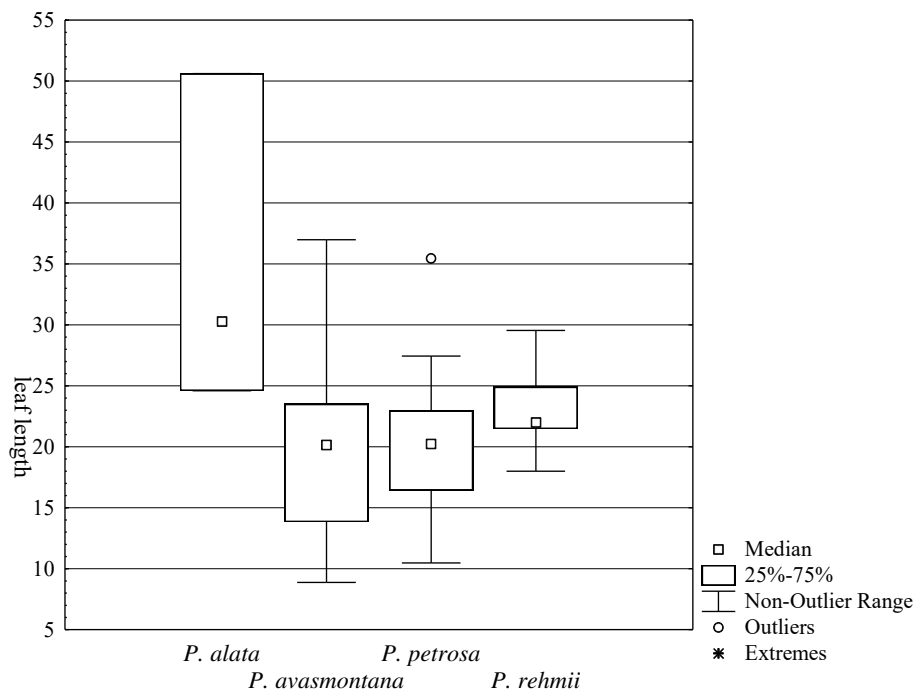
Figure 11: Principal Component Analysis (PCA) plot based on seven quantitative characters revealing two groupings (A & B). Cluster A contain *P. avasmontana* and *P. rehmi*, whilst cluster B include *P. alata* and *P. petrosa*. Clusters are given names according to the type specimens nested within them. OTU labels are according to Appendix 4.

Table 3: Character loadings in the PCA plot.

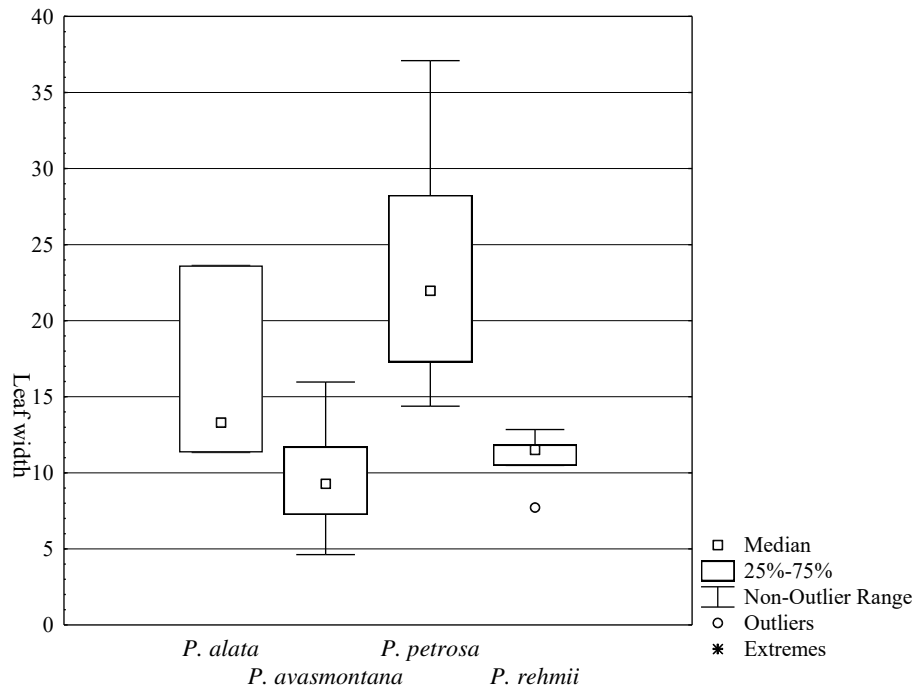
Component	Eigen value	Percent	Cumulative
1	3.87957509	55.4225	55.4225
2	1.08289757	15.4700	70.8925
3	0.96133610	13.7334	84.6258
4	0.58882416	8.4118	93.0376
5	0.29997874	4.2854	97.3230
6	0.14717567	2.1025	99.4255
7	0.04021267	0.5745	100.000

Sum of eigen values = 7.000000

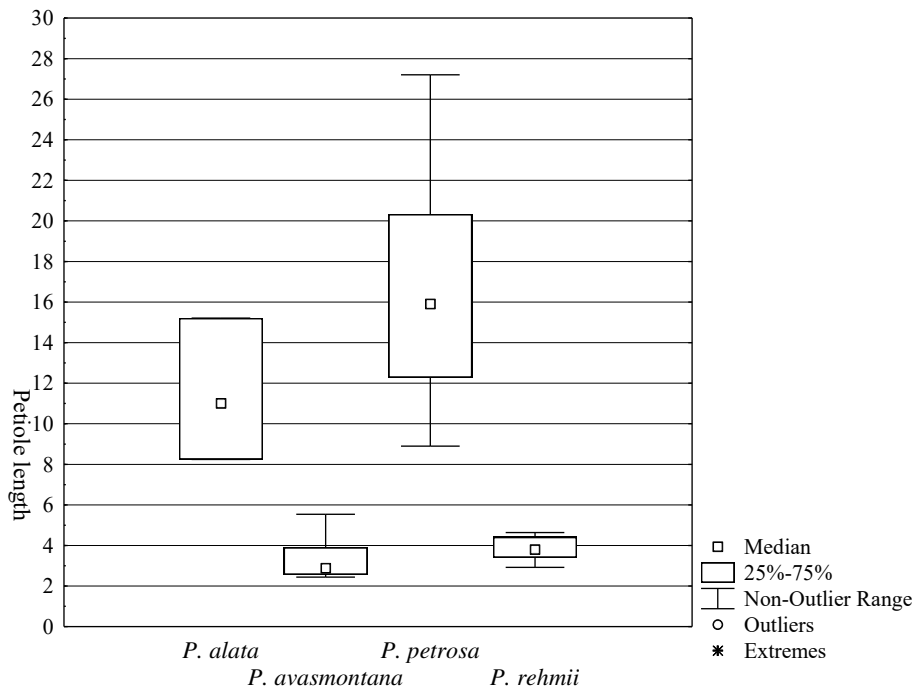
4.3 Univariate Analyses



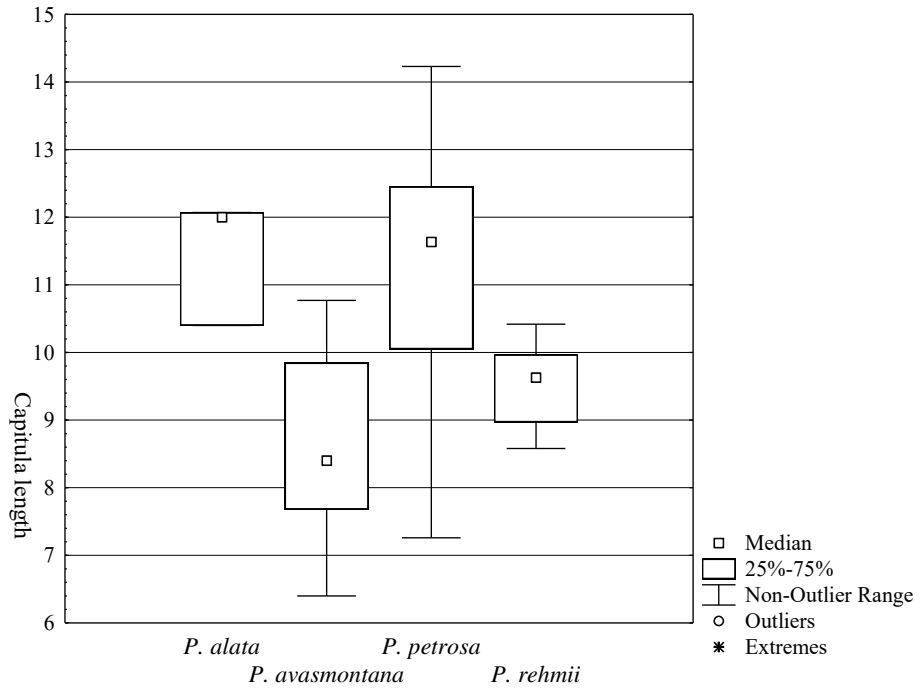
A Leaf length



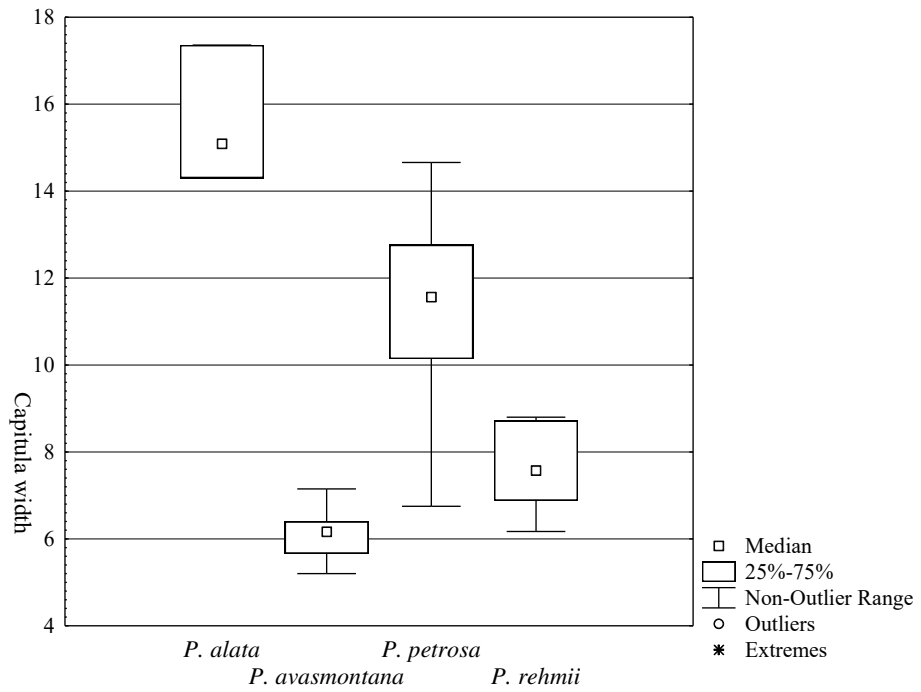
B Leaf width



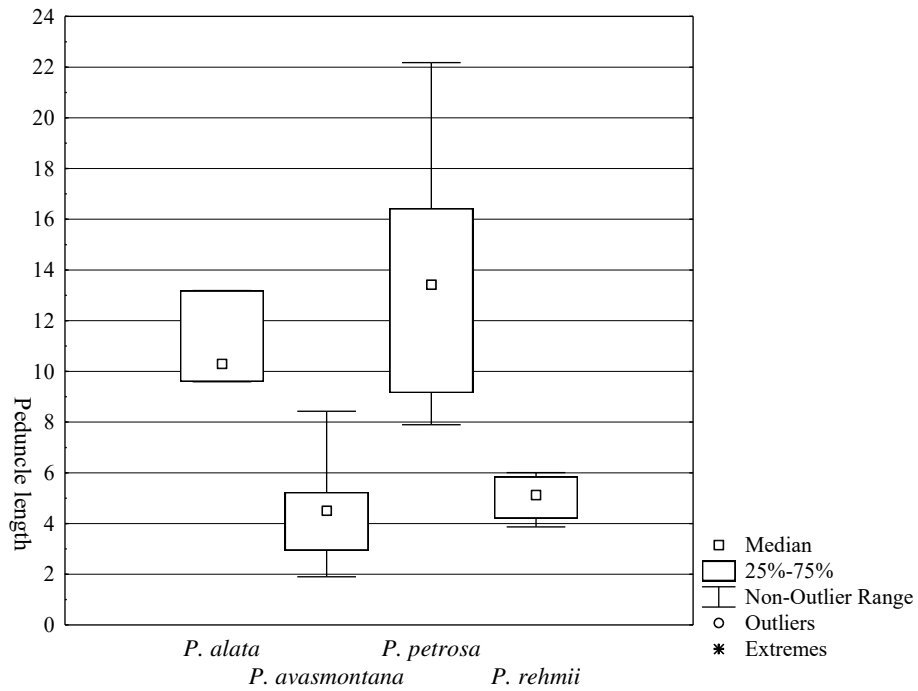
C Petiole length



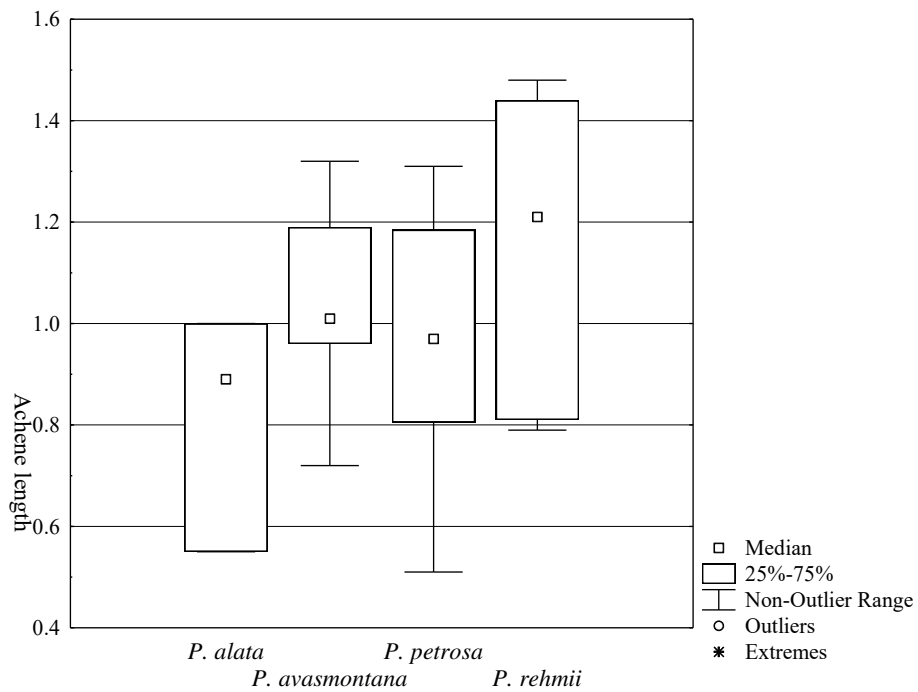
D Capitula length



E Capitula width



F Peduncle length



G Achene length

Figure 12: Box-and-whisker plots A–G showing variation in seven characters used in the quantitative multivariate analyses (measurements are in mm).

4.4 Phenology

Table 4: Flowering period for the genus *Pentatrichia*. The blank spaces indicate lack of information.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
<i>P. alata</i>												
<i>P. avasmontana</i>												
<i>P. petrosa</i>												
<i>P. rehmi</i>												

Key:

	information absent		flower remains		immature flowers		mature flowers
--	--------------------	--	----------------	--	------------------	--	----------------

Abbreviations:

(Jan: January; Feb: February; Mar: March; Apr: April; May; June; July; Aug: August; Sept: September; Oct: October; Nov: November; Dec: December)

4.5 Gross Morphology



Photo: E. Klaassen

A



Photo: E. Klaassen

B



Photo: E. Klaassen

C



Photo: M. Hochobes

D

Figure 13: Differences in capitula of *Pentatrichia*: **A**: *P. alata*, **B**: *P. avasmontana* **C**: *P. petrosa* and **D**: *P. rehmi*.



Photo: E. Klaassen

A

Photo: E. Klaassen

B

Photo: E. Klaassen

C

Photo: M. Hochobes

D

Figure 14: Different leaf shapes within the genus *Pentatrichia*: **A**: *P. alata*, **B**: *P. avasmontana* **C**: *P. petrosa* and **D**: *P. rehmi*.

CHAPTER 5: DISCUSSION

5.1 Habitat Preference

All species of *Pentatrichia* generally have a cremnophilous habit with the exception of *P. petrosa* which has a shrubby habit. Cliff habitats are amongst some of the harshest environments to survive in with high water run-off and exposure to elements. This type of habitat provides refuge from herbivory, shelter from wind and these plants seem to survive on detritus caught in crevices. Therefore plants inhabiting this type of habitat have evolved adaptations such as low heights, having wind dispersed seeds and cluster growth forms (Figure 15) to ensure their survival (Van Jaarsveld and Van Wyk, 2000). *Pentatrichia avasmontana* is an excellent example of this survival strategy. The fact that these species prefer the southern and eastern slopes indicate a preference for shade or short periods of sunlight. Although the genus is known to occur in one of the potential IPA's for Namibia (north-east Namibia including the Waterberg escarpment and Otavi Mountains within the Karstveld) it is not threatened by the possibility of altered land use practices as it grows on the cliff faces which are free from agricultural practices and not easily accessible to man.



Photo: E. Klaassen

Figure 15: Cluster growth form of *P. avasmontana*, Aredareigas Nature Estate.

5.2 Insect Visitors

During fieldwork visitors of the order Diptera was observed on *P. petrosa* and *P. rehmi* (Figure 16). Hierarchical classification of the visitors collected revealed that it belongs to the Kingdom: Metozoa (animals); Phylum: Arthropoda; Class: Hexapoda; Order: Diptera and Family: Bombyliidae (Iziko, 2006). The Bombyliidae are commonly known as bee flies, which are hairy nectar and pollen eating flies resembling bees (Yeates and Lambkin, 2004; Bee Flies – Family Bombyliidae, 2006; The free dictionary, 2006). Although pollination of the Asteraceae takes place in two stages as described by Turner (1977b), pollination of the genus is unknown and is in need of further study as the bee flies that were found during fieldwork are known to feed on the pollen (Yeates and Lambkin, 2004).



Photo: E. Klaassen

Figure 16: Insect visitors (bee flies) on *P. petrosa*.

5.3 Multivariate Methods

5.3.1 Cluster Analyses

Numerical Taxonomy is based on the study of as many morphological characters as possible to enhance greater stability in the determination of the overall similarity of OTUs through the use of computers (Pankhurst, 1991). Every character has equal weighting and the greater the amount of information for a taxon, the greater the strength of the classification. It has the advantages that it is reproducible, there is greater predictive value than other phenetic classifications, it is objective and free of bias, can integrate data from many sources and can handle large amounts of data. A similarity measure is computed and a dendrogram plotted showing similarity between OTUs (Pankhurst, 1991).

Sequential Agglomerative Hierarchical Nested Clustering (SAHN) method was used based on Manhattan distances and grouping algorithms used were single linkage, complete linkage and UPGMA to generate phenograms. The cophenetic correlation was calculated to test the goodness of fit of the different clustering algorithms (Table 1). According to Pankhurst (1991) the highest cophenetic correlation represents less distortion and a better classification and is thus an indication that the clustering is a good representation of the original dataset. The different algorithms can be explained as follows:

- 1) Single linkage algorithms link the two most similar objects and have the advantage of showing affinities of each item but are less good for forming groups.
- 2) Complete linkage attaches links to the two most dissimilar objects.
- 3) UPGMA computes the average of all similarities between pairs of objects and links them together.

The clusters are considered robust if the results of the different algorithms are relatively similar (Pankhurst, 1991).

Of the three clustering algorithms implemented the UPGMA obtained the highest cophenetic correlation coefficient of 0.78221 (Table 1) indicating the best fit between the phenogram and the original distance matrix. The Complete linkage and Single linkage yielded a cophenetic correlation coefficient of 0.76544 and 0.72413 respectively.

Analyses of the UPGMA phenogram revealed two distinct clusters A and B with a phenon line drawn at $r = 0.14$. Cluster A formed a combination of *P. alata*, *P. avasmontana* and *P. rehmi* whilst cluster B contained *P. petrosa*. The groupings A and B were formed on the basis of leaf shape. Group A contained all the taxa that had a lanceolate-ovate leaf shape whilst group B included species with a cordate leaf shape, *P. petrosa* being the only species with a cordate leaf shape. When a second phenon line is drawn at $r = 0.116$ three clusters (C, D & E) are formed. Cluster C contains *P. alata*, cluster D include a combination of *P. avasmontana* and *P. rehmi* and cluster E include *P. petrosa*. This grouping is mainly on the basis of leaf and capitula characters. The inclusion of *P. avasmontana* in *P. rehmi* suggests that it is morphologically similar to the latter and thus does not warrant specific status. Groupings were awarded names on the basis of the type specimens nesting within them.

5.3.2 Ordination Analyses

The aim of ordination analyses is to plot the objects in reduced space by using two or sometimes three of the components as dimensions (Neff and Marcus, 1980; Abbott *et al.*, 1985). Generally, axis 1 represents the main part of the total variation whilst axis 2 represents the main part of the remaining variation and should be independent to the first axis. OTUs were plotted in multidimensional character space and this technique is used in taxonomy to obtain taxonomic groupings (Abbott *et al.*, 1985). Ordination analyses do not necessarily produce the same results as cluster analyses

but is used to test the groupings of cluster analyses. To check the repeatability of the groupings obtained in the cluster analyses, PCO was employed.

The PCO analyses revealed three distinct groupings (Figure 9 & 10). This confirms the existence of three taxa in the genus as obtained by cluster analyses (Figure 8). PCO deals with distances between objects rather than correlations between attributes and have the advantages of being able to handle mixed and binary characters (Neff and Marcus, 1980). However, it is limited in that one cannot determine how much each character contributes to the final result. The computational procedure involved calculating a similarity matrix using Manhattan distances, double centering and the plotting of eigen vectors (characters). Double centering transforms the data to make it comparable to PCA.

The PCA groupings were not as distinct as in the PCO analyses and only revealed two clusters (Figure 11) due to the fact that fewer characters were used in the PCA. Within these two clusters *P. avasmontana* is still nested within *P. rehmi* and *P. alata* clusters within *P. petrosa*. These groupings are considered to be related to the leaf characters of these taxa. PCA constructs a new set of orthogonal coordinate axes such that projection of points onto them has maximum variance. PCA is sensitive to binary characters and was accordingly restricted to only seven quantitative characters (Appendix 4). The procedure involved calculating a similarity matrix using correlation coefficient to generate a correlation matrix, which was used to extract and project the eigen vectors and plot the OTUs. The Eigen values indicate how much of the total variation is explained by the different ordination axis (Table 2 and 3).

Projecting objects onto the principle components place them into space. PCA has the disadvantage of not being able to handle missing data. It is however good at determining how much each character contributes to the component as indicated by Table 3.

According to Table 3 the first three components or characters (leaf length, leaf width and petiole length) contribute to most of the variation. Although the petiole wing width delimits *P. alata* from *P. avasmontana*, *P. petrosa* and *P. rehmi*, it was not included in the multivariate analyses, because it was difficult to obtain accurate measurements of the petiole width of the other three species.

5.4 Univariate Analyses

Box plots were graphed both to determine the extent of overlap between quantitative characters, as well as to reveal characters of diagnostic value that could be used in the construction of a dichotomous key. Petiole length is the only character that clearly separates *P. avasmontana* and *P. rehmi* from *P. petrosa*. *Pentatrichia rehmi* reveals a constant overlap with *P. avasmontana* with regard to all characters. Outliers for the species may be possible as indicated by Figure 12. Analysis of measurements for all taxa revealed that the leaf length and leaf width for *P. petrosa* are inversely related; leaf width being bigger than the length compared to *P. alata*, *P. avasmontana* and *P. rehmi*.

5.5 Phenology

Mainly flower remains (empty involucre bracts) are present from November to April, although *P. alata* starts to flower in March. August to October form the peak for maturity of flowers. The development of achenes is directly linked to the flowering period, with maturity reaching a peak during August to October. This seems to be relevant to all species within the genus. Fieldwork has revealed that *P. avasmontana* starts to bud in July whereas mature heads are already present in *P. petrosa* during the same period. Generally the flowering periods of the different species overlap considerably, thus the possibility of hybridisation among species in contact zones is not inconceivable. However, no hybrids have been observed both in previous works as well as during this current study.

5.6 Gross Morphology

Examination of morphological characters revealed that *P. alata* and *P. avasmontana* have white ray florets and yellow disc florets (Figure 13). *Pentatrichia alata*, *P. avasmontana* and *P. rehmii* have a lanceolate-ovate leaf shape whilst *P. petrosa* has a cordate to rounded leaf (Figure 14).

5.7 Species Concept and Speciation

Biologists universally agree that a species form the basic natural unit. However, they do not agree on what a species is or how it should be defined. The controversy

arising from this debate is not of a practical nature but more of a theoretical nature e.g. taxonomists define a species in terms of easily identifiable characters. Rundle *et al.* (2001) point out that species are real evolutionary units and different species concepts place different emphasis on properties of species. Five species concepts are recognized namely the phenetic, recognition, biological, ecological and cladistic species concepts (Ridley, 1993). Morphology offers the most practical source of easily identifiable taxonomic characters and results in the identification of phenetic species. The current study follows this particular species concept. Phenetic classification is based on the overall resemblance among biological entities for characters assumed to be heritable (Abbott *et al.*, 1985; Pankhurst, 1991). Therefore phenetic classification seeks to express natural relationships among organisms by analysing large numbers of equally weighted, non-correlated, homologous characters in order to avoid the purposeful selection of characters thought to be important. Furthermore it makes no assumptions about phylogeny, no implications on ancestry and no statement about the evolution of the group.

The phenetic species offers the most important source of taxonomic characters for Asteraceae (Bohm and Stuessy 2001) and previous studies on the genus *Pentatrichia* have been based on morphological characters. This study, although based on morphological characters, differs from previous studies in that statistical approaches have been employed for objectivity. Conclusions from this study revealed that leaf length, leaf width, petiole length, petiole wing width and the presence or absence of ray florets proved to be the most important morphological characters delimiting the species in the genus.

Speciation refers to how a species can divide to give separately evolving lineages beginning with some form of differentiation which then becomes exaggerated and eventually consolidated into two (or more) distinct groups (Majerus *et al.*, 1996). The initial differentiation can come about by spatial separation through some form of geographic barrier. Geographic separation is one of the most common modes of speciation, especially in Asteraceae, and have historically been used as the basis for separating species (Majerus *et al.*, 1996; Bohm and Stuessy, 2001). Majerus *et al.* (1996) consider three forms of speciation: a) sympatric speciation where speciation occurs in the same region with the possibility of mixing of groups, b) allopatric (geographic) speciation where the groups are initially separated and where no mixing of groups are possible, and c) parapatric speciation where groups exist in adjacent regions with a zone of contact. However, the value of the latter is unclear. In allopatric speciation the separated groups can lead to the existence of a new population through the colonisation of a previously empty habitat or a single initial population may fragment into two or more smaller groups (Majerus *et al.*, 1996). The isolation of the groups may lead to divergent gene pools that accumulate enough differences to be recognised as a distinct species (Bohm and Stuessy, 2001). This seems to be true for the species within the genus *Pentatrichia* where geographical barriers separate Namibian species from the South African species, *P. alata*. However, sympatric speciation is also evident in the Namibian species where two taxa, *P. avasmontana* and *P. petrosa*, coexist in the same region or habitat as observed in the Waterberg Plateau Park. Observation of hybridisation was not evident, but may not be impossible between these species.

5.8 Taxonomic Implications

The specific status of *P. avasmontana* is reconsidered as a result of both the cluster and ordination analyses as well as the univariate analyses. The cluster and ordination analyses revealed that *P. avasmontana* is embedded within *P. rehmi* (Figure 8, 9 & 10). *Pentatrichia rehmi* showed close similarity with *P. avasmontana* taking into consideration the characters used for the univariate analyses (leaf size, petiole length, capitula size, peduncle length and achene length) as well as leaf shape, texture and petiole wing width as indicated by Figure 12. The extent of overlap of *P. rehmi* with *P. avasmontana* was such that no clear distinction between the two species could be made, further strengthening the view that these two may represent one heterogenous species. The only discernible morphological difference between the two species is the presence of ray florets in *P. avasmontana*. In addition the two taxa are distributionally distinct. *Pentatrichia avasmontana* has a predominantly central distribution and occur on sandstone, schist and quartzite whereas *P. rehmi* occurs only on quartzite in north-eastern Namibia although rock formations like dolomite and limestone is also present in the habitat of this species. Darwin (1872) states that subspecies are local forms, which are completely fixed and isolated, but they do not differ from each other by strongly marked characters. It is therefore concluded that the presence of only one variable character between these two species does not warrant *P. avasmontana* specific status as it was described later than *P. rehmi*. *Pentatrichia avasmontana* is thus reduced to a subspecies under *P. rehmi* as *P. rehmi* subsp. *avasmontana* (Merxm.) Klaassen & Kwembeya comb.nov.

Pentatrichia avasmontana was described in 1954 by Merxmüller whilst *P. rehmi* had already been described in 1950 by Merxmüller as *Inula rehmi* Merxm.

CHAPTER 6: TAXONOMY

6.1 Genus Description

Pentatrichia Klatt 1895

Klatt in Bulletin de L'Herbier Boissier 3:436-437 (1895); Merxmüller in Mitt.Bot.München 10:438-439 (1954); Merxmüller in FSWA 139:138-139 (1967); Anderberg in Op.Bot. 104:43 (1991); Anderberg in Asteraceae Cladistics and Classification 325 (1994); Herman *et al.* in Strelizia 10:154 (2000)

Type: *P. petrosa* Klatt

Shrublets or shrubs, varying from 0.2 to 1.50 m, much branched, branches curved, young shoots glandular pilose to glabrescent, densely leafy toward apex. *Leaves* alternate, cordate or lanceolate or ovate or lanceolate-ovate, petiolate or rarely sessile, usually narrowing into (almost to prominently) winged petiole, incised with obtuse lobes, glandular pubescent, often reticulate and pitted below. *Capitula* solitary or subcorymbose on apical branches, pedunculate, peduncles densely bracteate, heterogamous or homogamous. *Ray florets* when present marginal, female, white, tube slender, limb elliptical, shortly tridentate. *Disc florets* bisexual and fertile, yellow, tube cylindrical narrowing toward the hardly or expanding five dentate limb, teeth small, lanceolate or almost linear. *Receptacle* naked, pitted, honeycombed. *Ovary* oblong. *Style* filiform, basally inflated, bifid, style branches obtuse with sweeping hairs not reaching furcation. *Anthers* linear, tailed at the base. *Involucre* campanulate. *Involucral bracts* multi-seriate, 7 rows, imbricate, linear-lanceolate, acuminate, cutaneous, glandular to obscurely glandular to eglandular on back, inner

most 2 mm and outer most 7 mm long, recurved in dry state. *Achenes* 1 mm long, indistinctly 4-ribbed, sparsely hairy to glabrous, maturing to black. *Pappus* of free barbelate bristles in 1 row interspersed with a row of short scales, 3-5 (-8).

6.2 Key to Species

- 1a Leaves orbicular-cordate, membranous, capitula homogamous, growing mainly between boulders*P. petrosa*
- 1b Leaves lanceolate-ovate, thickening with maturity, capitula heterogamous or homogamous, cremnophilous.....2
- 2a Petiole more than 15 mm long, petiole wing prominent, up to 1.5 mm wide, capitula heterogamous, plants endemic to South Africa *P. alata*
- 2b Petiole less than 6 mm long, petiole wing obscure mainly visible as a ridge, less than 0.2 mm wide, capitula heterogamous or homogamous, plants endemic to Namibia*P. rehmi*

6.3 Species Descriptions

Pentatrachia alata S.Moore in Journ.Bot. 55:106 (1917)

Type: South Africa, Pilgrim's Rest, Rogers 18667 (PRE, iso!)

Synonyms: *Philyrophyllum alatum* Burt Davy in Kew Bull. 570 (1935)

Pulicaria alata Phill. in Gen.S.Afr.Fl.Pl. 2:805 (1951)

Derivation: *alatus* (L) = winged, referring to the winged petiole.

Perennial shrubby herb, up to 1 m high, much branched with curved branches, young shoots glandular pilose glabrescent, densely leafy toward apex. *Leaves* alternate, lanceolate-ovate, up to 51 x 24 mm, narrowing into a prominently winged petiole, petiole up to 15 mm long, incised with obtuse lobes, glandular pubescent, reticulate venation and pitted below. *Capitula* solitary or few together (2-4) on apical branches, up to 12 x 17 mm, pedunculate, peduncles up to 13 mm long, peduncles densely bracteate, heterogamous. *Ray florets* marginal, female, white, bi-dentate at apex, 7.5 mm long. *Disc florets* yellow, 6 mm long. *Receptacle* naked, pitted, honeycombed. *Style* filiform, bifid, style branches linear. *Anthers* linear, tailed at the base. *Involucral bracts* multi-seriate, imbricate, linear-lanceolate, acuminate, obscurely glandular on back, inner most 2 mm and outer most 7 mm long, slightly recurved in dry state. *Achenes* 0.5(-1.0) mm long, indistinctly 4-ribbed, pubescent. *Pappus* bristles 5.

Distribution: Occurs in the Limpopo and Mpumalanga Provinces of South Africa, which is included in the Wolkberg Centre of Endemism. *Pentatrichia alata* is considered to have a disjunct distribution as all other species within this genus occur in Namibia. This might be due to the much higher rainfall of up to 2 000 mm compared to about 600 mm in Namibia.

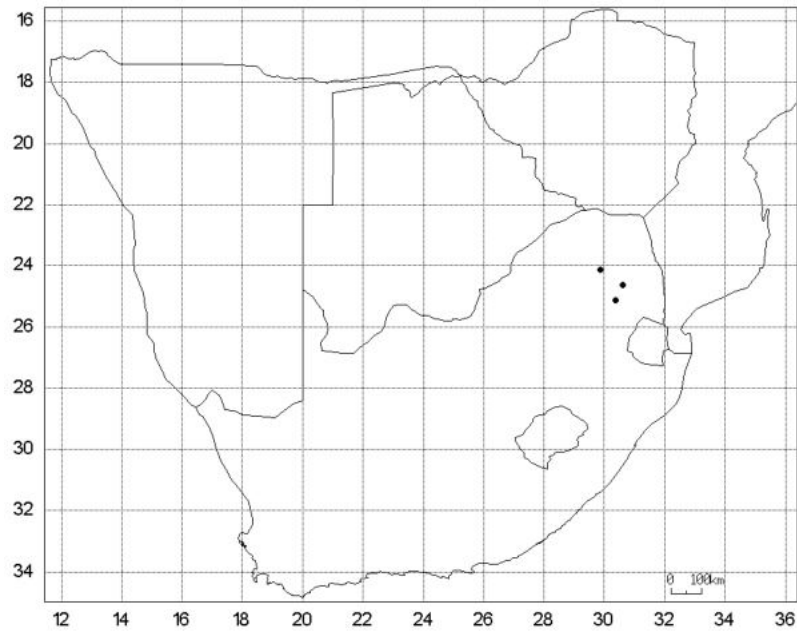


Figure 17: Distribution of *P. alata* in southern Africa (MAPPIT Geographical Mapping System).

Ecology: Rock crevices or mountain sides.



Figure 18: Habit of *P. alata*. (PRE, digital scan of type specimen)

Conservation status: Endemic, LR-lc (Lower Risk-Least Concern).

Specimens examined: Rau & Schlieben 9646 (M); Rogers 18667 (PRE);

Venter 9825 (PRE)

Pentatrachia rehmsii (Merxm.) Merxm. in Mitt.Bot.München 1:43 (1950)

Type: Namibia, Rehm s.n., Guchab Mountains (M)

Synonyms: *Pentatrachia rehmsii* (Merxm.) Merxm. in Mitt.Bot.München 1:43 (1950)

Inula rehmsii Merxm. in Mitt.Bot.München 1:43 (1950)

Derivation: After Dr. Rehm founder of the species.

Small perennial shrub, 0.5 m high, much branched, branches curved, young shoots glandular pilose to glabrescent, densely leafy toward apex. *Leaves* alternate, petiolate or rarely sessile, narrowing into almost winged petiole, wing often only visible as a ridge, petiole up to 5 mm long, ovate-lanceolate, 29-37 x 13-16 mm, incised with obtuse lobes, glandular pubescent, reticulate and pitted below, thickening with maturity. *Capitula* solitary or few together (4-10) on apical branches, up to 11 x 9 mm, pedunculate, peduncles 10 x 8 mm long, peduncles densely bracteate, heterogamous or homogamous. *Ray florets* when present marginal, female, white, tube 3 mm long, ligula 6 mm long. *Disc florets* yellow, ovary 6 mm long, limb 5-dentate. *Receptacle* naked, pitted, honeycombed. *Style* filiform, basally inflated, bifid. *Anthers* linear, tailed at the base. *Involucral bracts* multi-seriate, imbricate, linear-lanceolate, acuminate, obscurely glandular on back, inner most 2 mm and outer most 7 mm long, recurved in dry state. *Achenes* 0.7(-1.5) mm long, indistinctly 4-ribbed, sparsely hairy. *Pappus* bristles 3-5 interspersed with a row of short scales.

Two forms are closely related but distributionally and morphologically distinct and will be recognised on the subspecific level. These two are easily separated as follows:

- 1a Capitula heterogamous, ray florets white, mainly central Namibia, various rock types subsp. *avasmontana*
- 1b Capitula homogamous, north-eastern Namibia, quartzite subsp. *rehmii*

Pentatrichia rehmi Merxm. subsp. *avasmontana* (Merxm.) Klaassen & Kwembeya
comb.nov.

Basionym: *Pentatrichia avasmontana* Merxm.

Type: Dinter 7894, Lichtenstein in the Auas mountains (PRE, iso!, Z, iso!)

Synonyms: *Pentatrichia avasmontana* Merxm. in Mitt.Bot.München 1:441
(1954); Type: Dinter 7894, Lichtenstein in the Auas mountains (PRE, iso!, Z, iso!)

P. confertifolia Merxm. in Mitt.Bot.München 1:441 (1954); Type: Fleck 49a,
Gamsberg (Z!).

Tetratrichia avasmontana Dinter ex Merxm. in Mitt.Bot.München 1:440 (1954),
nom.nud. in syn. (Z!)

Pulicaria confertifolia Klatt ex Merxm. in Mitt.Bot.München 1:440 (1954), *nom.nud.*
in syn. (Z!)

Derivation: *avas* (L) referring to the Auas Mountains and *montana* (*montanus*) (L)
= mountain, pertaining to or growing on mountains or mountain dweller

Perennial shrub, 0.3 m high. *Leaves* ovate-lanceolate, up to 36 x 16 mm, petiolate or rarely sessile, petiole up to 5 mm long, *Capitula* solitary or few together (4-10) on apical branches, up to 10 x 7 mm, peduncle up to 8 mm long. *Ray florets* marginal, female, white, tube 3 mm long, ligula 6 mm long. *Disc florets* yellow, ovary 6 mm long. *Achenes* 0.7(-1.3) mm long, indistinctly 4-ribbed, sparsely hairy. *Pappus* bristles 3-5 interspersed with a row of short scales.

Distribution: Occurring mainly in central Namibia but also found in the Waterberg Plateau Park.

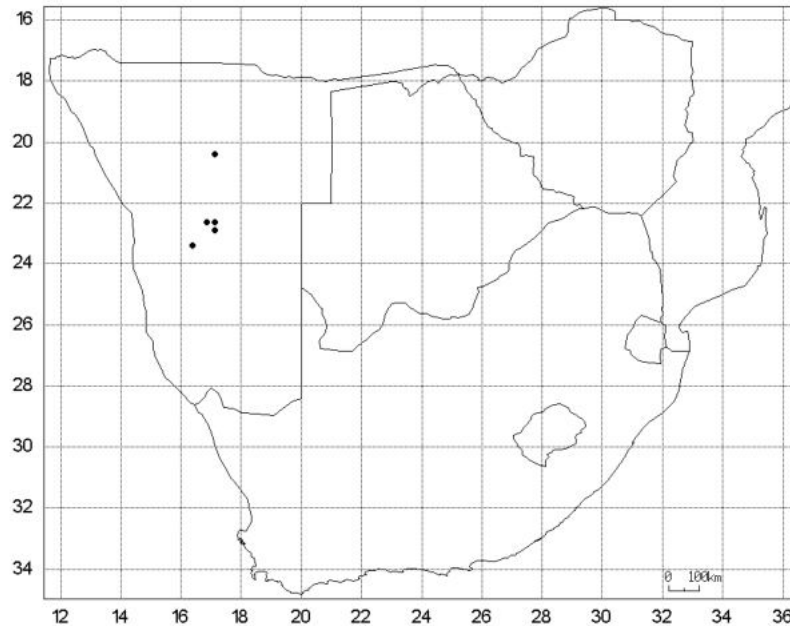


Figure 19: Distribution of *P. rehmi* subsp. *avasmontana* in southern Africa (MAPPIT Geographical Mapping System).

Ecology: Occurring in crevices of cliff faces, preferring S, SE, E and NE faces. Various rock types including sandstone, schist and quartzite have been noted. Altitudinal variation up to 2 326 m have been recorded. *Pentatrachia rehmi* subsp. *avasmontana* has been found at Waterberg Plateau Park which has an average rainfall of about 450 mm thus indicating that the distribution range of this species might be extended with closer investigation of other mountain ranges, such as the Baines Mountains in the Kaokoveld which has the same type of geology (sandstone, dolomite and conglomerate) as Waterberg Plateau Park, in the rest of the country. This would evidently give a clearer indication whether this species prefer the higher rainfall areas within the country or whether this species is just under collected compared to *P. petrosa* due to its habitat preference.



Photo: M. Hochobes



Photo: E. Klaassen

Figure 20: Habit of *P. rehmi* subsp. *avasmontana*. Fig Tree Walk, Waterberg Plateau Park.

Similar species: *Pentatrichia rehmi* subsp. *avasmontana* can be confused with *Jamesbrittenia acutiloba* (Pilg.) Hilliard when observed from a distance, displaying the same habit and habitat preference as indicated by Figure 20. However, *J. acutiloba* belongs to the family Schrophulariaceae and have white tubular flowers and opposite leaves with a serrate margin, which are densely glandular pubescent.



Photo: M. Hochobes



Photo: M. Hochobes

Figure 21: *Jamesbrittenia acutiloba*, habit and flowers. Okatjikona Environmental Education Centre, Waterberg Plateau Park.

Conservation status: Endemic, LC (Least Concern).

Specimens examined: Bradfield 575 (PRE); Dinter 7894 (PRE, Z); Meyer 1015 (M); Meyer 1013 (WIND, M); Merxmüller & Giess 32564 (WIND); Seydel 4063 (WIND); Seydel 4064 (M)

Pentatrichia rehmi (Merxm.) Merxm. subsp. *rehmi*

Small shrubs, 0.5 m high. *Leaves* ovate-lanceolate, up to 29 x 13 mm, petiole up to 5 mm long. *Capitula* solitary or few together (4) on apical branches, up to 10 x 8 mm, peduncle up to 6 mm long. *Disc* florets yellow, 7 mm long including ovary. *Achenes* 0.8(-1.5) mm long, indistinctly 4-ribbed, sparsely hairy. *Pappus* bristles 5 interspersed with a row of short scales.

Distribution: North-eastern Namibia

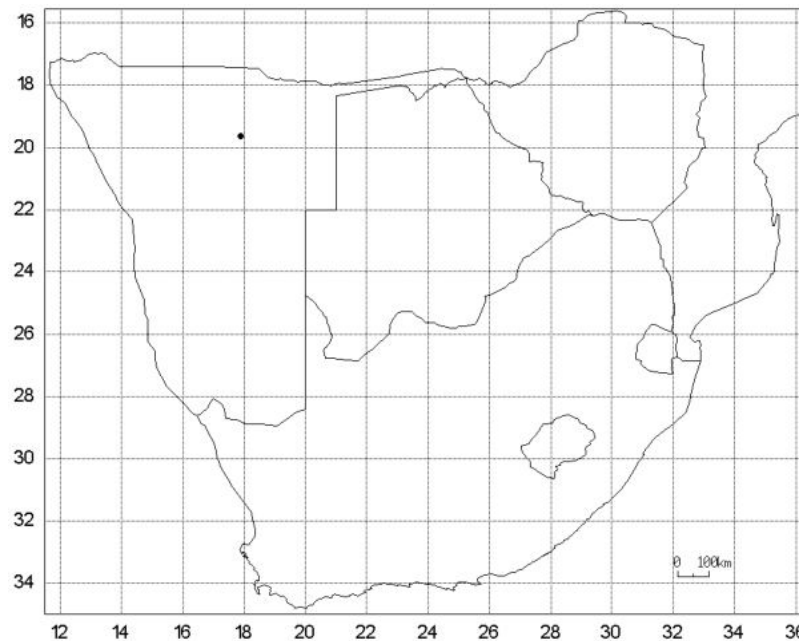


Figure 22: Distribution of *P. rehmi* subsp. *rehmi* in southern Africa (MAPPIT Geographical Mapping System).

Ecology: Crevices of quartzite cliff faces. Altitude between 1 646 and 1 729 m.



Photo: S. Rügheimer

Figure 23: Quartzite rock formation, Guchab Mountain.



Photo: M. Hochobes



Photo: M. Hochobes

Figure 24: Habit of *P. rehmi* subsp. *rehmi*, Guchab Mountain.

Similar species: *Pentatricchia rehmi* subsp. *rehmi* displays the same habit and habitat preference as *Jamesbrittenia dolomitica* Hilliard as indicated by Figure 25. However, *J. dolomitica* differs from the former in that it belongs to the family Schrophulariaceae, has yellow tubular flowers and opposite leaves.



Photo: E. Klaassen

Figure 25: *Jamesbrittenia dolomitica*, flowers, Guchab Mountain.

Conservation status: Endemic, VUD1 (Vulnerable)

Specimens examined: Rehm s.n. (M, digital scan); Klaassen & Hochobes 1751 (WIND); Klaassen & Hochobes 1752 (WIND); Klaassen & Hochobes 1754 (WIND); Klaassen & Hochobes 1755 (WIND); Klaassen & Hochobes 1756 (WIND); Klaassen & Hochobes 1757 (WIND)

Pentatrachia petrosa Klatt in Bull.Herb.Boiss. 3:437 (1895)

Type: Namibia, Steingröver 19, Aus (Z!)

Synonym: *Inula petrosa* Klatt ex Range in Feddes Repert. 38:279 (1935)

Derivation: *petros* (G) referring to rocky places

Shrubs, varying from 0.2 to 1.50 m, much branched, branches curved, young shoots glandular pilose glabrescent, densely leafy toward apex. *Leaves* alternate, long petiolate narrowing into almost winged petiole, petiole wing often only visible as a ridge, petiole up to 27 mm long, cordate, up to 37 x 37 mm, incised with obtuse

lobes, glandular pubescent, reticulate. *Capitula* solitary or twinned on apical branches, up to 14 x 14 mm, pedunculate, peduncles up to 22 mm long and densely bracteate, homogamous. *Disc florets* yellow. *Receptacle* naked, pitted, honeycombed. *Style* filiform, bifid, style branches linear. *Anthers* tailed at the base, with a lanceolate appendage. *Involucral bracts* white with a green median line, multi-seriate, imbricate, linear-lanceolate, acuminate, eglandular to obscurely glandular on back, margin serrulate, inner most 2 mm and outer most 7 mm long, slightly recurved in dry state. *Achenes* 0.8(-1.3) mm long, indistinctly 4-ribbed, sparsely hairy. *Pappus* bristles 5 occasionally more (8) in 1 row interspersed with a row of short scales.

Distribution: Widespread in Namibia extending into the Northern Cape region of South Africa.

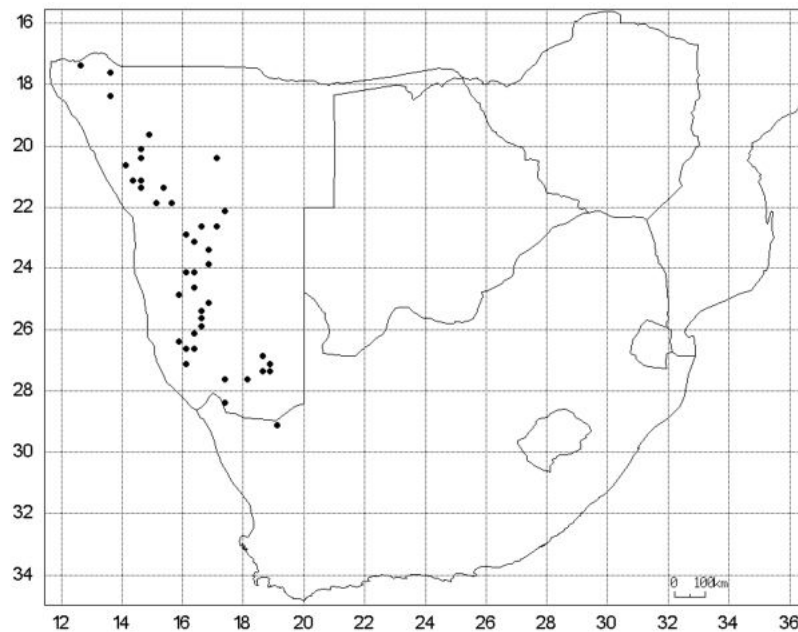


Figure 26: Distribution of *P. petrosa* in southern Africa (MAPPIT Geographical Mapping System).

Ecology: Rocky and mountainous areas along the escarpment, mainly at the base and in crevices of boulders, but are occasionally found hanging from crevices of cliffs, on koppies and rocky outcrops. Found on S, SE, SW, E, ESE, W, and N aspects. A variety of rock types including schist, granite, sandstone, quartzite and dolomite have been noted. Altitude between 490 and 1 719 m.



Photo: E. Klaassen



Photo: M. Hochobes

Figure 27: Habit of *P. petrosa*. **A:** Okatjikona Environmental Education Centre, **B:** Onjoka Conservation Station, Waterberg Plateau Park.

Similar species: *Pentatrichia petrosa* can be confused with *Cineraria canescens* Wendl. ex Link, displaying the same habit and habitat preference as indicated by Figure 28. However, *C. canescens* differ from *P. petrosa* in that the heads are heterogamous and the leaves are somewhat discoloured.



Photo: E. Klaassen



Photo: E. Klaassen

Figure 28: *Cineraria canescens*, habit and flowers, Fig Tree Walk, Waterberg Plateau Park.

Specimens examined: Bleissner 299 (M); Botha & Bredenkamp 3573 (PRE); Bradfield 524 (PRE); De Winter 3278 (WIND, M); De Winter & Leistner 5904 (WIND, PRE, M); Dinter 276 (NBG); Gassner 198 (M); Giess 3949 (WIND); Giess 10404 (WIND, PRE, M); Giess & Müller 11835 (WIND, M); Hardy & Venter 4601 (PRE, WIND); Kinges 2311 (M); Klaassen & Bartsch EK528 (WIND); Merxmüller & Giess 3561 (M); Nordenstam & Lundgren 578 (M); Örtendahl 269 (PRE); Schelpe 207 (M); Schwerdtfeger 4060 (WIND); Steingröver 19 (M); Strey 2122 (M, PRE)

CHAPTER 7: CONCLUSIONS AND RECOMMENDATIONS

This study has revealed the presence of only three distinct phenetic species in the genus *Pentatrichia*. The application of numerical methods has proved useful in the delimitation of these taxa. *Pentatrichia avasmontana* is here reduced to subspecific level under *P. rehmii* and will now accordingly be referred to as *P. rehmii* subsp. *avasmontana*. Morphological characters such as leaf length, leaf width, petiole length, petiole wing width and the presence or absence of ray florets proved to be the most useful characters delimiting the taxa.

Red List assessments have revealed that two taxa fall in the “Least Concern” category with *P. rehmii* subsp. *rehmii* emerging in the “Vulnerable” category.

It is hereby recommended that molecular methods, for example DNA sequencing, be used to further test species limits in this genus and to obtain information on the phylogenetic relationships among the species. Scanning Electron Microscopy (SEM) analyses are recommended to compare achene structures and surfaces as well as indumentum of leaf surfaces for comparison between other tribes and genera within the Asteraceae. Furthermore, more field studies need to be conducted to investigate the pollination biology and possible range extension of all the taxa.

No ethnobotanical information on the taxa could be obtained from literature as well as during field studies as a result of the unfamiliarity and habitat preference of the genus. The screening for economical important properties e.g. medicinal properties is

thus recommended. It is further recommended that the horticultural potential of the taxa be explored, possibly through seed germination, as it forms attractive displays against rock faces.

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APPENDIX 1

Definitions of terminology used in the text:

- Arenosols referring to sandy soil which was formed by windblown sand having a depth of up to 1 m
- Cambisols soils which are formed by recently eroded parent material which have been deposited by sporadic floods
- Cremnophilous stemming from the Greek word cremnos being defined as pertaining to cliffs
- Leptosols shallow, coarse textured soils formed in actively eroding landscapes, specifically hilly and undulating areas, which is limited in depth by the presence of hard rock
- Regosols medium or fine textured soils of actively eroding landscapes with thin layer of soil directly above the underlying rock surface from which it was formed
- Quartzite massive hard rock developed by metamorphism from sandstone and the quartzitic layers form the dominant ridges which are clearly visible from a distance

APPENDIX 2

Characters used in the phenetic analyses.

	Character	Character type	Selection criteria	Parts measured
1	leaf length	quantitative	completely visible	apex to base
2	leaf width	quantitative	completely visible	widest part
3	petiole length	quantitative	completely visible	base of leaf to attachment to stem
4	capitula length	quantitative	completely visible	apex to base
5	capitula width	quantitative	completely visible	widest part
6	peduncle length	quantitative	completely visible	base of capitula to corymb branching point
7	achene length	quantitative	completely visible	achene base to base of pappus bristles
8	ray florets	binary	0 = absent 1 = present	-
9	pappus bristles	binary	0 = absent 1 = present	-
10	pappus scales	binary	0 = absent 1 = present	-
11	capitula homogamous	qualitative	0 = no 1 = yes	-
12	capitula heterogamous	qualitative	0 = no 1 = yes	-

13	ray florets white	qualitative	0 = no 1= yes	-
14	ray florets yellow	qualitative	0 = no 1= yes	-
15	pappus bristles 3	qualitative	0 = no 1= yes	-
16	pappus bristles 5	qualitative	0 = no 1= yes	-
17	pappus bristles >5	qualitative	0 = no 1= yes	-
18	pappus bristles in two rows	qualitative	0 = no 1= yes	-
19	pappus bristles one row interspersed with scales	qualitative	0 = no 1= yes	-
20	achene glabrous	qualitative	0 = no 1= yes	-
21	achene pubescent	qualitative	0 = no 1= yes	-
22	achene immature	qualitative	0 = no 1= yes	-
23	achene mature	qualitative	0 = no 1= yes	-
24	florets immature	qualitative	0 = no 1= yes	-

25	florets mature	qualitative	0 = no 1= yes	-
26	involucral bracts strongly recurved	qualitative	0 = no 1= yes	-
27	involucral bracts not strongly recurved	qualitative	0 = no 1= yes	-
28	involucral bracts obscurely glandular	qualitative	0 = no 1= yes	-
29	involucral bracts eglandular	qualitative	0 = no 1= yes	-
30	leaves alternate	qualitative	0 = no 1= yes	-
31	leaves opposite	qualitative	0 = no 1= yes	-
32	leaves sessile	qualitative	0 = no 1= yes	-
33	leaves petiolate	qualitative	0 = no 1= yes	-
34	leaves palmately lobed	qualitative	0 = no 1= yes	-
35	leaves not palmately lobed	qualitative	0 = no 1= yes	-
36	leaves pubescent	qualitative	0 = no 1= yes	-

37	leaves glabrous	qualitative	0 = no 1= yes	-
38	petiole prominent	qualitative	0 = no 1= yes	-
39	petiole not prominent (leaf narrowed into petiole)	qualitative	0 = no 1= yes	-
40	petiole wing prominent	qualitative	0 = no 1= yes	-
41	petiole wing obscure	qualitative	0 = no 1= yes	-
42	leaves cordate	qualitative	0 = no 1= yes	-
43	leaves orbicular	qualitative	0 = no 1= yes	-
44	leaves reniform	qualitative	0 = no 1= yes	-
45	leaves lanceolate	qualitative	0 = no 1= yes	-
46	leaves ovate	qualitative	0 = no 1= yes	-
47	venation reticulate	qualitative	0 = no 1= yes	-
48	venation not reticulate	qualitative	0 = no 1= yes	-

49	leaves pitted	qualitative	0 = no 1= yes	-
50	leaves not pitted	qualitative	0 = no 1= yes	-

APPENDIX 3

OTUs used in the analyses

OTU: Abbreviation		Name	Collector number	Status	Taxon
1	Rog18667	Rogers, F.A.	18667	Type	<i>P. alata</i>
2	Ven9825	Venter, F.	9825		<i>P. alata</i>
3	R&S9646	Rau & Schlieben	9646		<i>P. alata</i>
4	Sey4063	Seydel, R.	4063		<i>P.</i> <i>avasmontana</i>
5	M&G32564	Merxmüller, H. & Giess, W.	32564		<i>P.</i> <i>avasmontana</i>
6	Bra575	Bradfield, R.D.	575		<i>P.</i> <i>avasmontana</i>
7	Sey4064	Seydel, R.	4064		<i>P.</i> <i>avasmontana</i>
8	Mey1015	Meyer, P.G.	1015		<i>P.</i> <i>avasmontana</i>
9	Din7894	Dinter, K.	7894	Type	<i>P.</i> <i>avasmontana</i>
10	EK&MH1759	Klaassen, E & Hochobes, M	1759		<i>P.</i> <i>avasmontana</i>

11	EK&MH1760	Klaassen, E & Hochobes, M	1760		<i>P.</i> <i>avasmontana</i>
12	Mey1013	Meyer, P.G.	1013		<i>P.</i> <i>avasmontana</i>
13	H&V4601	Hardy & Venter	4601		<i>P. petrosa</i>
14	K&Bek528	Klaassen, E. & Bartsch, S.	EK528		<i>P. petrosa</i>
15	Ort269	Örtendahl, I.	269		<i>P. petrosa</i>
16	Sey4060	Seydel, R.	4060		<i>P. petrosa</i>
17	Gas198	Gassner, G.	198		<i>P. petrosa</i>
18	M&G3561	Merxmüller, H. & Giess, W.	3561		<i>P. petrosa</i>
19	Gie14462	Giess, W.	14462		<i>P. petrosa</i>
20	Din276	Dinter, K	276		<i>P. petrosa</i>
21	Str2122	Strey, R.G.	2122		<i>P. petrosa</i>
22	D&L5904	De Winter, B. & Leistner, O.A.	5904		<i>P. petrosa</i>
23	DeW3278	De Winter, B.	3278		<i>P. petrosa</i>
24	Ble299	Bleissner, B.	299		<i>P. petrosa</i>
25	Kin2311	Kinges, H.	2311		<i>P. petrosa</i>
26	Ste19	Steingröver	19	Type	<i>P. petrosa</i>
27	Gie10404	Giess, W.	10404		<i>P. petrosa</i>

28	G&M11835	Giess, W. & Müller, M.	11835		<i>P. petrosa</i>
29	N&L578	Nordenstam, B. & Lundgren, J.	578		<i>P. petrosa</i>
30	Sch207	Schelpe, A.S.L.	207		<i>P. petrosa</i>
31	B&B3573	Botha & Bredenkamp	3573		<i>P. petrosa</i>
32	Bra524	Bradfield, R.D.	524		<i>P. petrosa</i>
33	EK&MH1751	Klaassen, E & Hochobes, M	1751		<i>P. rehmi</i>
34	EK&MH1752	Klaassen, E & Hochobes, M	1752		<i>P. rehmi</i>
35	EK&MH1754	Klaassen, E & Hochobes, M	1754		<i>P. rehmi</i>
36	EK&MH1755	Klaassen, E & Hochobes, M	1755		<i>P. rehmi</i>
37	EK&MH1756	Klaassen, E & Hochobes, M	1756		<i>P. rehmi</i>
38	EK&MH1757	Klaassen, E & Hochobes, M	1757		<i>P. rehmi</i>
39	Rehsn	Rehm, S.	s.n.	Type (scan)	<i>P. rehmi</i>

APPENDIX 4

Quantitative character matrix (measurement are in mm)

OTU		ll	lw	pl	cl	cw	pel
1	Rog18667	24.6	13.3	11	12	14.3	10.3
2	Ven9825	50.62	23.66	15.21	10.4	15.09	9.59
3	R&S9646	30.29	11.34	8.24	12.07	17.36	13.19
4	Sey4063	13.84	7.25	2.88	6.4	5.88	3.51
5	M&G32564	15.41	9.45	5.54	9.05	5.51	5.24
6	Bra575	30.08	15.97	3.27	9.87	7.15	4.5
7	Sey4064	8.88	4.26	2.56	7.68	6.26	2.94
8	Mey1015	13.80	6.04	2.44	7.66	6.16	1.90
9	Din7894	20.16	8.75	3.98	8.30	6.56	8.32
10	EK&MH1759	36.99	11.72	2.52	10.77	5.20	5.05
11	EK&MH1760	22.17	9.28	2.70	9.85	5.66	2.59
12	Mey1013	23.52	12.89	3.91	8.40	6.40	8.43
13	H&V4601	14.94	15.37	11.2	11.08	14.56	8.27
14	K&Bek528	10.48	19.06	21.83	11.5	14.66	15.34
15	Ort269	27.45	37.09	27.20	8.53	9.27	16.62
16	Sey4060	21.06	21.24	9.82	13.24	11.89	20.23
17	Gas198	21.06	15.88	9.38	8.35	8.12	8.21
18	M&G3561	26.98	30.62	19.85	11.77	13.09	22.18
19	Gie14462	21.23	25.97	21.47	14.23	12.77	17.92
20	Din276	17.67	20.90	15.60	8.43	6.75	8.44

21	Str2122	14.66	16.13	8.90	11.87	12.5	13.58
22	D&L5904	35.46	36.49	20.35	10.22	10.82	8.36
23	DeW3278	21.23	23.68	11.82	11.23	10.52	7.90
24	Ble299	16.78	17.57	15.13	10.65	10.13	13.26
25	Kin2311	17.67	20.28	12.73	9.88	10.15	9.86
26	Ste19	14.18	14.38	13.91	13.55	13.5	12.34
27	Gie10404	24.30	28.87	20.68	12.35	12.63	16.25
28	G&M11835	16.07	16.99	15.17	7.26	12.76	16.81
29	N&L578	19.41	22.71	17.47	11.92	9.54	10.03
30	Sch207	19.41	24.11	17.15	12.56	11.85	13.70
31	B&B3573	21.64	27.65	16.23	12.81	11.28	16.21
32	Bra524	27.01	30.94	20.32	12.30	10.32	12.64
33	EK&MH1751	29.55	12.85	2.92	9.91	8.72	5.12
34	EK&MH1752	24.92	11.72	4.34	9.63	6.88	6.01
35	EK&MH1754	22.01	10.49	3.43	10.42	7.57	3.87
36	EK&MH1755	18.00	7.72	3.40	8.97	6.17	4.20
37	EK&MH1756	21.53	11.52	3.79	9.14	8.80	4.76
38	EK&MH1757	22.01	11.23	4.42	9.97	7.52	5.85
39	Rehns	21.47	11.85	4.64	8.58	8.17	5.56

ll: leaf length; lw: leaf width; pl: petiole length; cl: capitula length; cw: capitula width; pel: peduncle length; achene length

APPENDIX 5

Type specimens of *Pentatrichia*.

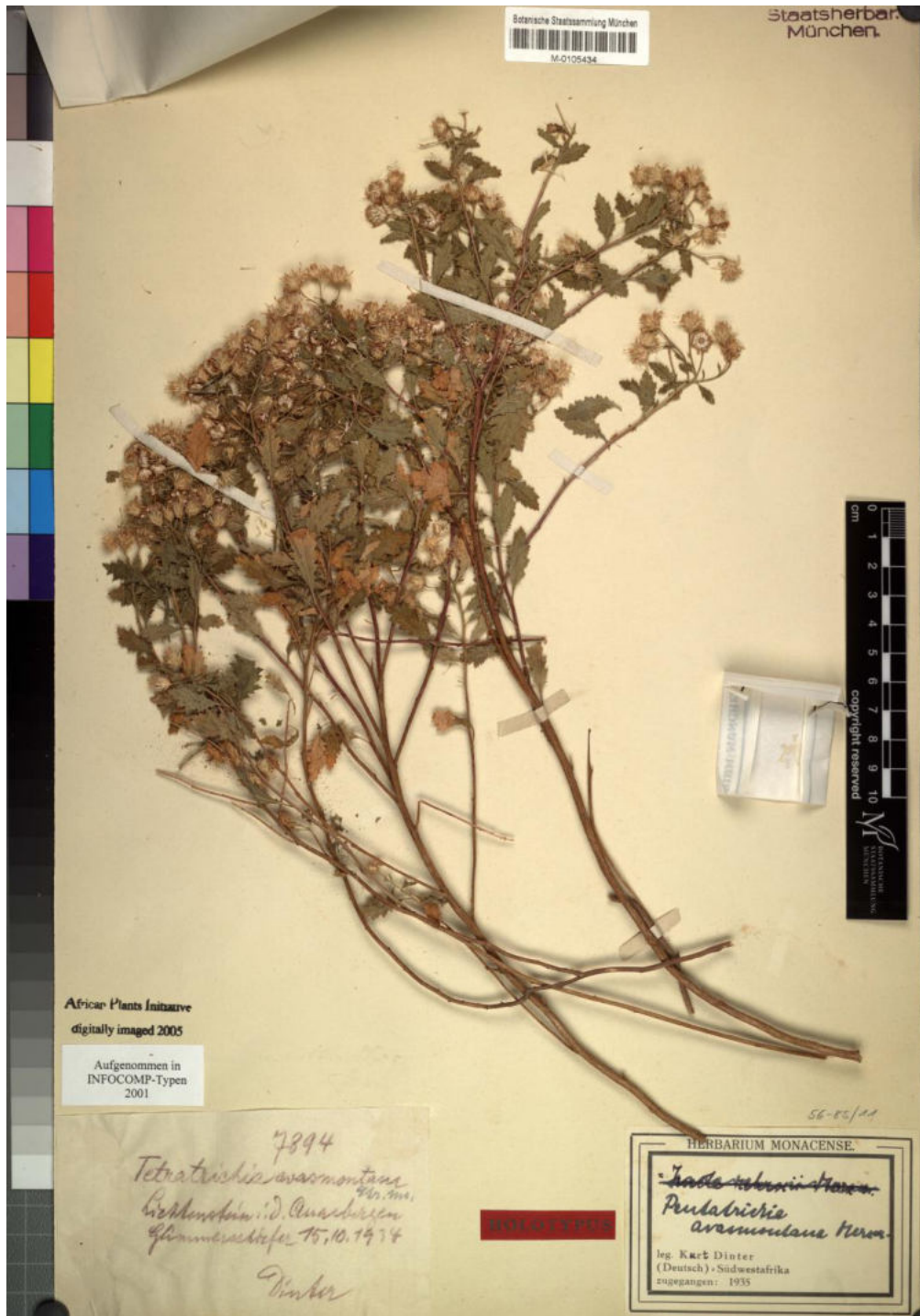
Pentatrichia alata S.Moore

Type: South Africa, Pilgrim's Rest, Rogers 18667 (PRE, iso!)

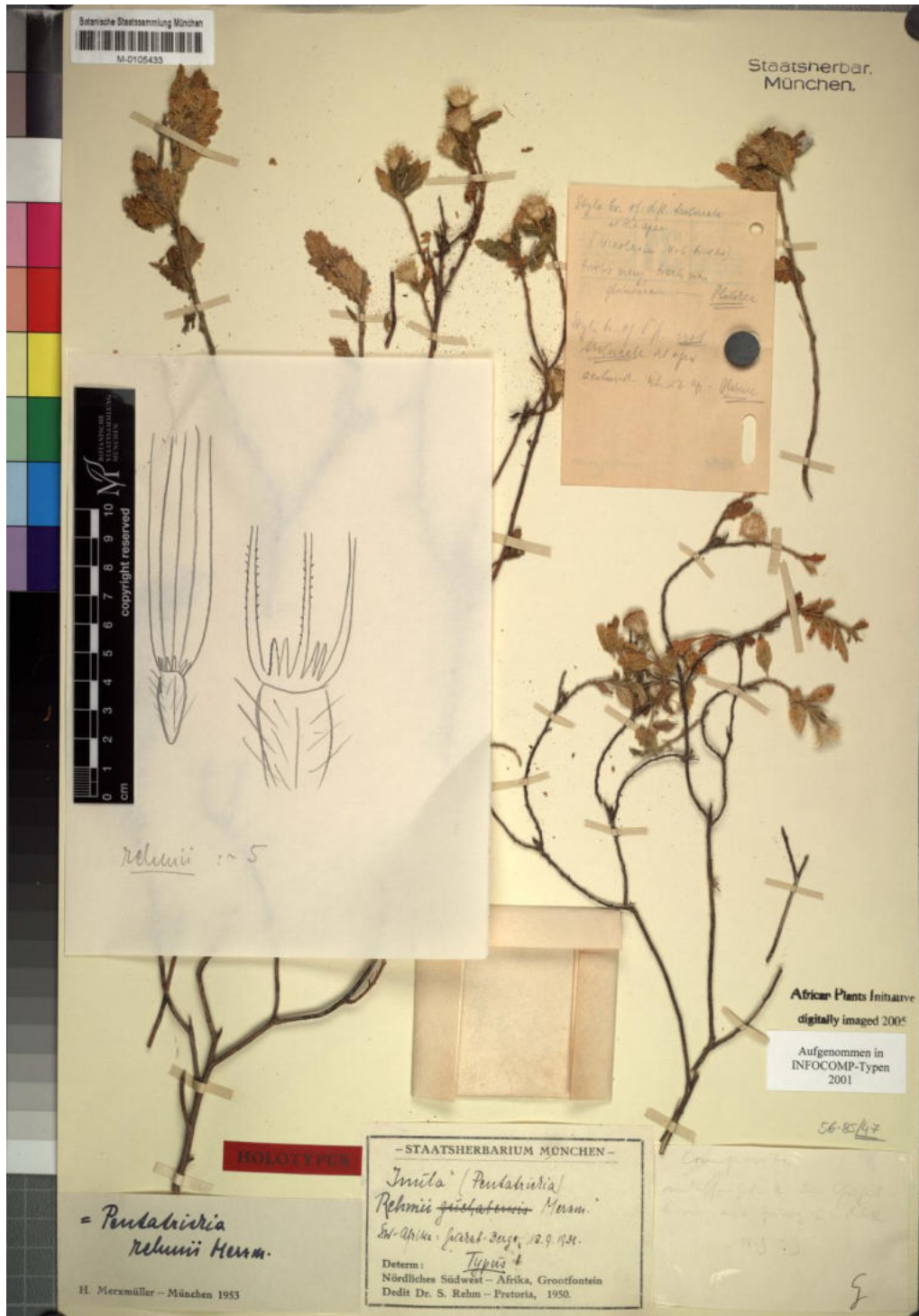


Pentatrichia rehmsii (Merxm.) Merxm. subsp. *avasmontana* (Merxm.) Klaassen & Kwembeya comb. nov.

Type: Dinter 7894, Lichtenstein in the Auas mountains (PRE, iso!, Z, iso!)



Pentatrichia rehmsii (Merxm.) Merxm. subsp. *rehmsii*
 Type: Namibia, Rehm s.n., Guchab Mountains (M)



APPENDIX 6: Mixed character data matrix

No of rows: 39		No of columns: 53																				
OTU	ll	lw	pl	cl	cw	pel	al	ra	rp	pba	pbp	psa	psp	ch	che	rw	ry	pb3	pb5	pb>5	pb2r	pb1s
Rog18667	24.6	13.3	11	12	14.3	10.3	0.55	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Ven9825	50.62	23.66	15.21	10.4	15.09	9.59	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
R&S9646	30.29	11.34	8.24	12.07	17.36	13.19	0.89	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Sey4063	13.84	7.25	2.88	6.4	5.88	3.51	0.72	0	1	0	1	0	1	0	1	1	0	1	0	0	0	1
M&G32564	15.41	9.45	5.54	9.05	5.31	5.24	1.26	0	1	0	1	0	1	0	1	1	0	1	0	0	0	1
Bra575	30.08	15.97	3.27	9.87	7.15	4.5	1.32	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Sey4064	8.88	4.62	2.56	7.68	6.26	2.94	1.19	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Mey1015	13.8	6.04	2.44	7.66	6.16	1.9	1.01	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Din7894	20.16	8.75	3.98	8.3	6.56	8.32	1.16	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
EK&MH1759	36.99	11.72	2.52	10.77	5.20	5.05	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
EK&MH1760	22.17	9.28	2.70	9.85	5.66	2.59	0.80	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Mey1013	23.52	12.89	3.91	8.4	6.4	8.43	0.96	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
H&V4601	14.94	15.37	11.2	11.08	14.56	8.27	0.75	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
K&Bek528	10.48	19.06	21.83	11.5	14.66	15.34	1.12	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Ort269	27.45	37.09	27.2	8.53	9.27	16.62	1.25	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Sey4060	21.06	21.24	9.82	13.24	11.89	20.23	1.18	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Gas198	21.06	15.88	9.38	8.35	8.12	8.21	0.98	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
M&G3561	26.98	30.62	19.85	11.77	13.09	22.18	0.94	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Gie14462	21.23	25.97	21.47	14.23	12.77	17.92	1.16	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Din276	17.67	20.9	15.6	8.43	6.75	8.44	0.53	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Str2122	14.66	16.13	8.9	11.87	12.5	13.58	1.17	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
D&L5904	35.46	36.49	20.35	10.22	10.83	8.36	0.86	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
DeW3278	21.23	23.68	11.82	11.23	10.52	7.9	0.85	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Ble299	16.78	17.57	15.13	10.65	10.13	13.26	0.76	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Kin2311	17.67	20.28	12.73	9.88	10.15	9.86	0.72	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1

Stel9	14.18	14.38	13.91	13.55	13.5	12.34	0.91	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Gie10404	24.3	28.87	20.68	12.35	12.63	16.25	1.19	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
G&M11835	16.07	16.99	15.17	7.26	12.76	16.81	1.28	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
N&L578	19.41	22.71	17.47	11.92	9.54	10.03	0.51	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Sch207	19.41	24.11	17.15	12.56	11.85	13.7	1.31	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
B&B3573	21.64	27.65	16.23	12.81	11.28	16.21	0.96	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Bra524	27.01	30.94	20.32	12.3	10.32	12.64	1.21	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1751	29.55	12.85	2.92	9.91	8.72	5.12	0.81	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1752	24.92	11.72	4.34	9.63	6.88	6.01	1.44	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1754	22.01	10.49	3.43	10.42	7.57	3.87	1.11	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1755	18.00	7.72	3.40	8.97	6.17	4.20	0.79	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1756	21.53	11.52	3.79	9.14	8.80	4.76	1.48	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
EK&MH1757	22.01	11.23	4.42	9.97	7.52	5.85	1.21	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1
Rehsn	21.47	11.85	4.64	8.58	8.17	5.56	1.36	1	0	0	1	0	1	1	0	0	0	0	1	0	0	1

OTU	ag	ap	aim	am	fim	fm	ibsr	ibnr	iogl	iegl	la	lo	ls	lp	lpa	lnpa	lpu	lgl	ppr	pnw	pwp	pwo	lc	lor	lr	lla	lov	vr	vnr	lpi	lnpi
Rog18667	0	1	1	0	1	0	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0
Ven9825	0	1	1	0	0	1	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0
R&S9646	0	1	1	0	0	1	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0
Sey4063	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
M&G32564	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Bra575	0	1	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Sey4064	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Mey1015	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Din7894	0	1	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1759	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1760	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Mey1013	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
H&V4601	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
K&Bek528	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Ort269	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Sey4060	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Gas198	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
M&G3561	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Gie14462	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Din276	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Str2122	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
D&L5904	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
DeW3278	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Ble299	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Kin2311	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Ste19	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Gie10404	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1

G&M11835	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
N&L578	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Sch207	0	1	0	1	0	1	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
B&B3573	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
Bra524	0	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1
EK&MH1751	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1752	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1754	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1755	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1756	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
EK&MH1757	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Rehns	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0

ll: leaf length; lw: leaf width; pl: petiole length; cl: capitula length; cw: capitula width; pel: peduncle length; ra: ray florets absent; rp: ray florets present; pba: pappus bristles absent; pbp: pappus bristles present; ch: capitula homogamous; che: capitula heterogamous; rw: ray florets white; ry: ray florets yellow; pb2r: pappus bristles 2 rows; pb1s: pappus bristles 1 row; ag: achenes glabrous; ap: achenes pubescent; aim: achenes immature; am: achenes mature; fim: florets immature; fm: florets mature; ibsr: involucre bracts strongly recurved; ivnr: involucre bracts not recurved; ibg: involucre bracts obscurely glandular; ieg: involucre bracts eglandular; la: leaves alternate; lo: leaves opposite; ls: leaves sessile; lp: leaves petiolate; lpa: leaves palmately lobed; lnpa: leaves not palmately lobed; lpu: leaves pubescent; lgl: leaves glabrous; ppr: petiole prominent; pnw: leaf narrowing into petiole; pwp: petiole wing prominent; pwo: petiole wing obscure; lc: leaves cordate; lor: leaves orbicular; lr: leaves reniform; lla: leaves lanceolate; lov: leaves ovate; vr: venation reticulate; vnr: venation not reticulate; lpi: leaves pitted; lpni: leaves not pitted.