A systematic study of *Berkheya* and allies (Compositae)

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B. cardopatifolia (Picture by Dr. R. Clarke)

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To my family, particularly to my loving mother; God’s one true gift to me. Thank you for your undying love, support and for never giving up on me through all the madness. This one is for you.

Declaration

This thesis is the result of the author's original work except where acknowledged or specifically stated in the text. It has not been submitted for any other degree or examination at any other university or academic institution.

Signed: Ntombifikile Phaliso
05p3358

Abstract

Berkheya Ehrh. is a genus of daisies in the tribe Arctotideae, subtribe Gorteriinae with over 80 species, most of which occur in southern Africa. This genus has centres of diversity associated with the montane regions of South Africa, including the Drakensberg Alpine Centre and Mpumalanga escarpment regions. Previous molecular and morphological studies indicate that *Berkheya* is paraphyletic. I present phylogenies based on nrDNA (ITS; Internal Transcribed Spacer) and cpDNA (*psbA-trnH*) sequence data analysed with Bayesian Inference and Parsimony. A phylogeny of combined cp- and nrDNA is also presented. These phylogenies are used to assess generic limits and to investigate the biogeographic patterns of *Berkheya* and its allies. The ITS phylogeny shows five well supported clades of *Berkheya,* two of which (Clades I and 2) are monophyletic summer rainfall region clades. Clades 3 to 5 are all paraphyletic winter rainfall clades with *Cullumia* occurring in the third clade, *Cuspida* occurring in the fourth and *Didelta* in Clade 5. Both *psbA-trnH* and combined phylogenies show concordance with the clade distribution shown in the ITS phylogeny. The ITS phylogeny was used to analyse correspondence with Roessler's (1959) Series. It was found that the phylogeny showed considerable agreement with Roessler's series, but *B. bipinnatifida* and *B. spinosa* of Series Speciosae may require some revision as well as taxa of monotypic series Cruciatae and Angustae. It is suggested that the latter series be merged with *Cullumia* species to form a single series. Some consideration should be taken to include *Didelta* species into Series Fruticosae as *Didelta* occurs in subclade 5b of Clade 5 with other Series Fruticosae taxa. Achene morphology was examined from species from each of the five clades to investigate the relationships of *Berkheya* and its allies, as well as to determine if there were any consistent achene features for each clade. The structure of surface cells on the fruit, the presence, absence and morphology of twin hairs as well as the structure of the

pappus scales were found to be most useful in reflecting phylogenetic relationships within the clades. When compared with the clades of the ITS phylogeny, achene morphology showed consistent characters between taxa occurring in the same clades. As the most comprehensive study involving *Berkheya*, this phylogenenetic investigation was able to confirm that *Berkheya* is a paraphyletic genus with *Didelta*, *Cullumia* and *Cuspida* needing to be subsumed into *Berkheya*. An alternative classification is that taxa of Clade 5 could possibly be erected as an expanded *Didelta*, separate and sister to *Berkheya*.

Chapter 1: General Introduction

The Compositae (Asteraceae) family is one of the largest angiosperm families worldwide with an estimated 24,000 species in 1600-1700 genera (Funk *et al.*, 2009). On a global scale, Compositae occur on all continents except Antarctica (Funk *et al.*, 2004). At an estimated 250 genera and 2250 species, the Compositae accounts for 10% of the botanical diversity in Southern Africa, with 80% of its species being endemic to this region (Koekemoer, 1996). Morphological characters which define the family are: florets arranged on a receptacle in a flower head (capitulum) surrounded by involucral bracts (a series of these serving a protective function are known as phyllaries) which develops centripetally; anthers typically fused with styles that brush or push pollen out; achenes that are one-seeded and indehiscent (Funk *et al.*, 2009).

The classification of the Compositae has experienced three major milestones; the first was Cassini's (1816) treatment of the family, in which he defined 20 tribes. In this classification he placed Heliantheae at the centre, Eupatorieae and Vernonieae at one end (grouped together) and Cichorieae (Lactuceae) and Mutisieae on the opposite end (Funk *et al.*, 2009). The second landmark was Bentham's (1873) treatment, developed independently to Cassini's classification, in which he defined two subfamilies and 13 tribes. This treatment prevailed until the 1890s with revisions showing minor deviations from the original treatment such as concepts surrounding the tribes Vernonieae, Liabeae, Senecioneae and Helenieae. This classification was soon followed by that of Hoffman in 1890-1894 which corresponded to Bentham's treatment, defining 13 tribes which mostly corresponded with Cassini's original 20 tribes (Alfonso *et al.*, 2006; Funk *et al.*, 2009).

The development of molecular techniques, especially the use of DNA sequence data, to infer phylogenetic relationships amongst taxa led to a paradigm shift in the systematics of Compositae (Funk and Chan, 2008), and represents the third major milestone in the classification of the family. The pioneering study by Jansen and Palmer (1987) based on cpDNA data led to the description of a third subfamily (the Barnadesioideae). Many systematic studies of Compositae have since included the use of molecular data.

According to Funk and Chan (2008) the recent increase in the use of molecular methods (together with a range of modern phylogenetic analytical methods) led to two main alterations to the higher-level classification of Compositae: firstly, basal clades were identified which re-arranged previous ideas of evolution within the family, and secondly, revisions undertaken using molecular data have lead to the family being divided into 12 subfamilies and 43 tribes.

The Cichoriodeae s.s. (Panero and Funk, 2002, Funk *et al.*, 2005) is one of the subfamilies which has required extensive modification. Prior to the use of molecular data, morphological studies showed that the subfamily was paraphyletic, comprising four large and two small tribes (Karis, 1992). The larger tribes are Arctotideae (African daisies), Lactuceae (dandelions), Liabeae (Andean sunflowers) and Vernoniae (ironweeds), while the smaller tribes are Eremothamneae, Gundelieae and Moquineae. Two unplaced genera, *Platycarpha* and *Heterolepsis*, also occur in the subfamily.

Considerable attention has recently been given to the tribe Arctotideae, with both molecular and morphological studies having being undertaken (Wortley *et al*., 2008; Karis, 2006; Funk *et al*., 2004; Funk and Chan, 2008, McKenzie *et al*., 2006a; McKenzie *et al*., 2006b; McKenzie and Barker, 2008, Karis *et al*., 2009). The Arctotideae was first described by Cassini (1819) and subsequently merged with the tribe Cardueae by Lessing (1831, 1832). In

1873, Bentham re-established the Arctotoideae and divided the tribe into three subtribes: Arctotidinae, Gorteriinae and Gundeliinae. Between 1890 and 1894, Bentham's subtribes were adapted by Hofmann (1890-1894), who introduced a few differences in the generic level classification.

Recent studies have suggested that Gundeliinae, a subtribe within Arctotideae, is incorrectly placed within this tribe and may be a sister group to the tribe Lactuceae (Funk and Chan, 2008; Funk *et al*., 2009). Members of the Arctotideae occur mainly on the African continent, but three species of Arctotideae are indigenous to Australia and a few species (such as *Arctotheca populifolia* (Merino & Donat 2011) and *Arctotheca calendula* (Medina, 2006.) have become naturalised weeds in a range of countries around the world.

The Arctotideae is a fairly small tribe composed of two well-supported monophyletic subtribes; Arctitidinae and Gorteriinae and the poorly supported subtribe Gundeliinae. These subtribes, together with monotypic subtribe Gundeliinae, which is still considered within this tribe, contain 251 species and 17 genera (Funk and Chan, 2008; Funk *et al*., 2009).

The focus of the present study is the subtribe Gorteriinae. Gorteriinae occurs mainly in southern Africa, with a few species occurring in East Africa. A number of the species are endemic to the Cape Floristic Region (CFR). Karis (2006) gives a detailed description of morphological characters that are characteristic of Gorteriinae, viz.: latex-containing shrubs or herbs bearing leaves that are either spiny or tomentose to hispid; connate involucral bracts; sterile ray florets that often have 4-lobed limbs; disc corolla lobes with sclerified margins; a pappus of scales; and deeply alveolate receptacles.

Roessler (1959) revised the taxonomy of Gorteriinae based on morphological characters and accepted eight genera: *Gazania*, *Gorteria*, *Cuspidia*, *Didelta*, *Heterorhachis*, *Cullumia*, *Berkheya* and *Hirpicium*. *Berkheya* contains the largest number of species (78 species, 40 subspecies; Funk and Chan, 2008; Funk *et al*., 2009), followed by *Gazania* (17 species). Molecular phylogenetic analyses by Funk *et al*. (2007) suggest that there are three clades within the Gorteriinae: the *Gazania* clade (GAZ; comprising *Gazania*, *Hirpicium* and *Gorteria),* the *Didelta* clade (DID; comprising *Didelta* and *Berkheya spinosissima)* and the *Berkheya* clade (BER which includes *Cullumia*, *Cuspidia*, *Heterorachis* and the remaining *Berkheya* species). Their study, however, only included 20 *Berkheya* species.

In his treatment Roessler (1959) classified the species of *Berkheya* into eight series using morphological characters such as envolucral bract structure, receptacle alveole margins, achene morphology (pappus scale morphology); plant growth forms; leaf shape and capitulum structure. However, current phylogenies only support five of these series (Funk and Chan, 2008), which was in part a consequence of the very limited sampling of the large genus *Berkheya*. Despite this, *Berkheya* was indicated to be paraphyletic because *Didelta* and *Cullumia* were embedded in *Berkheya* (Figure 1, source Karis *et al*., 2009).

The phylogeny obtained by Karis *et al.* (2009) [Figure 1] indicates that the generic limits of *Berkheya* require reappraisal, and the genus (and subtribe) is hence of great taxonomic interest

Distribution and chorology

A chorological analysis of the distributions of species of *Berkheya* within southern Africa shows that most species of *Berkheya* are concentrated within 10 chorological centres of diversity (Figure 2). Some of these are associated with the montane regions of South Africa with the highest species diversity being in the Drakensberg and Mpumalanga escarpment regions. Some species, such as *B. johnstoniana, B. tysonii* and *B. angusta,* are narrowly distributed and occur in single centres of endemism. A topographic map of approximate margins of rainfall regimes (Figure 3) shows the importance of rainfall data in a holistic understanding of the distribution of species. An understanding of the evolutionary relationships of the species of *Berkheya* will aid in explaining these distribution patterns.

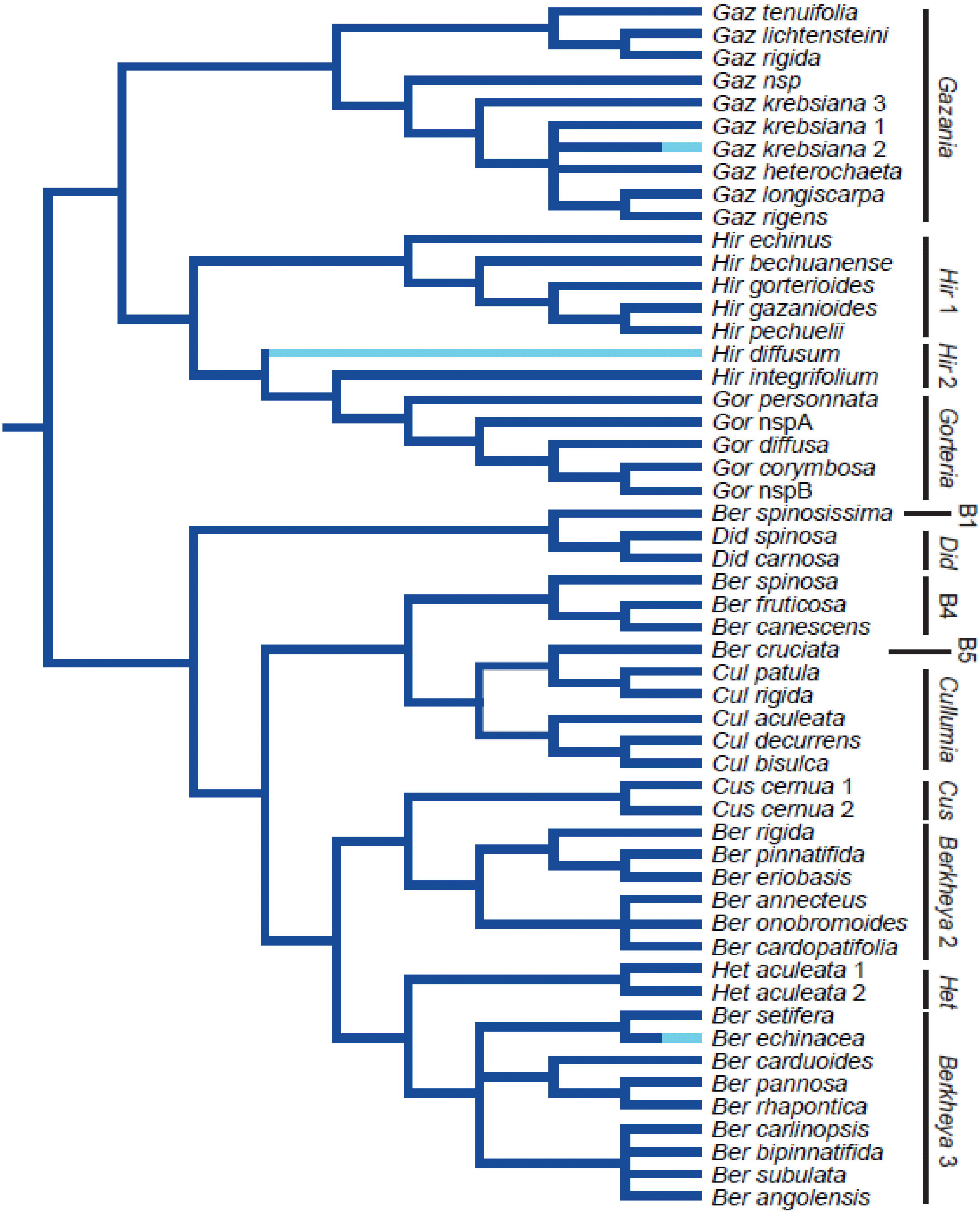


Figure 1: Phylogeny of the subtribe Gorteriinae based on ITS data showing resolution of five *Berkheya* clades (source: Karis *et al.*, 2009).

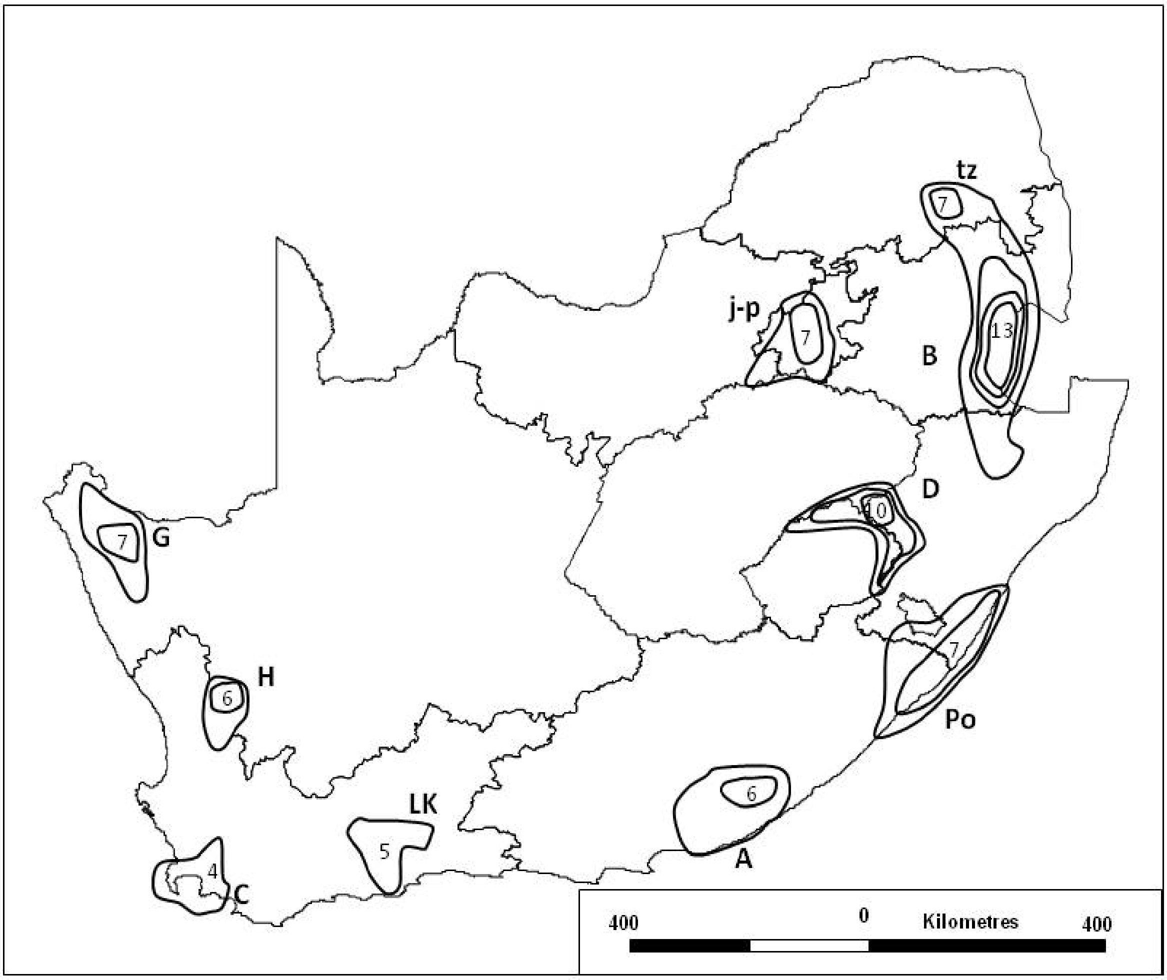


Figure 2: Chorology of Berkheya based on PRECIS data at quarter degree resolution. Isochores are in 3-species intervals. Capital letters indicate centres of endemism, named following a variety of authors, lower case letters are ad hoc names used here: A=Albany, C=Caledon, H=Hantam, G=Gariep, Po=Pondoland, D=Drakensberg, LK=Little Karoo, B=Barberton, t-z=Tzaneen, j-p=Johannesburg-Pretoria.

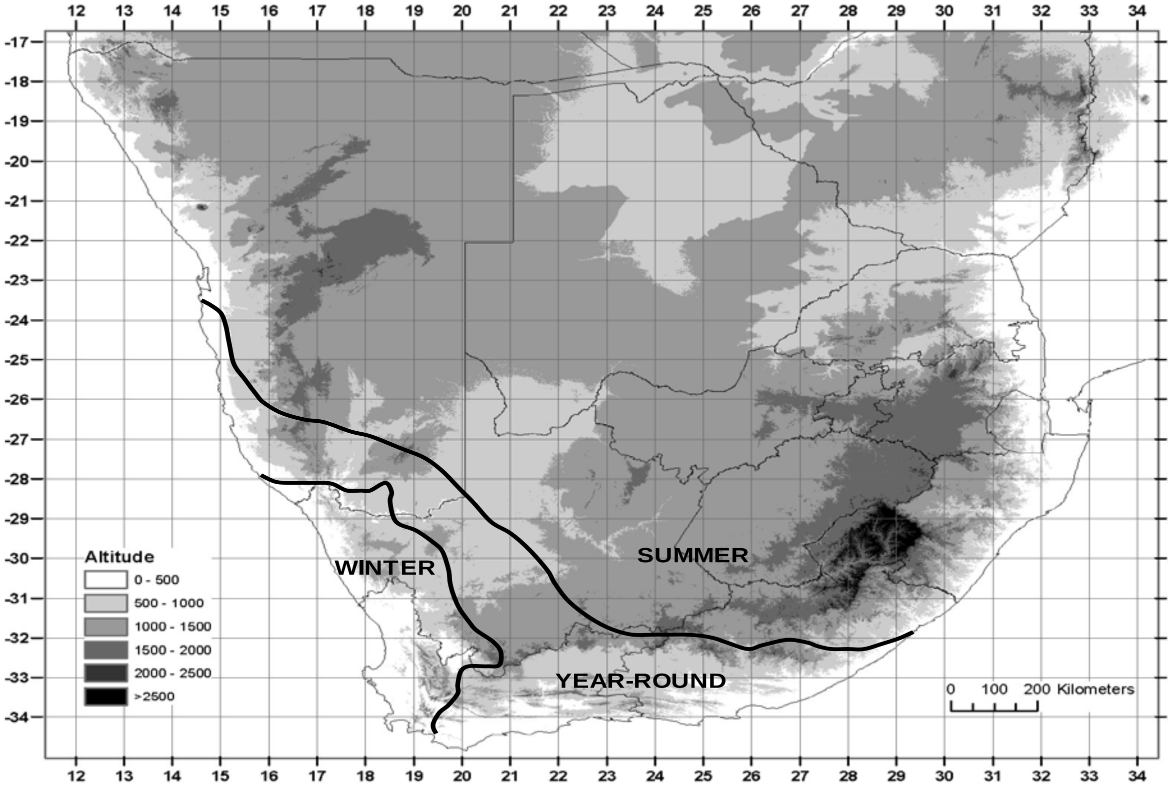


Figure 3: Topographic map showing approximate margins of rainfall regimes in southern Africa. (Based on McKenzie and Barker 2008)

The aims of this study are thus:

1) To reconstruct a comprehensive species-level molecular phylogeny of *Berkheya* and allied genera using DNA sequence data (nrDNA and cpDNA).

2) To use the resultant phylogeny to assess generic monophyly of *Berkheya* and clarify the relationships of the genera *Didelta, Cuspidia* and *Cullumia.*

3) To use the resultant phylogeny to test the validity of Roessler's infrageneric taxonomy of eight series within *Berkheya*.

4) To use the resultant phylogeny to explore biogeographic patterns.

5) To examine the morphology of the achenes of selected species of *Berkheya* to obtain novel morphological characters that might support the molecular findings.

Aims 1-4 will be addressed in Chapter 2, while aim 5 will be addressed in Chapter 3. Thereafter, Chapter 4 will synthesise and summarise the findings.

Chapter 2: The molecular phylogeny of *Berkheya* and allies

The aims of the study presented in this Chapter are:

1) To reconstruct a comprehensive species-level molecular phylogeny of *Berkheya* and allied genera using DNA sequence data (nrDNA and cpDNA).

2) To use the resultant phylogeny to assess generic monophyly of *Berkheya* and clarify the relationships of the genera *Didelta*, *Cuspidia* and *Cullumia.*

3) To use the resultant phylogeny to test the validity of Roessler's infrageneric taxonomy of eight series within *Berkheya*.

4) To use the resultant phylogeny to explore biogeographic patterns.

Molecular (DNA-based) systematics:

The introduction of DNA-based molecular techniques has resulted in a paradigm shift in systematics. DNA sequencing is a direct method of detecting genetic variability of taxa at the DNA level (Galeta, 2007). Originally, plant systematics was reserved for taxa which had sequences that were too divergent for easy interpretation through restriction site mapping. This led to taxa with moderate to slow evolving DNA sequences being predominantly focused on in phylogenetic studies (Baldwin 1995). In recent years however, the ease of generating DNA sequence data through Polymerase Chain Reaction (PCR) technology has allowed for an explosion of molecular genetic analyses. This advancement in PCR technology led to the affordable generation of sequences, which made the use of comparative DNA sequences widespread. This provided a fast, convenient, robust and informative tool for accumulating data for phylogenetic and systematic studies. Sequence data thus essentially allows an increased precision in phylogenetic data by providing better homology assessment of molecular characters and character states (Baldwin, 1995; Small, *et al*., 1998; Soltis *et al*., 1998).

DNA sequences can be used comparatively in various organisms at different taxonomic levels. Baldwin (1995) noted that the major challenge in the use of nucleotide characters in low-level phylogenetic studies was identifying easily amplifiable and relatively rapidly evolving yet unambiguously alignable regions of DNA with which to undertake a study. Three different types of genetic material may be found within the plant cell; chloroplast DNA (cpDNA), nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) which have been explored to varying degrees in phylogenetics (Caputo, 1997). These different genomes show differences in characteristics as per the organelle in which they evolve (Hamza, 2010). Chloroplast DNA (cpDNA) has been recognized as the molecular marker of choice in systematic studies involving plants since the discovery of this genome (Small *et al*., 2004). However, the use of a second independent source of data in the form of nuclear DNA (nDNA) data has also long been the norm.

The simple genetics of cpDNA makes it ideal for phylogenetic investigations in plant taxa. The abundance of cpDNA within plant tissue is due to the high number of chloroplasts present in each cell in each leaf. Multiple copies of cpDNA are present in each chloroplast within a plant cell, which greatly facilitates the amplification process (Galeta, 2007). Chloroplast DNA typically comprises a circular covalently closed haploid chromosome that occurs within the organelle as monomers and multimers. The main difference between cpDNA and nDNA is thus the fact that nDNA exhibits evidence of both parents, meaning that gene conversion may go in the direction of either parent. For this reason, nuclear genes show greater genetic variability and thus provide a greater evolutionary signal than cpDNA (Albach and Chase, 2004). The uniparentally (maternally) inherited cpDNA genomes tend to have a genome size of 135-160kb in angiosperms and 135-217kb in photosynthetic land plants. Two identical segments of roughly 10-75kb (average 25) kb occur in cpDNA which form inverted repeats (IR), which act to separate the rest of the genome into two single-copy sections; one large region (LSC) and a small region (SCC). Structurally the cpDNA molecule in angiosperms is estimated to be ten times the size of the mtDNA of mammals (Caputo, 1997; Galeta, 2007; Hamza, 2010).

As chloroplast DNA is inherited uniparentally, it will report only on the maternal lineage in instances of hybridization. This poses the problem of it not being able to resolve relationships within taxa, which have evolved via processes such as hybridization (including allopolyploidy; Zimmer and Wen, 2012). The slow rates and clonal mode of evolutionary change within cpDNA compared to those of nDNA is attributed to the differences in how nuclear and organelle genomes are transmitted (Hamza, 2010), thus meaning cpDNA will not provide as much resolution (Chapman *et al*., 2007).

Though many cpDNA regions have been identified and exist for phylogenetic study, the most frequently and widely used regions are the *rbcL* and *matK* genes, and the introns and spacers between tRNA genes, most notably the *trnT-trnL* spacer, the *trnL* intron and the *trnL-trnF* spacer. In Compositae studies, the most commonly used intergenic spacer is the *trnL-trnF* spacer which is a non-coding region which often shows enough variation to be used at or below the species level (Barker *et al*., 2009). Other frequently used regions are the *matK* gene and *psbA-trnH* spacer (Kim *et al*., 1997; McKenzie *et al* 2006; Howis, 2006; Hamza, 2010).

The *psb*A-*trn*H region is a highly variable non-coding region which has been used in phylogenetic studies in the Compositae at the intrageneric and intraspecific levels. (Smissen *et al*., 2003).

Kim and colleagues (1999) investigated the phylogenetic viability of the spacer between cpDNA genes *psbA* and *trnH* in phylogenetic investigations of Compositae taxa at lower taxonomic levels. They compared ITS phylogenies with *psbA-trnH* phylogenies in the Sonchinae (Compositae). Their results showed that ITS sequences provided three times more variable sites and four times the number of phylogenetically informative sites than *psbA-trnH*. ITS phylogenies were shown to have more resolved nodes as illustrated by bootstrap and other phylogenetic indices. Although this was expected, this study was also able to illustrate the viability of *psbA-trnA* as they showed that data from this region showed a strong phylogenetic signal despite slower rates of substitution. They showed *psbA-trnH* to be highly informative in phylogenetic studies at generic rather than interspecific levels, which was found to be congruent with other studies at a generic level; however, this region lacked variation to resolve recently radiated Compositae taxa or congeneric species.
This and related studies thus serve as a testament to the validity of *psbA-trnH* in phylogenetic studies of Compositae.

Of the nuclear regions routinely used in plant systematics, the most commonly used region by far is the nuclear ribosomal DNA (nrDNA). Structurally nrDNA has three coding regions; 18S, 5.8S and 26S which are separated by two highly variable Internal Transcriber Spacers ITS1 and ITS 2. Each of these transcriptional units is further separated by a highly variable intergenic spacer (IGS) region. This genome has a high copy number of exceedingly variable sites with numerous well-conserved regions with some being variable enough for microevolutionary studies (Caputo, 1997). With tandem repeats of genes with hundreds to thousands of copies per array, this structure of nrDNA facilitates amplification through the PCR process (Galeta, 2007).

Due to non-coding regions being less functionally constrained, they are found to be more useful in phylogenetic studies at the lower taxonomic levels, as these fragments accumulate phylogenetically informative characters more rapidly (Clegg *et al*., 1994). In plant studies, and more specifically in Compositae (Asteraceae), the use of the ITS for phylogenetic purposes has been widespread. The utility of this region was first highlighted by Baldwin (1993) who recognized that the intraspecific variability of ITS sequences in Compositae could prove beneficial in resolving species level relationships (Baldwin *et al*., 1995; Barker *et al*., 2009). This region has subsequently been widely used in investigating species, genus and most recently intertribal level relationships (Markos and Baldwin, 2001; Wagstaff and Brietwieser, 2004; Lantz and Bremer, 2005; Howis, 2006; McKenzie *et al*., 2006; Galeta, 2007; Feliner and Rossello, 2007; Funk and Chan, 2008; Barker *et al*., 2009;). As previously stated, the ITS region occurs in high copy numbers, and hence comprises many paralogous copies within each cell. Numerous analyses have been undertaken to investigate the attributes of ITS which possibly make this an ideal nDNA region for phylogenetic investigations in Compositae (Baldwin, 1992; Baldwin *et al*., 1995; Kim *et al*., 1997; Small *et al*., 1998; Cronn and Wendel, 2003; Alverez and Wendel, 2003; Eidesen *et al*., 2007). Many of these studies highlight attributes which show ITS to be a robust marker. Biparental inheritance which allows detection of past cases of reticulation, hybrid speciation and parentage in taxa is a fundamentally favourable character of ITS. The simplicity of the region (500-700bp in angiosperms and high number of tandem repeats) as well as its intragenomic uniformity, due to rapid concerted evolution via crossing over and gene conversion has resulted in its extensive use. It mutates at a faster rate than chloroplast DNA and therefore provides a good phylogenetic signal. However, the use of ITS is controversial, as some authors have stated that this region has pitfalls in the form of possible issues with orthology and paralogy, occurrence of pseudogenes, concerted evolution, hybridization and lineage sorting of ancestral polymorphism (Alverez and Wendel, 2003; Bailey *et al*., 2003; Small *et al*., 2004; McKenzie *et al*., 2006). This is said to give potentially misleading phylogenies and it is stated that caution needs to be taken in the interpretation of resultant phylogenies. Despite this, ITS is widely used and as long as limitations are understood, data from this region may still provide meaningful insight into evolutionary history among taxa (Feliner and Rossello, 2007).

One way in which the potentially misleading signals which are given by ITS-based phylogenies may be identified and assessed is through incongruencies. This requires the use of independent sources of evidence such as morphological data or chloroplast DNA data. This can increase one’s confidence in the phylogenies in instances where congruence is found between the data sources (Doyle, 1992; Kim *et al*., 1997; Caputo, 1997; Cronn and Wendel, 2003; McKenzie *et al*., 2006).

On the basis of the above precedent, nrITS, *psbA-trnH* and *trnL-trnF* regions were initially selected for this study. However, *trnL-trnF* failed to consistently amplify and produce sufficient data, and the use of this region was not pursued beyond the pilot survey phase of the project. For this reason, the cpDNA data set comprises sequences of the *psbA-trnH* spacer.

Methods:

Sampling:

Samples of 65 of the possible 72 species of *Berkheya* were obtained from a number of collectors, including Dr. L. Mucina and associates, Dr. R.J. McKenzie and Dr. P.O. Karis from Stockholm, Sweden. Specimens are available both as DNA voucher specimens and as herbarium specimens housed at the Selmar-Schonland Herbarium (GRA). DNA voucher specimens received from Sweden were coupled with digital pictures as well as locality data. In the case of species where samples were not immediately available, efforts were made to outsource representative samples from other botanists and collectors. As a consequence a few key species were obtained but most could not be added to the current study.Many of these specimens were simply to old to extract DNA from. A key example of this is *Heterorachis* Sch. Bip which was received but was difficult to amplify and sequence, which lead to this genus not being included in the final dataset of this study. Where possible, multiple samples per species or subspecies were sequenced so as to confirm species monophyly. *Didelta* L' Herit, *Cuspida* Gaertn and *Cullumia* R. Br. specimens were included in the analyses as these taxa are integral in testing the generic limits of *Berkheya*. All species used in the study were identified using Roessler's key for *Berkheya* and sister genera.

DNA extraction, amplification and sequencing:

DNA was extracted from 1cm^2 of dried leaf material from each sample using the CTAB extraction method as described by Doyle & Doyle (1987). The ITS regions was amplified using the primer pairs of "ITS4" and "ITS5" or "ITS1" and "ITS4" (White *et al*., 1990). The intergenic spacer *psbA-trnH* was amplified using primers "psbA" and "trnH" (Sang *et al*., 1997) PCR reactions contained 1µl 0,1% Bovine serum albumen (BSA), 2,5µl 10x PCR buffer (bioline, London, UK), 1μl dNTPs (Bioline, London, UK), 1μl 0,1μM solution of each forward and reverse primer, 0.2μl BioTaq® DNA polymerase (5 U/μl, Bioline, London, UK) and 0,75-1,5μl DNA extract. The volume of 50mM $MgCl_2$ ranged between 0,75-2μl (1,5-4mM), and was often optimised for each sample. For all samples, the thermal cycling parameters were as follows:

Denaturation: 95°C for 45s; Primer annealing: at 54°C - 56°C (primer dependent) for 30 sec; Extension: 72°C for 3min. This was followed by a final extension cycle at 72°C for 10min.

The number of amplification cycles ranged from 30 to 35 cycles, depending on the quality of the DNA extracts. Amplification success was assessed by running the PCR products through 1% Agarose gel. Successful PCR reactions were then purified using PRC purification kit (Promega, Invesco) and resuspended in 10-15μl elution buffer. Purified PCR products were then sequenced in both forward and reverse directions using the BigDye® Terminator v.3.1. cycle sequencing kit according to manufacturer's protocol. Cycle-sequenced products were precipitated using the sodium acetate/EDTA protocol, and dried down prior to being sequenced using a ABI 3100 Genetic Analyzer (Rhodes University). For ITS, internal primers were also used for ITS. These were: "Chrysanth-5.8F", "Chromo-5.8R" (Barker *et al.,* 2005).

Sequence alignment:

Sequenced data (trace files) were edited using Seqencher 4.2.2 (Gene Codes Corp, Ann Arbor). Forward and reverse sequences from each sample were compiled into contigs and edited visually. Edited sequences were manually aligned using MacClade 4.06 (Maddison and Maddison, 2000), and additional data from GenBank was also included. As a consequence of some samples having quite divergent ITS sequences, an initial process of automatic alignment was carried out using the CLUSTAL W option as implemented in MEGA 5.05. Default settings were used. Following this process, the automatic alignment was edited by eye to remove minor inconsistencies.

Representatives of related genera in the subtribe (*Hirpicium* and *Gorteria*) were included as outgroup taxa. Roessler stated that the closest relatives to *Berkheya* were *Hirpicium alienatum* and *H. integrifolium*, although he provided no morphological evidence in support of this. However, we were guided by both Roessler and studies by Karis (2006) and elected to use *Gorteria diffusa* Thunb. and *Hirpicium echinus* Less.as outgroup taxa.

A "combined" data set comprising *psb*A-*trn*H and ITS data for species in common between the data sets was also produced (hereafter termed COMBINED). However, as the *psb*A-*trn*H data set was much smaller than the ITS data set, and the subset of species in common even fewer, the COMBINED data set included only 37 ingroup species. Some of these were obtained by merging ITS and *psb*A-*trn*H data from different specimens, with the assumption that species were monophyletic. Such taxa are termed "fictive taxa" sensu Kellogg & Linder (1995) or ‘‘hybrid taxa’’ (Wiens & Reeder, 1995). Prior to combination, the reduced ITS and *psb*A-*trn*H data sets were analysed and the topologies compared to assess if any well supported incongruence could be detected. Owing to the much smaller sample size of the *psbA-trnH* data set compared to the ITS data sample size, an Incongruence Length Difference test (Farris, 1994) was not conducted. According to Weins (1998), analyses based on reduced data are problematic, as they have the disadvantage of restricting the taxonomic scope of the study, and where taxa are removed or incomplete, the accuracy of such analyses would be diminished. This makes such analyses far less reliable than phylogenies with more complete datasets, hence the lack of an ILD analysis in the present study.

Phylogenetic Analyses:

Phylogenetic relationships were assessed by means of Maximum Parsimony (MP) and Bayesian Inference (BI). The MP analysis was performed using PAUP* 4.0b10 (Swofford, 2002). Uninformative characters were excluded and all nucleotide characters were equally weighted and unordered. Gaps were treated as missing data. An initial random input analysis (1000 iterations) was done to ensure all islands of equally parsimonious trees were sampled, followed by a Full Heuristic search on the trees saved in memory using TBR branch swapping with MAXTREES set at 10000. From the Parsimony analyses, a strict consensus tree was constructed with branch support being assessed using the Quick Bootstrap (BS) method (Felsenstein, 1985) for the ITS data set, and a full heuristic bootstrap for the *psb*A-*trn*H and COMBINED data sets.

Prior to the BI analysis, The most appropriate model for sequence evolution for each data set was selected using the Akaike Information Criterion (AIC) test (Akaike, 1974) as implemented in MrModeltest v.2.2 (Nylander, 2004). Bayesian analyses were conducted using MrBayes v.3.1.2 (Huelsenbeck and Roquist, 2001). Each analysis comprised four independent runs of 10 million generations each, using random starting trees with four chains (one cold, three hot), sampling every 1000 generations.

Results

Resultant analysis and tree statistics from the MP analyses of both data sets and a combined analysis on both datasets are presented in Table 1.Table 1: Statistics for phylogenetic analysis of data.

Dataset	Number of ingroup taxa	No. variable/parsimony informative characters	Number of Maximum Parsimony Trees	Tree length	ci	ri	Number of nodes with >75% Bootstrap support	Number of nodes with >0.9 BI posterior probabilities
ITS	116	247/184	10000	537	0.486	0.821	26	33
psbA	467	96/31	72	57	0.614	0.847	11	5
Combined data	28	255/152	178	305	0.607	0.751	11	8

The ITS data set

One hundred and sixteen samples of *Berkheya* are used in this study, representing 63 species of *Berkheya.* One *Cuspida,* three *Cullumia* and two *Didelta* samples were included as previous studies have shown these to be embedded in *Berkheya*, and are required to test generic monophyly (Funk *et al*., 2008. Karis 2006. Wortley *et al*., 2008). The final ITS alignment was 667bp long. Of these, 247 sites were variable and 184 were parsimony informative (Table 1). This alignment is presented in Appendix A. The MP analysis of ITS region yielded 10000 Parsimonious trees (i.e. the MAXTREES limit) of 537 steps (CI = 0, 490; RI = 0, 840; consensus tree not shown). The BI analysis of the ITS data was obtained using the GTR+G+I model estimated using AIC (Figure 4). Both MP and BI analyses recovered five clades. The clades in the BI analysis correspond entirely with the clades retrieved by the MP analysis (tree not shown). Support for the clades shown in Figure 4 is high, with the lowest being the probability of Clade 1 (PP = 0,95).

The BI tree shows five main lineages of *Berkheya* [Figure 4 (Clade 1-5)]. Of these, Clade 3 has three subclades, one of which being a clade composed of the three samples *Cuspida cernua* (L.f.) B.L.Burtt.

The five clades show a correlation with rainfall regimes (summer rainfall in the Eastern areas of southern Africa and Africa (Clade 1 & 2), a winter rainfall in the west (Clade 4 & 5) as well as a year-round rainfall region in the central regions of southern Africa (Clade 3).

The *psb*A-*trn*H data set

Due to a number of laboratory and equipment problems, the *psbA-trnH* dataset is considerably smaller than the ITS dataset. Thirty seven ingroup taxa were used in the *psbA-trnH* data, comprising 34 *Berkheya* species, and three sister taxa, namely; one *Didelta*, one *Cuspida* and one *Cullumia* species. The final *psbA-trnH* dataset was 563bp long, 96 of which were variable and 31 were parsimony informative. Parsimony analysis of the *psbA-trnH* region resulted in 72 equally parsimonious trees of 57 steps (Ci = 0, 614; Ri = 0, 847). A consensus tree reveals four lineages of *Berkheya* (tree not shown) The BI phylogeny was obtained using the GTR+G+I model and also recovered four clades (Figure 5) and matched the MP topology in this respect. The clades represented in the *psb*A-*trn*H data corresponds with the ITS phylogeny, with a distribution of winter and summer rainfall taxa into separate clades. Clade A corresponds with ITS Clade 5, Clade B with ITS Clades 1 and 2, Clade C with ITS Clade 3 and Clade D with ITS Clade 4.

All posterior probability values for the clades are reasonably high, with the exception of Clade A (PP = 0,41) being the lowest. However, in this clade, *B. schinzii* is sister to a well supported subclade of the remaining taxa (PP = 0.95; Figure 5).

The COMBINED data set

This analysis included only twenty six ingroup and two outgroup taxa. *Cuspida cernua* and *Didelta spinosa* were also included, but as no *Cullumia* species were found to be common between the two data sets, the genus was omitted. Parsimony analyses resulted in 1178 most parsimonious trees with 305 steps (Ci= 0 .607, Ri: 0.751). As in the *psb*A-*trn*H analysis, four clades were recovered (tree not shown).

The BI phylogeny was obtained using the GTR+G+I model and also recovered four clades (Clades I-IV; Figure 6).

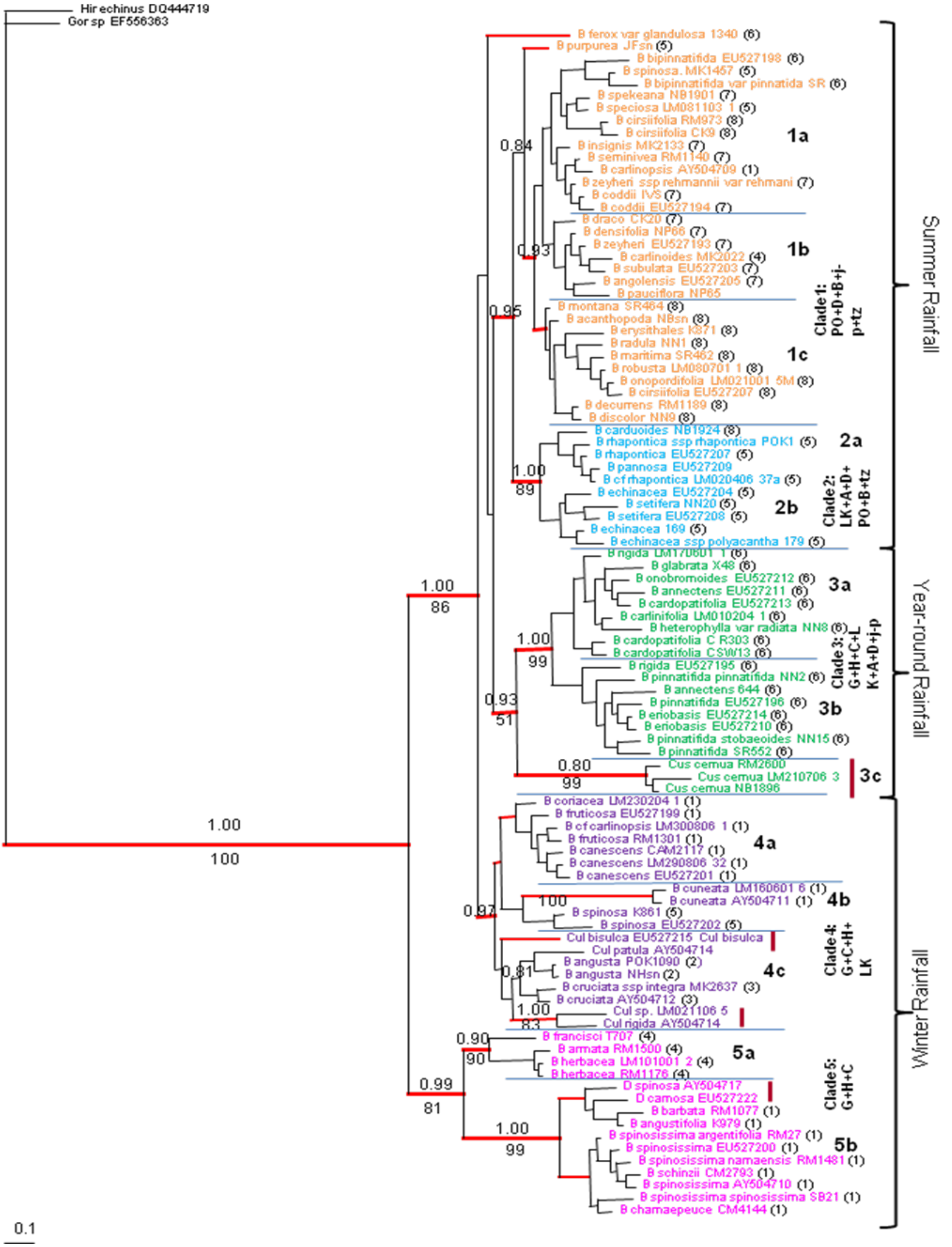


Figure 4: Phylogram obtained from Bayesian inference analysis of the ITS data set. The values at branch nodes represent Bayesian posterior probabilities (above branch) and MP bootstrap percentages (below branch). CI = 0,490, RI = 0, 840. Clades 1– 5 (subclades are designated a, b and c) are indicated together with the region of occurrence and centre of diversity, which corresponding to regions in the chorology (Figure 1) [ad hoc names used: A=Albany, C=Caledon, H=Hantam, G=Gariep, Po=Pondoland, D=Drakensberg, LK=Little Karoo, B=Barberton, t-z=Tzaneen, j-p=Johannesburg-Pretoria.]. Branches highlighted in red are branches common to both MP and BI analyses. Vertical brown bars indicate segregate genera that were placed within the *Berkheya* clade. The series in which Roessler (1959) placed each *Berkheya* taxon is indicated by the numbers 1–8 in parentheses after the accession name (Table 3 indicates the names of each of these series).

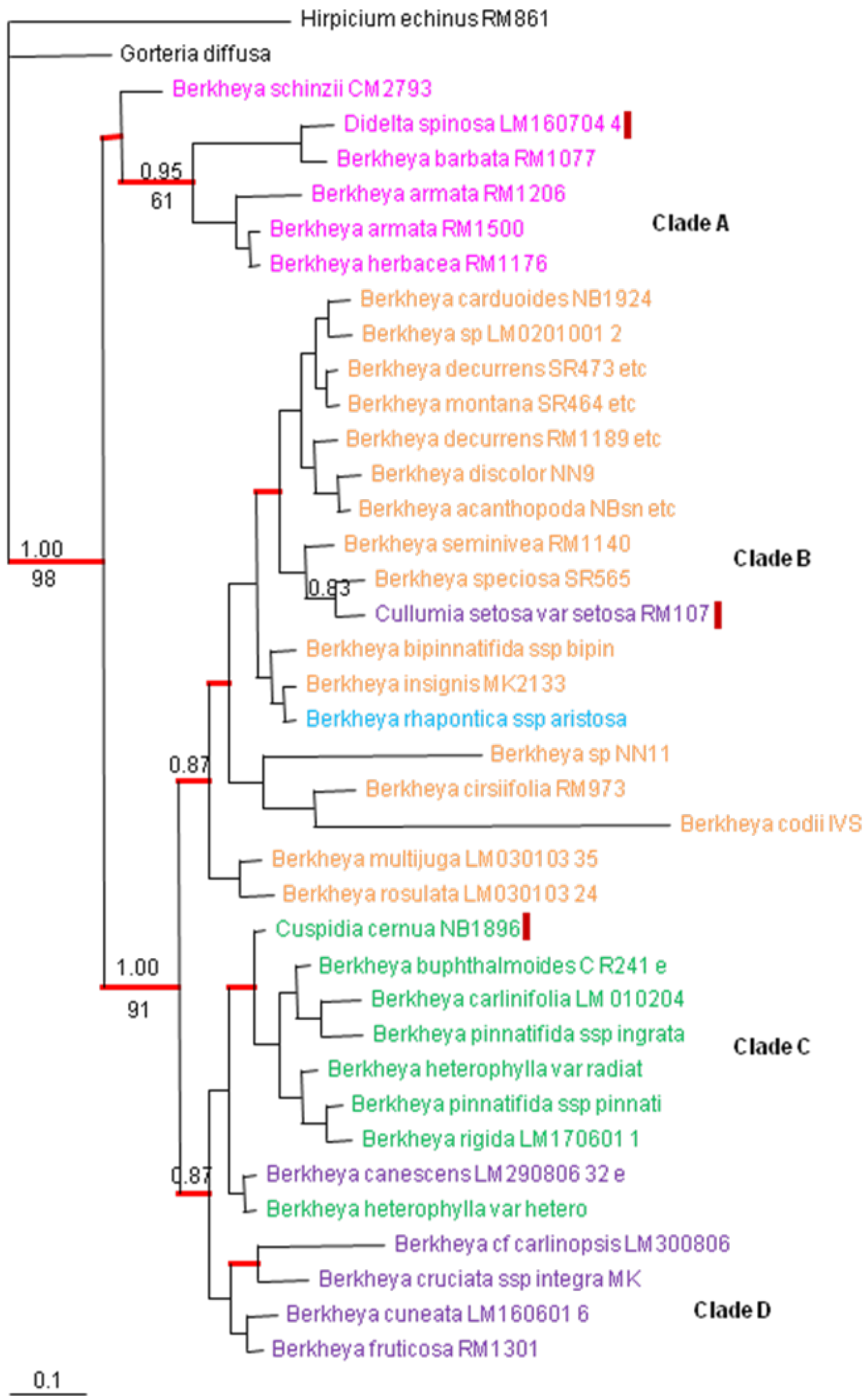


Figure 5: Phylogram obtained from Bayesian inference analysis of the *psb*A-*trn*H data set. The values at branch nodes represent Bayesian posterior probabilities (above branch) and MP bootstrap percentages (below branch). Clades A-D are labelled. The clade colour corresponds with the clade colours in the ITS phylogram (Figure 4). Branches in the phylogeny highlighted in red represent branches common to the MP and BI phylogenies. Vertical brown bars indicate segregate genera that are placed within the *Berkheya* clade.

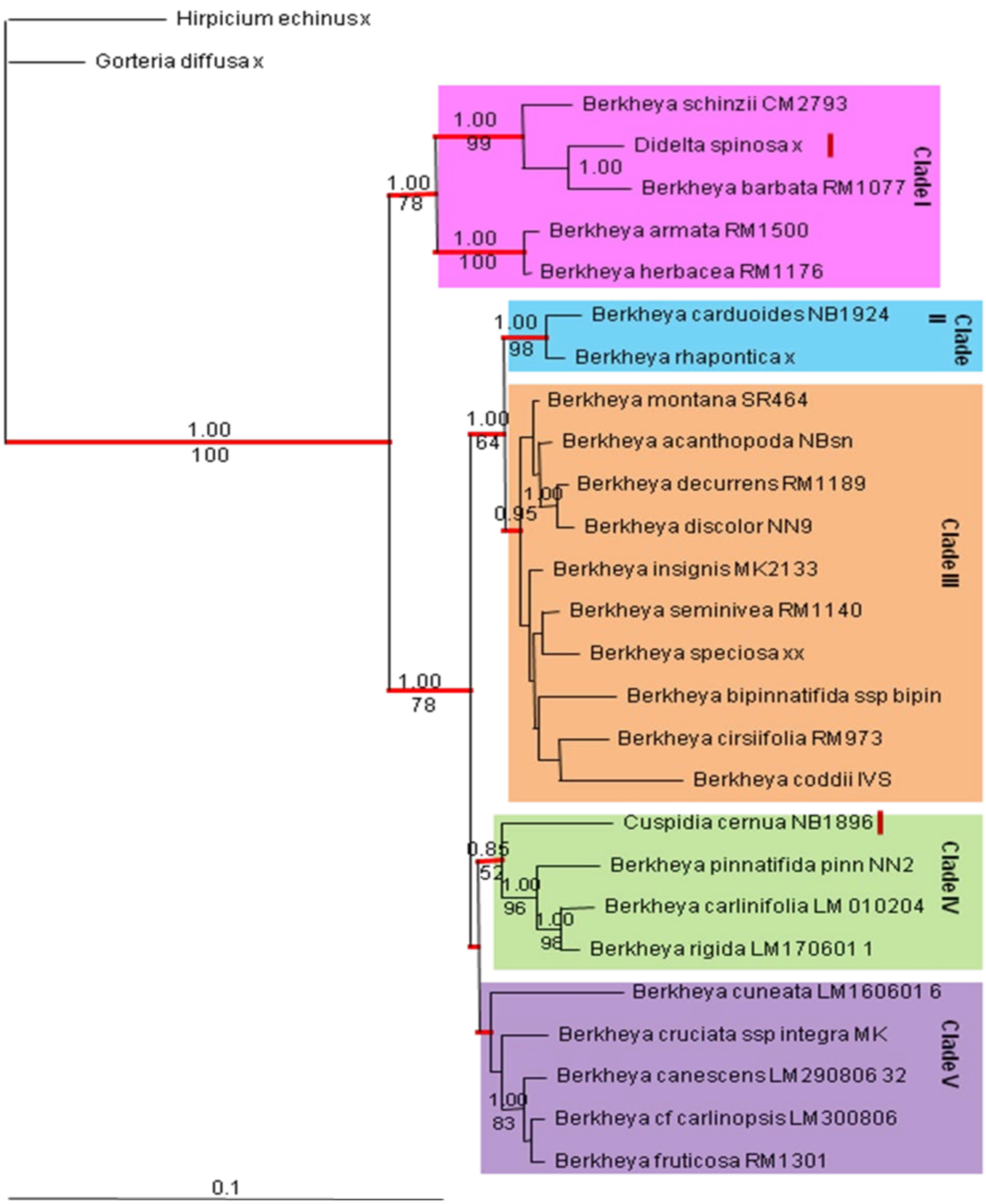


Figure 6: Phylogram obtained from Bayesian inference analysis of the combined (ITS + *psb*A-*trn*H) data set. The values at branch nodes represent Bayesian posterior probabilities (above branch) and MP bootstrap percentages (below branch). Clades I-Vare shown, which are coloured to correspond with those in the ITS phylogram (Figure 4). Branches highlighted in red represent branches common to the MP and BI phylogenies. Vertical brown bars indicate segregate genera that were placed within the *Berkheya* clade. xx represents fictive taxa that are species common to the ITS and *psb*A-*trn*H data sets but sequences were not derived from the same specimen.

Discussion:

Previously, the most comprehensive molecular phylogenetic study of the subtribe Gorteriinae included 39 samples of 30 species representing the *Berkheya* clade (Funk and Chan, 2008). With 116 samples in total, representing 63 *Berkheya* species, the ITS phylogenies in the present study represent the most complete analysis of the *Berkheya* clade to date and this analysis will thus be the main focus for discussion in this chapter.

Funk and colleagues (Funk *et al*., 2004; Funk and Chan, 2008) both used nuclear and chloroplast DNA sequence data to analyse phylogenetic relationships within Gorteriinae. In their analyses, two main groupings were identified within this subtribe, namely the *Gorteria* clade containing the genera *Gazania*, *Gorteria* and *Hirpicium*, and the *Berkheya* clade containing *Berkheya*, *Cullumia*, *Cuspida*, *Didelta* and *Heterorhachis*. Most taxa used in the *Berkheya* clade of Funk *et al*. (2004, 2008) were included in the present study with the exception of *Heterorachis*, which gave great difficulty in sequencing and thus had to be excluded.

Phylogenetic relationships within the *Berkheya* clade:

Analysis of the ITS data yielded a phylogeny (Figure 4) in which five clades were resolved. Within these clades, species groupings (although often not well supported) were distinguished as subclades (designated with lower-case letters a, b and c in Figure 4). These clades will be discussed sequentially from the earliest diverging Clade 5 to the terminal Clade 1.

Clade 5

The well-supported Clade 5 is sister to the remaining *Berkheya* clades. This clade is distributed in the Succulent Karoo and Fynbos biomes with species occurring mainly in the Caledon, Gariep and Hantam-Roggeveld centres of diversity (Figure 2). Subclade 5a comprises *B. armata*, *B. herbacea* and *B. francisci*, which all occur in the Fynbos biome in the Western Cape. The two *Didelta* species are embedded in subclade 5b and are related to *B. barbata* and *B. angustifolia,* and these species collectively sister to a lineage comprising *B. spinosissima*, *B. schinzii* and *B. chamaepeuce*. The geographic range of the species within subclade 5b is in the Fynbos and Nama-Karoo biomes (*B. barbata* and *B. angustifolia*) and the Succulent Karoo biome and extends northwards through Namibia into Angola. The two subclades (5a and 5b) were both well supported (PP = 0.90, BS = 90%; and PP = 1.00, BS = 99%, respectively). When the distributions of the species in this clade are mapped (based on map information provided by (Roessler 1959) species of subclade 5a are limited to the Cape Floristic region with species also occurring in the Worcester-Robertson Karoo (as per Van Wyk and Smith, 2001) and Little Karroo (Figure 7). This distribution overlaps with that of subclade 5b in the Cape Floristic region. Species of subclade 5b are shown to have a slightly larger range which includes the CFR, Succulent Karoo, Hantam, Gariep and Albany centres of endemism, and overlaps with the range of *Didelta* species, which also form part of the subclade, in the Gariep and Succulent Karoo centres of endemism.

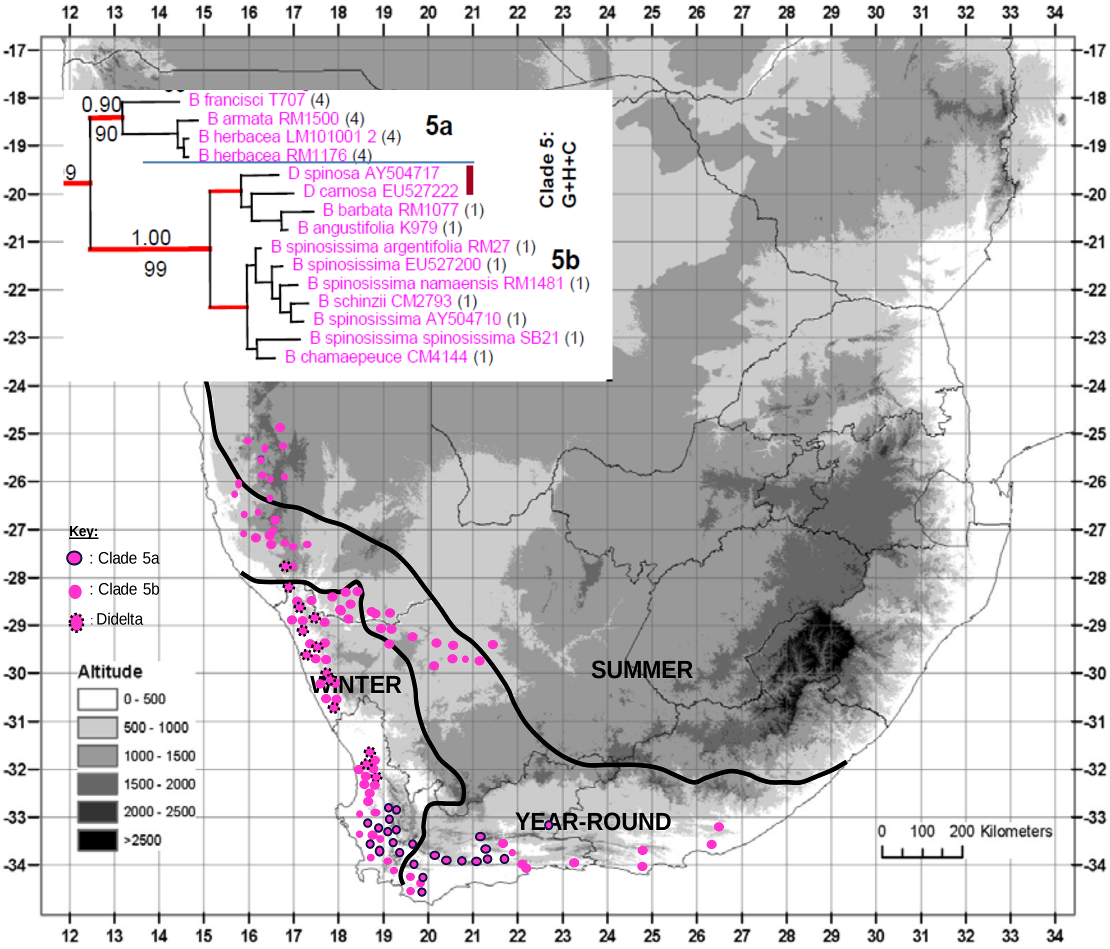


Figure 7: A topographical map showing approximate margins of rainfall regimes. Map shows species distribution of Clade 5 data plotted with Clade 5 from ITS phylogeny superimposed on the top left. (Based on McKenzie and Barker 2008)

Clade 4

The relationships between the remaining clades were not strongly supported, although each individual clade was well supported. Clade 4 is comprised of species restricted to the winter rainfall region of southwestern Africa. This clade contains the four specimens of *Cullumia* for which data was available (in subclade 4c), although these do not form a monophyletic lineage. Currently considered to be a genus separate to *Berkheya*, *Cullumia* was also found to be closely related to *Berkheya* by Funk *et al*. (2004) and Funk and Chan (2008), who reported that *Cullumia* species formed a subclade embedded within the *Berkheya* clade. In the present study the *Cullumia* samples were placed in a weakly supported clade (PP = 0.81) with *B. angusta* and *B. cruciata* (subclade 4c in Figure 4). The relationship with *B. cruciata* is consistent with the findings of Funk and Chan (2008), but *B. angusta* was not included in these authors' study. Karis (2006) reported that two noteworthy morphological features were common between *B. cruciata* and *Cullumia* species. Firstly, the endothecial wall thickening plate is displaced towards the connective-facing side and is sickle-shaped and, secondly, all of the taxa have glabrous achenes. Roessler (1959) states that *B. angusta* is morphologically very closely related to *Cullumia,* speculating that the species may assume an intermediate position between the two genera (Roessler, 1959). This relationship is thus not all that surprising.

As noted above, Clade 4 is distributed in the winter rainfall region (Figure 8). Subclade 4a is distributed along the coastal western regions of South Africa and the south of Namibia. This range includes the Succulent Karoo, Gariep, and CFR centres of endemism. In the CFR, subclade 4a overlaps with the known distribution of *B. angusta* which is in the Worcester-Robertson Karoo centre. Few species, namely *B. coriacea*, are found in the coastal CFR and Little Karoo region. Subclade 4b species, *B. spinosa* and *B. cuneata* are found in the higher altitude regions of the CFR where the Worcester-Robertson centre of endemism (Van Wyk and Smith, 2001). Here the distribution of these species overlaps with subclade 4c species, *B. cruciata* and *Cullumia* species. *Cullumia* species are found in the CFR and Little Karoo regions. In the CFR region, *Cullumia ciliaris, C. bisulca* and *C. rigida* overlap with subclade 4a species. *C. rigida* is found in the Succulent Karoo centre, while *C. ciliaris* is distributed in the CFR. In the little Karoo we see an overlap with *C. patula*, *B. cruciata* and subclade 4b species. Common among the taxa within this clade is a woody, shrubby structure which may be as a result of the arid habitat in which they occur.

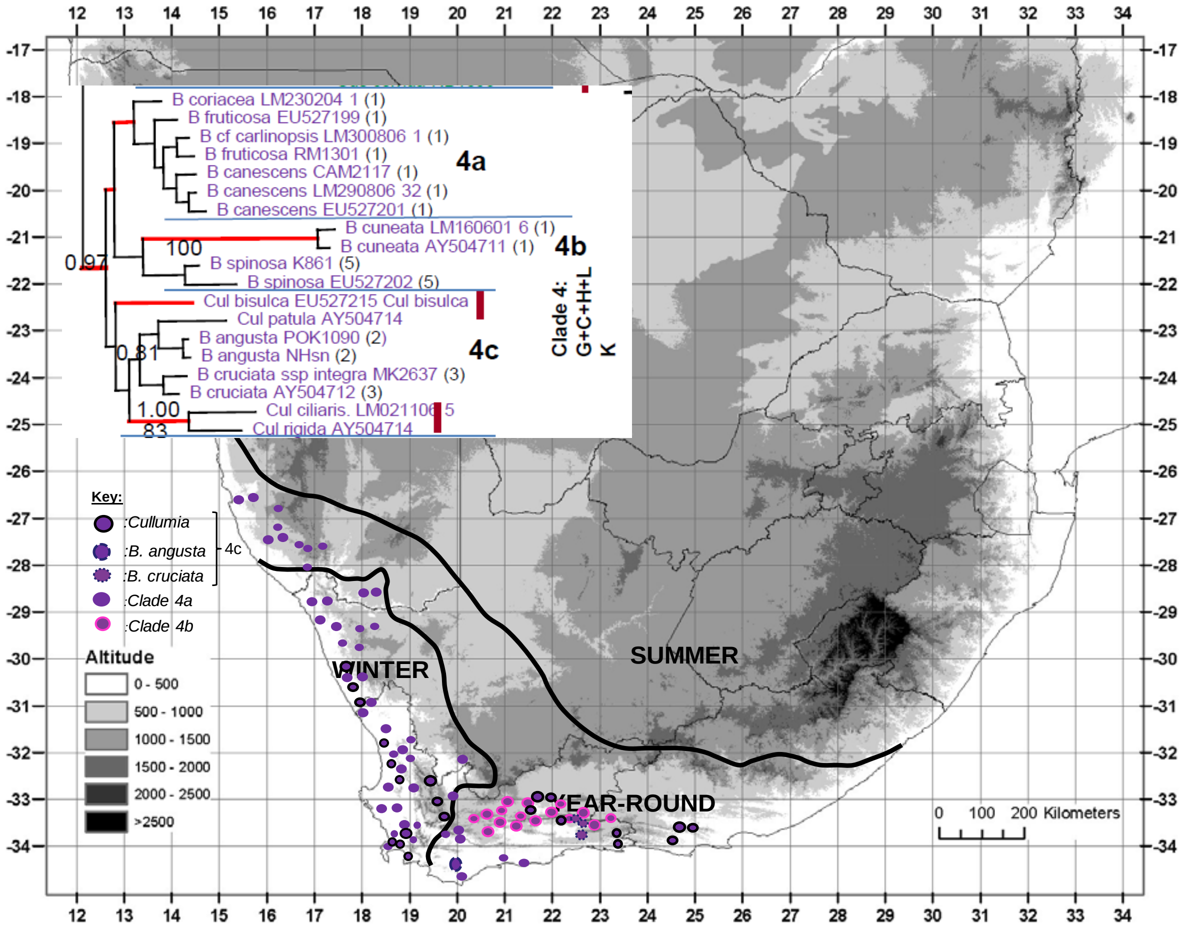


Figure 8: A topographical map showing approximate margins of rainfall regimes. Map shows species distribution of Clade 4 data plotted with Clade 4 from ITS phylogeny superimposed on the top left. (Based on McKenzie and Barker 2008)

Clade 3

Clade 3 is made up of widespread taxa that are mainly found in the year-round rainfall region, which is distributed across the central portion of southern Africa. Species such as *B. pinnatifida* sensu Roessler are found in the Drakensberg and Johannesburg–Pretoria centres of endemism. This clade includes *Cuspidia cernua*, which forms subclade 3c and is sister to the remaining members of Clade 3, but with weak support (PP = 0.83, BS = 51%) therefore suggesting an unclear relationship with the rest of the clade. However, the placement of *C.*

cernua corresponds with previous phylogenetic analyses (Funk *et al*. 2004, Funk and Chan 2008).

The distribution of the species within this clade is shown in Figure 9. Species from this clade are predominantly distributed in the year-round rainfall regions which include the Albany and Little Karoo centres of endemism. Species of subclade 3a are found along the coastal belt of the southwestern regions of South Africa, covering the Succulent Karoo, CFR and Albany centres of endemism. Clade 3b has a split distribution with most species of the subclade being found in the grassland biome which is in the summer rainfall region that overlaps with the Highveld biome. The remaining species of subclade 3b are found in the western Hantam, Gariep and CFR centres of endemism. *B. annectens* occurs in the Gariep centre, *B. eriobasis* in the Hantam centre. *Cuspida cernua* is restricted to the Albany centre and has a fairly wide distribution in this region. Overlap is shown in the occurrence of *Cuspida* species (subclade 3c) and subclade 3a species. It must also be noted that although the phylogeny suggests this, *B. rigida* and *B. pinnatifida* are not monophyletic species. The occurrence of this in Figure 9 may be attributed to false identification of species, most likely *B. rigida* EU527195, which is a GENBANK specimen, the identity of which could not be verified.

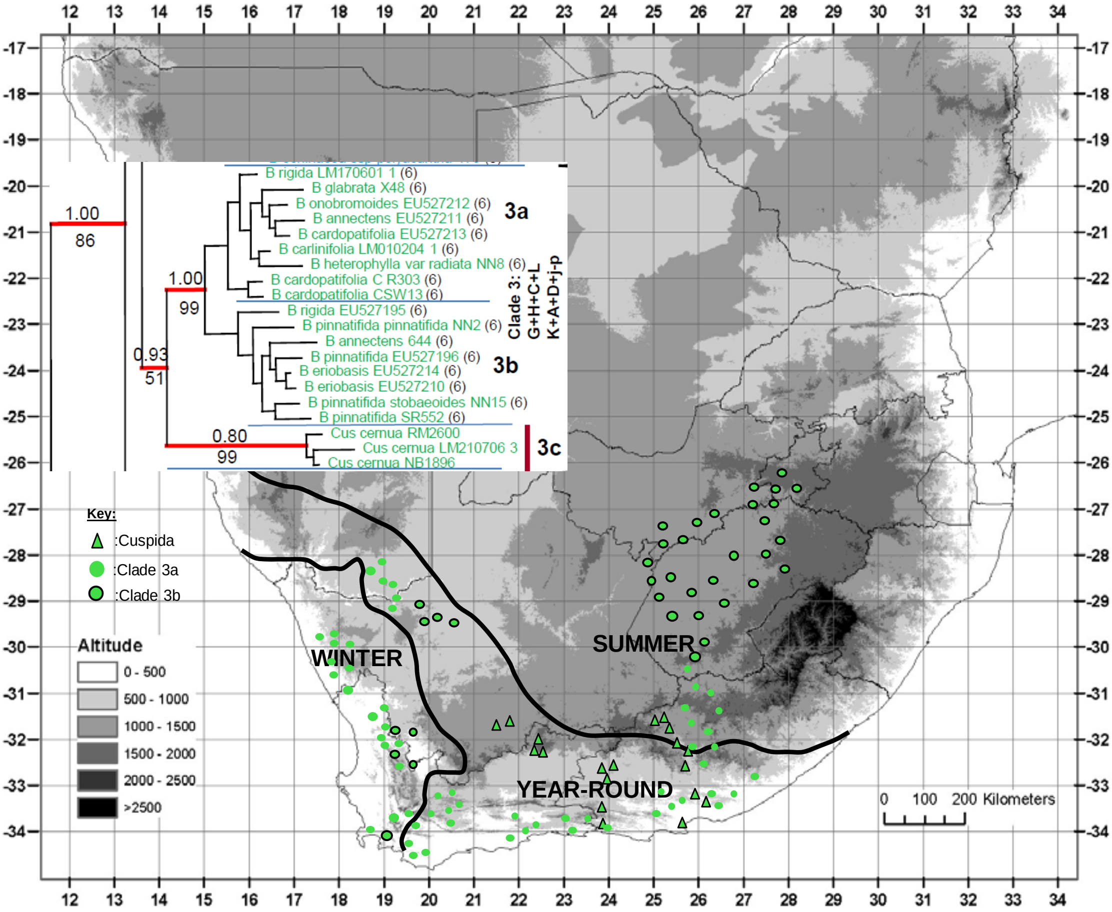


Figure 9: A topographical map showing approximate margins of rainfall regimes. Map shows species distribution of Clade 3 data plotted with Clade 3 from ITS phylogeny superimposed on the top left. (Based on McKenzie and Barker 2008)

Clade 2

Clade 2 (Figure 10) is composed of taxa that are distributed in the summer rainfall region with the exception of *B. carduoides*, which is found from the Swellendam district to East London (Roessler 1959) and thus mainly occurs in the year-round rainfall region. *Berkheya setifera* and *B. echinacea* subsp. *echinacea* are found as far north as Tzaneen and Zimbabwe, respectively, and *B. echinacea* subsp. *polyacantha* occurs in East Africa.

Distribution of species of Clade 2 (Figure 10) show that this clade has a restricted range which occurs from the Tzaneen centre of endemism down to the Barberton and Pondoland centres along the Sekhukhuneland and Wolkberg Centres. This clade thus occupies Savana and grassland biomes of South Africa. These regions experience summer rainfall and no species occur in the winter rainfall regions.

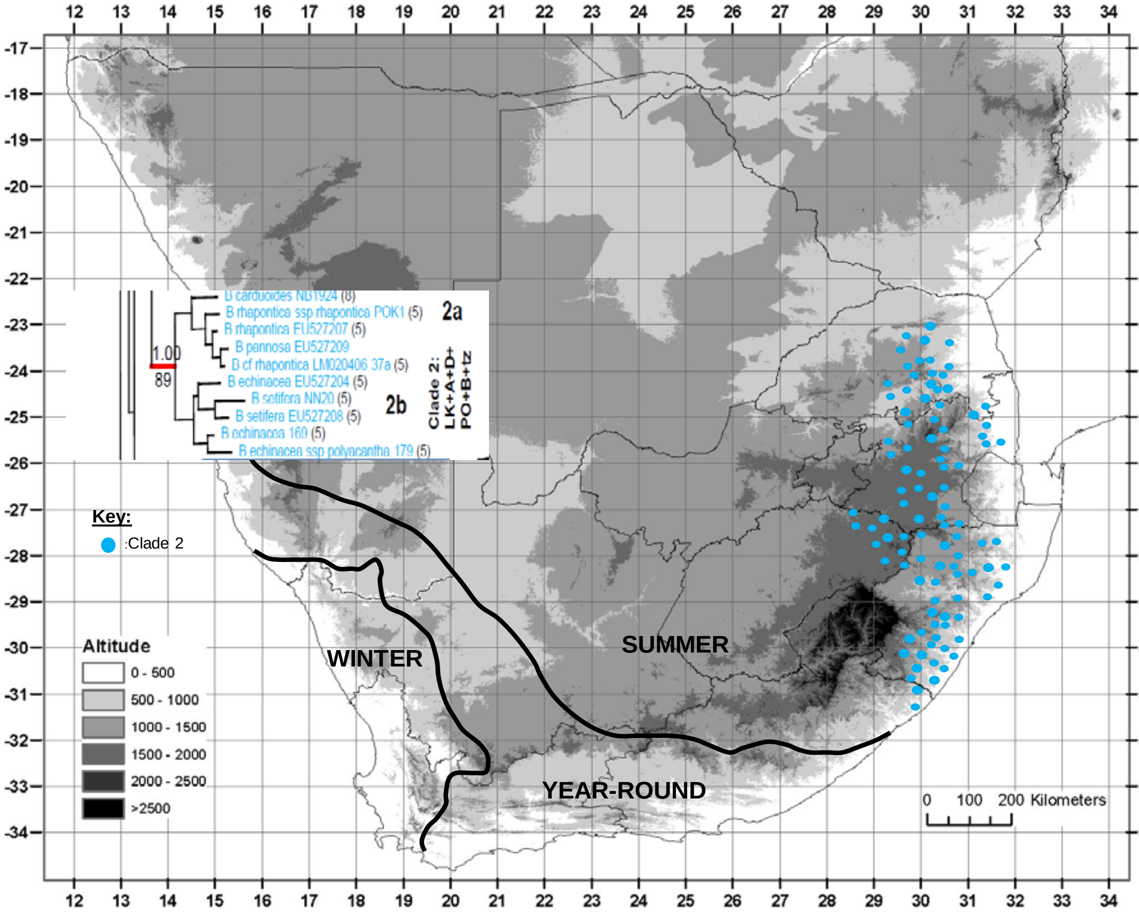


Figure 10: A topographical map showing approximate margins of rainfall regimes. Map shows species distribution of Clade 2 data plotted with Clade 2 from ITS phylogeny superimposed on the top left. (Based on McKenzie and Barker 2008)

Clade 1

Clade 1 is also a summer rainfall clade. Most of the species are distributed in eastern parts of South Africa (Figure 11), but *B. spekeana* and *B. angolensis* occur in Central and East Africa, and Angola, respectively. This clade is fairly well supported (PP = 0.93).

Three subclades are found in Clade 1, the branching of which is not very well supported, and the distribution of these subclades illustrates 3 distinct patterns. Subclade 1a is distributed close to the coast, along the Maputoland-Pondoland regions or the Indian Ocean Coastal Belt sensu Mucina and Rutherford (2006), with some species being distributed inland as far as the Drakensberg Alpine centre and the Johannesburg-Pretoria Centre.

Subclade 1b's distribution forms a 'belt' which extends from the Albany region to the Tzaneen Centre, forming a curved distribution along the escarpment mountains, including the Drakensberg Alpine Centre and Barberton centres of endemism. Subclade 1c species are distributed from the Albany region along the Pondoland region, moving inland to the DAC and Highveld regions towards the Johannesburg-Pretoria region.

Unplaced taxa

B. purpurea and *B. ferox* var. glandulosa were placed sister to the remainder of the clade. These taxa showed no distinct molecular sequences and are thus not expected to separate from the other taxa in this way as both are found in the Eastern parts of South Africa. It is notable that *B. purpurea* is unusual in that is possesses a purple inflorescence which is atypical of *Berkheya* species, which normally have yellow capitulum. Further analyses into these taxa would aid in the understanding of their current placement.

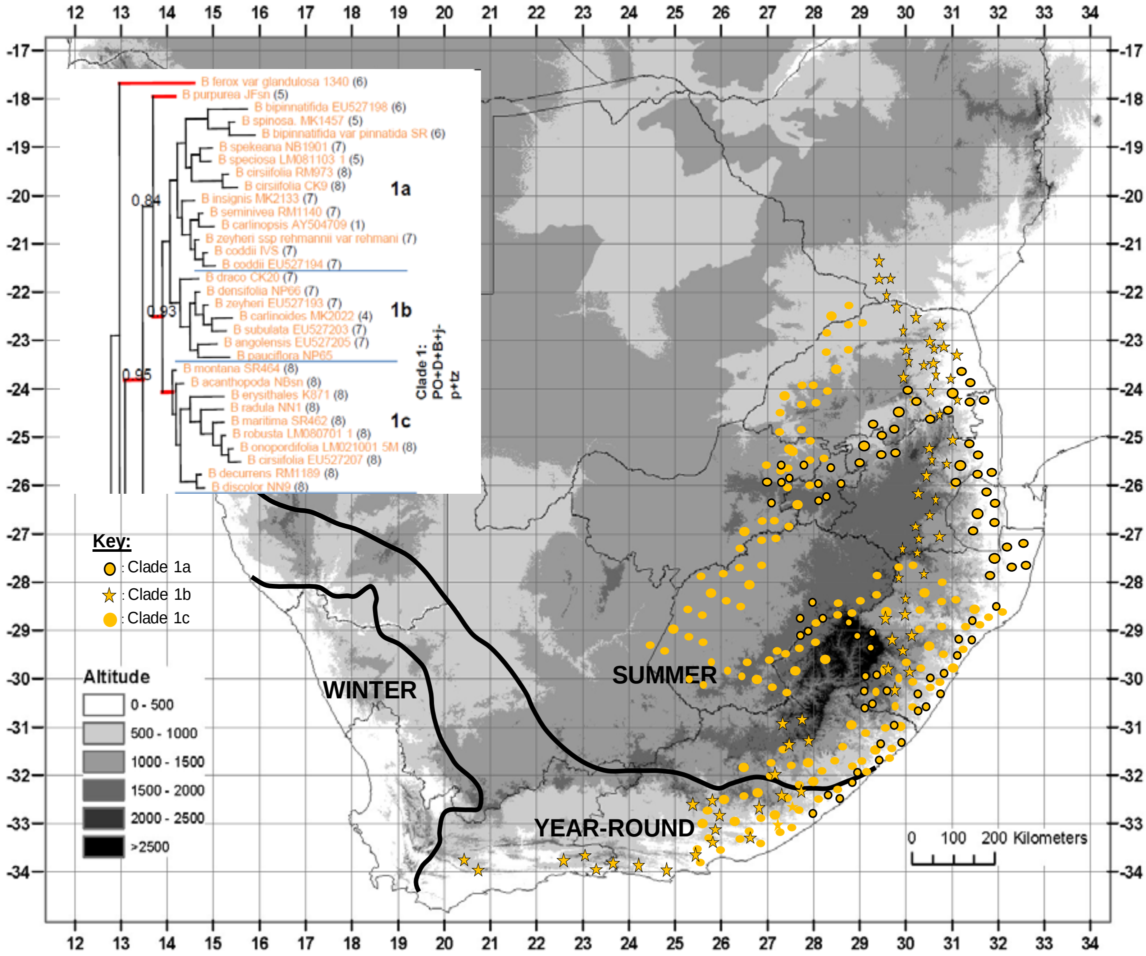


Figure 11: A topographical map showing approximate margins of rainfall regimes. Map shows species distribution of Clade 1 data plotted with Clade 1 from ITS phylogeny superimposed on the top left. (Based on McKenzie and Barker 2008)

Insights from the *psb*A-*trn*H and combined data set phylogenies

The structure of the *psb*A-*trn*H tree differed from that of the ITS phylogeny, although the number of taxa for which *psb*A-*trn*H data were available was far fewer than for the ITS region. Another contributing factor for the differences in the phylogenies is the difference in the independent evolution of *psbA-trnH* as compared to that of the nuclear ITS. Four clades were resolved in the *psb*A-*trn*H phylogeny (Clades A to D). Although much correspondence was observed between the clades retrieved in the ITS and *psb*A-*trn*H phylogenies, the *psb*A-*trn*H phylogeny was not as well supported as the ITS phylogeny, with the strongest support of PP= 1.00 shown for the separation of Clade A from the other clades. *Didelta spinosa* was embedded in Clade A, *Cuspidia cernua* was placed in Clade C and *Cullumia setosa* was placed in Clade B. *Cullumia* was embedded in the summer rainfall clade, Clade B, which does not correspond with where it occurs in the ITS phylogeny or the known distribution of *Cullumia* species inwinter rainfall regions of South Africa. This is one of the main incongruences between the two datasets.

The combined ITS and *psb*A-*trn*H data set was analysed to investigate the robustness of the findings. Combination of data sets with congruent phylogenetic signal would be expected to yield a phylogeny with increased support owing to the increased number of informative sets.

The BI phylogeny of the combined data set reveals four clades (Clades I to IV; Figure 6), which correspond with those retrieved in the *psb*A-*trn*H phylogenies. Clade I is a winter rainfall clade comparable to Clade 5 and Clade A in the ITS and *psb*A-*trn*H phylogenies, respectively, and contains *Didelta spinosa*. Clade II is a summer rainfall clade that corresponds with Clade 2 and Clade B in the ITS and *psb*A-*trn*H phylogenies, respectively. Clade III contains *Cuspida cernua* and corresponds with Clade 3 and Clade C in the ITS and *psb*A-*trn*H phylogenies, respectively. No *Cullumia* species were in common between *psb*A-*trn*H and ITS data, therefore *Cullumia* was not included in the combined data analysis. Posterior probability values for Clades I and II were both strongly supported (PP = 1.00). Clades III (PP = 0.95) and IV (PP = 0.85) have much lower posterior probability values, and the sister relationship of these two clades received poor support (PP = 0.50). The decrease in clade support could be a consequence of the incongruence between the ITS and *psb*A-*trn*H data sets. The possibility of *Cullumia* (which was not included in the COMBINED data set) having arisen as a consequence of an ancient hybridization event cannot be excluded; the *psbA-trnH* data resolve the maternal ancestry, while the ITS indicates the paternal ancestry.

Taxonomic implications: paraphyly of *Berkheya*

Previous studies (Funk *et al*., 2004, 2008. Karis, 2006, 2009) included species from sister genera so as to investigate the possibility of *Berkheya* being a paraphyletic genus. However, despite some results suggesting paraphyly, *Berkheya* was retained as a monophyletic genus. Here I present a comprehensive ITS dataset which includes a majority of *Berkheya* species. From the phylogenies presented here, it is clear that *Berkheya* is paraphyletic, as *Cullumia*, *Didelta* and *Cuspida* are deeply embedded within *Berkheya*.

Funk and Chan (2008) previously noted the close relationship between *Didelta* and *B. spinosissima*. We concur with their findings but would further suggest that the *Didelta* clade, shown in this study as Clade 5 (ITS), may be a clade worthy of generic status. *Berkheya* species are said to have convex phyllaries as a distinctive morphological character, while *Didelta* has free phyllaries (Karis, 2006). *Didelta* species have also been shown to have a close similarity to morphological structures in *B. spinosissima* and *B. angustifolia*, such as pollen structure (Wortley *et al*. 2008); this group has sub-lophate, elliptic and echinate pollen grains with spines clumped on ridges of the pollen. This further illustrates the morphological similarities of *Didelta* to these *Berkheya* species as shown in previous studies (Karis, 2006; Funk and Chan, 2008; Funk *et al*., 2009). Such studies could be used to support the recognition of an expanded *Didelta*. However, similar data from other species in this clade (eg. *B. armata* and *B. herbacea*) is required to confirm these morphological synapomorphies, and hence any such taxonomic change is premature. Thus, while the need for appropriately names monophyletic taxa is recognised

Within taxonomy, great debate has occurred over the years over the recognition of paraphyletic groups as opposed to monophyletic taxa, with monophyly being the recognized criterion for grouping taxa in phylogenetic studies (Horandl, 2006). The identification of "good" genera is defined by Humphreys and Linder (2009) as being those that are predictive and stable. The former implies taxa that have not yet been characterized whose attributes may be easily predicted, while the latter refers to taxa which have increased communication power in their classification using already known and accepted names. Humphreys and Linder (2009) argue that monophyly only becomes important as it increases the probability of a genus being both stable and predictive. In this study, an enlarged and monophyletic *Berkheya* is an appropriate solution, as is the recognition of an expanded *Didelta* and slightly smaller monophyletic *Berkheya*.

Taxonomic Implications: Correspondence with Roessler's classification.

Roessler identified eight series within *Berkheya*. In his revision of Gorteriinae, he lists *Berkheya* species by numbering them (1 to 72), a number system in which each species has a single number under which its subspecies would also fall. The allocation of each species to series is given in Table 3.

Table 2: Table showing Berkheya Classification by Roessler (1959) with species used in this study, coupled with distribution of taxa in centres of diversity

Series	Type	Roessler's sp. No.	Taxa sampled (ITS)	Centre of Diversity as indicated in Figure 2 (ad hoc names used here: A=Albany, C=Caledon, H=Hantam, G=Gariep, Po=Pondoland, D=Drakensberg, LK=Little Karoo, B=Barberton, t-z=Tzaneen, j-p=Johannesburg-Pretoria.)
1.Fruticosae	*B. fruticosa* (L.) Ehrh.,	1-13	*B. barbata,*	G, H, LK, C

			B. angustifolia, *B. schinzii,* *B. cuneata,* *B. coriacea,* *B. chamaepeuce,* *B. canescens,* *B. fruticosa,* *B. spinosissima,* *B. carlinopsis*	
2.Angustae	*B. angusta* Schlechter	14	*B. angusta*	LK
3.Cruciatae	*B. cruciata* (Houtt.) Willd.,	15	*B. cruciata*	LK
4. Armatae	*B. armata* (Vahl) Druce	16-21	*B. armata,* *B. herbacea,* *B. carlinoides,* *B. francinsci*	C, LK
5.Speciosae	*B. speciosa* (DC.) O. Hoffm.,	22-30	*B. purpurea,* *B. rhapontica,* *B. setifera* *B. echinacea,* *B. speciosa,* *B. spinosa*	A, D, Po, B, tz,
6. Rigidae	*B. rigida* (Thunb.) Adams. & Salt.	31-44	*B. rigida,* *B. heterophylla,* *B. onobromoide,* *B. pinnatifida,* *B. cardopatifolia,* *B. eriobasis,* *B. bipinnatifida,*	G, H, D, j-p, C, LK, A,

			B. calinifolia, *B. annectance,* *B. ferox,* *B. draco*	
7.Subulatae	*B. subulata* Harv.	45-55	*B. zeyheri, B. seminivea, B. coddii, B. subulata, B. spekeana, B. insignis, B. angolensis,*	Po, D, tz, j-p, B,
8.Decurrentes	*B. decurrens* (Thunb.) Willd.	56-72	*B. decurrens,* *B. radula,* *B. maritima,* *B. montana,* *B. erysithales* *B. carduoides,* *B. cirsiifolia,* *B. acanthopoda,* *B. robusta,* *B. discolor,* *B. onopordifolia,*	A, D, Po, B, tz,

The ITS phylogeny obtained here corresponds reasonably well with some of Roessler's series, but discrepancies were also found.

Species from series Fruticosae are found to occur in the ITS phylogeny in Clades 4 and 5. Subclade 4a is composed entirely of Series Fruticosae species, while in Clade 5, Subclade 5b is all Series Fruticosae species, which is the subclade with *Didelta* embedded in it. However, not all species from this Series occur in these clades as *B. spinosa* and *B. carlinopsis* are found in Clade 1, completely separated from other Series Fruticosae species. The occurrence of these species in Clade 1 is unexpected. As previously stated, *B. carlinopsis* is a winter rainfall species and is therefore unexpected in the clade in which it occurs. The identification of this specimen cannot, however, be checked due to this being a sequence from GENBANK.

As discussed earlier, *Berkheya cruciata* of the monotypic Series Cruciata has been shown earlier to be closely related to *Cullumia* species in subclade 4c. Similarly, *B. angusta* which forms the monotypic Series Armatae, is also found in sublade 4c with *Culumia*. *B. armata* and *B. cruciata* are found to be closely related to *Cullumia*. It could be hypothesised that the reason why these species were each grouped into separate Series by Roessler was due to morphological characters which liken them to *Cullumia* and not *Berkheya* species. A detailed morphological study of this subclade is needed to form a better understanding of the results shown in this study.

Series Armatae species, namely *B. herbacea*, *B. francisci* and *B. armata* form subclade 5a.

With the exception of *Cuspida*, Clade 3 is composed entirely of species of Series Rigidae. Similarly, with the exception of *B. carduoides* which is in Series Decurrentes species, Clade 2 corresponds to Series Speciosae.

Species of Series Subulatae are found in Subclades 1a and 1b of Clade 1. Series Decurrentes exclusively makes up subclade 1c with the exception of *B. cirsiifolia* that is found in subclade 1a.

Molecular data presented here thus supports much of Roesler's Series. The phylogeny shows species of Series Fruticosae, Angustae, Cruciatae and Armatae to occur in the Winter rainfall clades, Series Subulatae and Decurrentes taxa falling in the Summer rainfall clades and Series Rigidae species occurring entirely in the year-round rainfall clade. A summary tree (Figure 12) shows the distribution of the Series according to the clades shown in the ITS phylogeny.

Few species were found not to correspond with Roesler's series. Firstly, it may be suggested that in the instance of *B. bipinnatifida* and *B. spinosa* of Series Speciosae, that the series be revised as Series Speciosae taxa are found to occur in Clade 2 and these species do not occur here in this review. Also, taxa of series Cruciatae and Angustae be merged with *Cullumia* species to form a single series. Furthermore, consideration should be taken to include *Didelta* species into Series Fruticosae, if subclade 5b and Clade 5 as a whole is not considered a separate genus.

Biogeographic implications:

Funk and Chan (2008) identified five of Roesler's series within the *Berkheya* clade (Figure 1), but their molecular analysis was based on far fewer species that shown in this study. Their study separated *Didelta*, *Cullumia* and *Cuspida* from *Berkheya.* We propose that once revised using both molecular and morphological data, the relevant series should include these other genera as it has been conclusively shown that these genera to be embedded within *Berkheya.*

According to the oldest pollen fossil evidence, Calyceraceae and Asteraceae diverged within the last 60 million years (Zavada and de Villiers, 2000), followed by divergence within the Liabeae-Arctotideae-Vernonieeae clade approximately 25Mya. Gorteriinae diverged from Arctotidinae 24Mya. Within the subtribe Gorteriinae, according to the structure of our phylogenies, it may thus be hypothesised that the five clades diverged from a common ancestor, Clade 5 diverging first from the remaining clades forming a winter rainfall clade. Taxa in the remaining clade then radiated eastward, resulting in the formation of the Clade 4 (also a winter rainfall clade) and the remaining Eastern clades. From this we can see a clear

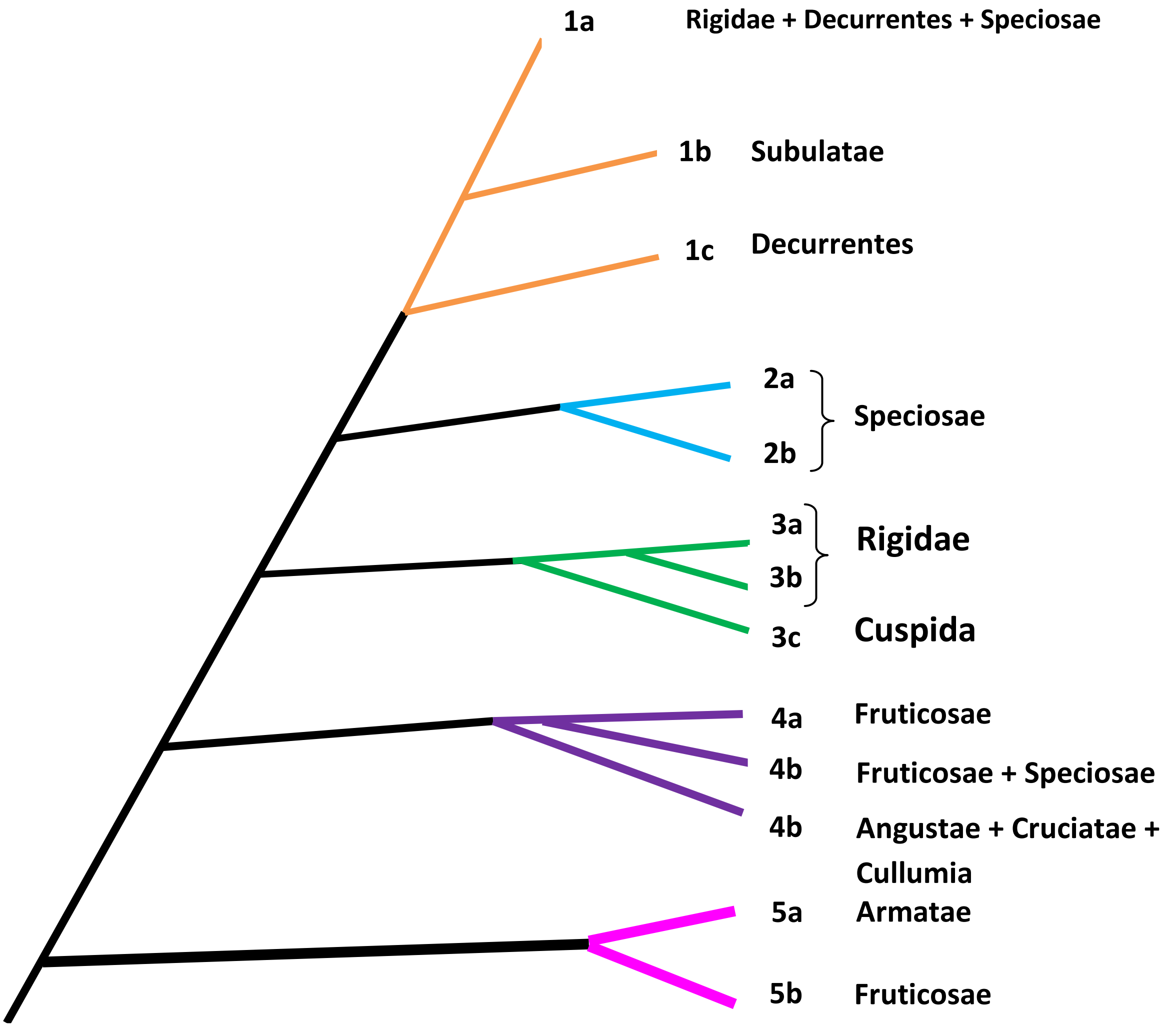


Figure 12: Line diagram summarizing Roessler's Series within clades according to ITS data.

distinction of species that occur in the Eastern and Western parts of southern Africa. This is supported by Karis *et al*. (2009) who hypothesise that Gorteriinae has its centre of origin in the Greater Cape Floristic Region, which includes the Cape Floristic region (CFR) and its surrounding winter rainfall areas. These findings correspond with those of *Gazania* (Howis 2009), which also illustrate a pattern of species originating in the CFR radiating outwards.

This chapter has thus presented the most comprehensive molecular phylogenetic investigation of *Berkheya* and its allies to date. For the present study, ITS sequence data therefore provides further evidence, along with previous phylogenies that *Berkheya* is a paraphyletic genus, with *Cuspida*, *Didelta* and *Cullumia* embedded within it.

In addition, this study highlights the necessity for further phylogenetic analyses of plastid data for Gorteriinae, as the limited amount of data in the present *psb*A-*trn*H data set does not allow robust comparative analyses of nrDNA and cpDNA sequence data. Further studies into morphology would also be beneficial within this subtribe and *Berkheya* in particular. The following chapter focuses on the use of achene morphology as a possible additional data set for the investigation of *Berkheya* and its closely related genera.

Chapter 3: Achene morphology of *Berkheya*

The aim of the study presented in this Chapter is:

1) To examine the morphology of the achenes of selected species of *Berkheya* to obtain novel morphological characters that might support the molecular findings.

Morphology Introduction

In his taxonomic revision of the subtribe Gorteriinae, Roessler (1956) used morphological data to delimit taxonomic groupings. He noted that diagnostic features within the group were; presence or absence of latex; conate involucral bracts; deeply alveolate receptacles with 4 lobes and sterile ray florets. This recognition of diagnostic features for Gorteriinae is maintained in the more modern work done on the subtribe (Funk *et al*., 2009 Ch11). For his delimitation of his series for *Berkheya*, Roessler used receptacle alveole margins, achene morphology (focussing mainly on pappus scale morphology); growth form; leaf shape and capitulum structure to divide the group into eight sections.

In 1977 Norlindh retained the Benthamian subtribes with an additional monotypic subtribe, Eremothamninae, which was first proposed by Leins (1970) based on palynological data. Subsequent morphological studies of Gorteriinae have looked at diagnostic morphological features for species and genera within the group (Karis, 2006; Bremmer, 1994). These studies have highlighted various features over the years. Synapomorphies identified as crucial are: Deeply alveolate receptacles, connate phylleries, four-lobed ray florets, sclerified disc corolla and most recently, laticifers have been discovered as alleged synapomorphies. A study on external achene anatomy by Reese (1989) stated that the fruits of all Gorteriinae species analysed had laticifers within the capitula, which allowed further use of this feature by

Bremer (1994), for cladistics research of the tribe Arctotidae. Here 24 species, representative of all genera of the subtribe Gorteriinae, were found to have conspicuous laticifers in fresh cross sections of their leaves. External achene morphology, ray limb epidermis, embryology and cladistics analyses have also since been identified as essential features in species delimitation in this group

In his 2006 study of Gorteriinae, Karis analysed morphological data from 43 taxa which showed that within the subtribe two clades could be found, namely the *Gorteria* and *Berkheya* clades (Karis, 2006). The idea of these two lineages was first introduced by Leins and Thyret (1971) based on pollen features and later confirmed by phylogenetic analyses of molecular data by Funk *et al*. (2004) and Funk and Chan (2008), which resolved two lineages within the Gorteriinae. One lineage included *Gazania, Gorteria* and *Hirpicium,* which they called the Gazania Clade (GAZ), The second lineage identified in this analysis included both the Didelta Clade (DID) comprising *Didelta* and *Berkheya spinosissima*, as well as the Berkheya Clade (BER) which included *Cullumia*, *Cuspida*, *Heterorachis* and *Berkheya*, but excluding *B. spinosissima* (Funk *et al*., 2008). The two analyses done by Funk *et al*.(2004, 2008), which focused on molecular data, and Karis (2006), which was based solely on morphological data, clearly illustrate two separate lineages. This showed that use of morphological data as shown by Karis was able to produce a phylogeny which successfully resolved the clades which the subtribe is currently understood to comprise.

Karis (2006) also demonstrated that according to morphological data, *Berkheya* and *Hirpicium* were both paraphyletic. He found floral micromorphological data to be phylogenitically informative, and also found both sister groups to be defined by sets of diagnostic synapomorphies within the anthers, styles and external morphologies. His studies showed that *Heterorachis, Cullumia, Cuspida* and *Didelta* were embedded within *Berkheya* (Karis, 2006).

Authors have differed in the characters emphasised when delimiting genera. For example, Lessing (1832) placed emphasis on fruit morphology, pappus morphology, ray floret fertility as well as filament ornamentation when revising the subtribe Arctotidinae, but pappus characters and fruit pubescence were subsequently seen as unreliable (Beauverd, 1915; Lewin, 1922). The use of fruit morphology in the taxonomic classification of Compositae species, in particular external achene and pappus characters has been exploited by workers in a number of tribes in the family, notably the Calendulae, Anthemideae and Arctotideae, which show striking evolution in achene morphology during diversification (Funk *et al.*, 2009).

Value of achene morphology to systematics of the Compositae

Cheheregani and Mahanfar (2007) used achene data to study 11 species which represented five genera of the tribe Anthemideae (Compositae). Achene morphology was important to distinguish the genera, even when used alone, and these workers examined characters of the achenes which they found to be most suitable for systematic application and used these to delineate taxa. The character found to be most taxonomically informative were achene length, as there were few minor variations between the achenes of different species. Shape was found to be highly specific to genera and differed only between species. Pappus scales, where present, were found to show a great degree of variation among species. Their surface features, sulcus, wart, tubercule and lacune morphologies were also studied, with lacune morphology being found to be most informative within the group as it was found to be distinct at a species level (Cheheregani and Mahanfar, 2007).

Furthermore, the use of morphological data in conjunction with DNA data has become more popular over the years as this allows comparative analyses of taxa. In their study, Cheheregani and Mahanfar (2007) found that a combination of their achene morphological data with existing molecular data of the same group showed clear boundaries within the monotypic genera and distinct achene morphologies in homogenous genera.

McKenzie *et al.* (2005) studied Arctotidinae which allowed them to identify “natural” species groups within this subtribes, using external morphological characters of the achenes. Following this example I used scanning electron micrographs of achenes taken from herbarium specimens, supplemented with observation with a dissecting microscope, to examine the external achene morphology of representative species in the *Didelta* and *Berkheya* clades. The information obtained was used to infer relationships among the species, and to assess if there is a correlation between the groupings suggested by the morphological data and the clades resolved by molecular data in the Chapter 2.

Methods and Materials:

Mature achenes were obtained from herbarium specimens found in the Selmar Schonland Herbarium, Grahamstown. As these samples were dry, no treatment was necessary prior to them being mounted on stubs and sputter coated with gold-palladium. The achenes were examined using the JEOL JSM 840 Scanning Electron Micrograph (SEM) found at the Rhodes University Electron Microscope Unit. Various features of the achene and pappus scales were noted as being variable. In particular twin hairs, surface sculpturing of the fruit, ribs on the achene, and pubescent cells are described and assessed for their taxonomic utility.

These features were initially described and analysed for each species, but subsequently species were grouped according to clades found in the molecular phylogeny of Figure 4 in

Chapter 2, and features specific to, or consistent within, each clade or subclade were determined.

The maturity of a fruit is important in such a study and it is for this reason that mostly mature fruits were selected and used in this study. Where mature fruits could not be found, immature fruits were used and were labelled as such.

Observations of pappus morphology and trichome structure were made. Where necessary, further examinations were done using a dissecting microscope. Care was taken to standardize achenes selected and features studies so as to avoid features which are highly variable according to stages in development and growth conditions. (Breitwieser & Ward, 2003)

Results:

Achene data is presented in the form of a table of all characters (Table 4.1), an appendix of plates (pictures of achenes from each clade; Appendix B) as well as tables with corresponding achene pictures illustrating character state descriptions within the discussion below.

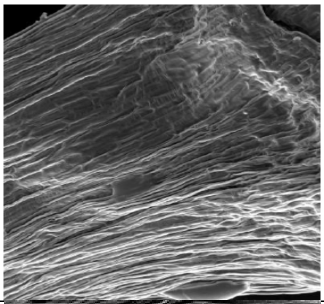
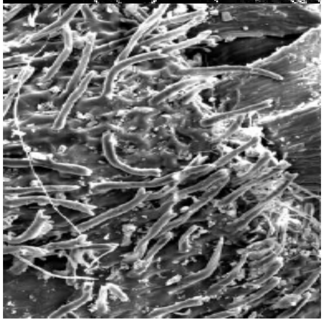
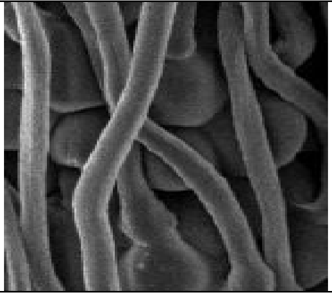
Table 3: Table showing achene data with character marked for presence and absence and where relevant, with codes: (**Twinhairs**: 0-absent, 1-long,2-short,3-swollen basal cells,4-twisted,5-basal,6-apex,7-dense,8-sparse; **Surface cells:** 1-Reticulate,2-swollen,3-sunken; **Scale shape:** 1-truncate,2-acuminate,3-erose,4-dentate,5-crenate; **Scale margins:** 0-entire,1-serrate,2-spinescent; **Scale series:** 0-uniseriate,1-biseriate.

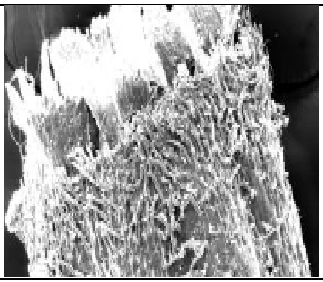
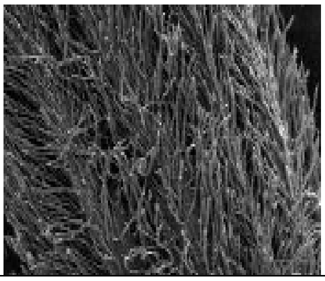
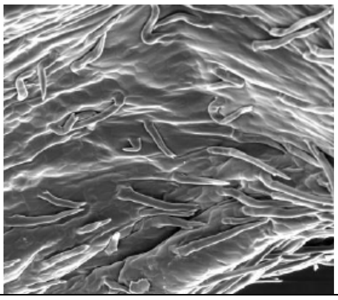
	Achene						Pappus scales						
Characters	Twinhairs	Twinhair character	Swollen cells	Surface cells	Cell structure	ribs	Pappilae	praemorsus	Scale margins	Scale structure	coronate	Scale series	no. scales
Species name:													
B. cirsiifolia	0	0	0	1	2	1	1	0	2	3	0	1	20
B. bipinnatifida	1	2,4,8	0	1	3	1	1	0	2	5	0	1	10
B. speciosa (immature)	0	0	0	1	1,3	0	0	1	2	3	1	1	14
B. subulata	1	1,4,7	1	0	0	0	1	0	2, 3	3	0	1	30
B. acanthopoda	0	0	1	1	1,2	1	0	1	1	1,4	0	1	10
B. draco	0	0	1	1	1, 3	0	1	0	2	3	1	1	8
B. erysthales	0	0	1	0	1,3	1	0	0	2	3	0	1	20
B. maritima	0	0	1	0	1	1	0	1	2	3	0	2	20
B. onopordifolia	0	0	1	0	1, 3	1	0	1	1	3	1	1	8
B. robusta	0	0	1	0	1,3	0	0	1	1	1,3	1	1	20
B. discolor	0	0	0	1	0	0	0	1	1	4	0	1	10
B. decurrens	0	0	0	1	1,3	1	0	0	2	4	1	2	10
B. rhapontica	1	1,3,4,7	1	0	2	0	0	1	2	4	0	2	20
B. echinacea	1	1,4,7	0	0	0	0	1	0	2,3	1,3	0	1	20
B. setifera	0	0	1	1	1	1	0	1	1	5	1	1	8
B. carlinifolia	1	2,4,7	0	0	3	1	0	0	2	5	1	2	18
B. onobromoides	1	2,4,6,8	1	0	3	1	1	1	1	1	0	1	20
B. cardopatifolia	1	2,6,8	1	1	2	1	1	1	2	1,4	0	1	
B. pinnatifida	1	2,4,7	0	0	0	1	1	0	2,3	2	0	1	24
B. heterophylla	1	2,4,6,8	1	0	3	1	0	1	1	1	0	1	20
Cuspida cernua	1	1,4,7	0	1	0	0	1	0	2,3	2	0	1	12
B. canescens	1	1,4,7	0	0	0	0	1	0	2,3	2	0	1	20
B. fruticosa	1	1,4,7	0	0	0	0	1	0	2	2,3	1	2	20
B. cruciata	1	1,4,7	1	0	2	1	1	0	2	2,3	0	1	8
B. coriacea	1	1,4,7	0	0		0	1	0	2	2,3	1	1	10
B. cuneata	1	1,4,7	0	0	0	0	1	0	2,3	2	0	1	20
B. herbacea	1	1,4,7	0	0	0	0	1	0	2,3	2	0	1	20-30
B. armata	1	1,4,7	0	0	0	0	1	0	2,3	2	0	1	20
B. spinosissima	1	1,4,7	0	0	0	0	1	0	2,3	2,3	0	1	10

Twin hairs:

The structure and position of the twin hairs (when present) differed considerably among the species. As shown in Table 4.2 below, seven character states were identified.

Table 4: Illustrated character states describing variability in twinhair structure.

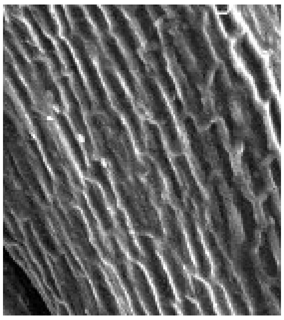
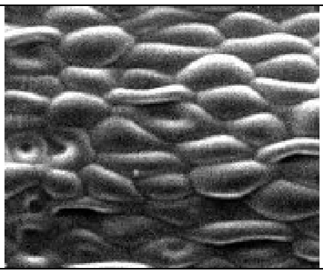
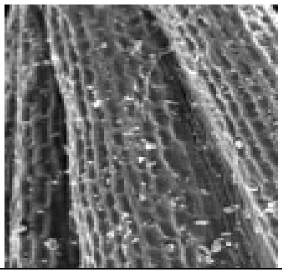
Twinhair character states:	
0: Absent	
1: Long given approximate length compared to fruit	
2: Short given approximate length in relation to fruit	
3: Swollen basal cell	

4: Twisted	
5: Twin hairs arise from base of achene	
6: Twin hairs arise from apex of achene	
7: Achene densely covered in twin hairs	
8: Achene sparsely covered in twin hairs	

Epidermal cells of the achene:

As previously stated, the relative maturity of sampled achenes was of great importance in this study (Table 5). Although concerted attempts were made to select mainly mature samples for use, in some instances it must be acknowledged that these varying degrees of maturity are expected to affect the physical appearance of selected features. An example of this would be a seemingly reticulate achene which may have been colliculate, but over time dried out possibly due to being immature at the time of collection, resulting in a reticulate appearance.

Table 5: Illustrated character states describing surface sculpturing of achene with very sparse or no twin hairs.

Surface sculpturing	
1: Reticulate: cells on surface have a rectangular appearance	
2: Swollen/Colliculate	
3: Sunken	

Pappus scales:

All achenes examined possessed pappus scales, and a number of features of these were identified as variable. The presence / absence of papillae, whether or not they are praemorse (has a bitten impression; Figure 13), the presence of coronate scales and the number of scales were assessed. In addition, the following multistate characters were selected with multiple character states.

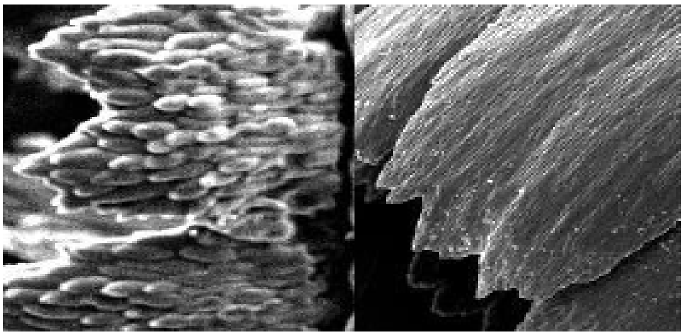
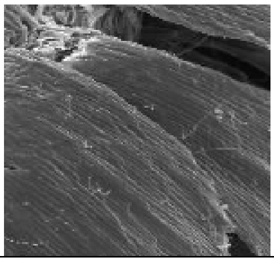
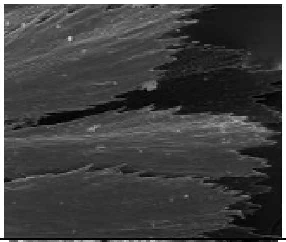
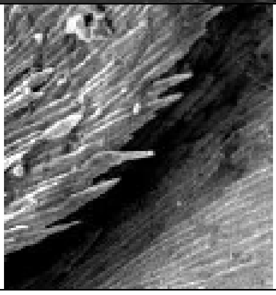


Figure 13: Images illustrating pappus scale characters. A: Papillate scale, B: praemorse scale.

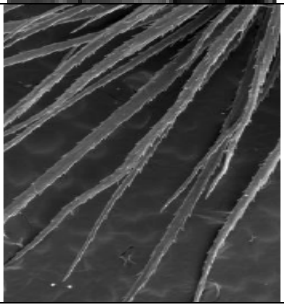
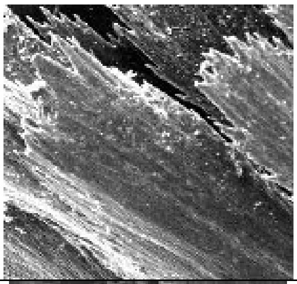
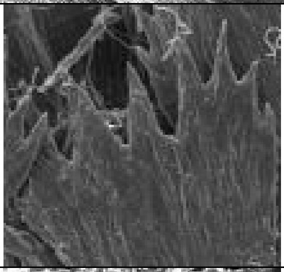
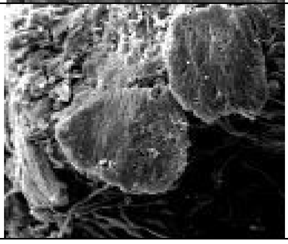
Pappus scale margins:

Table 6: Pappus scale margin structure.

Scale margins	
1: Entire	
2: Serrated	
3: Spinescent: deeply serrated resulting in spine-like protrusions	

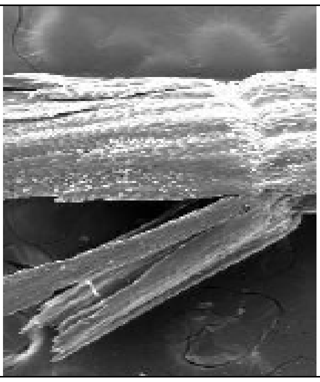
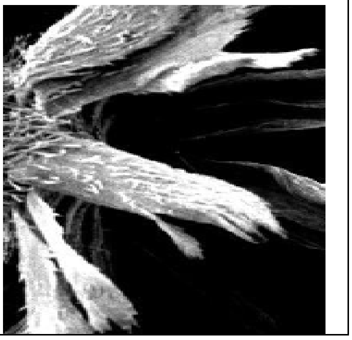
Pappus scale shape:

Table 7: Pappus scale shape

Scale shape	
1: Truncate: square apex	Truncate 
2: Accuminate: gradually taper off to a highly acute tip	
3: Erose: irregular structure at the apex	
4: Dentate: regular “teeth” at the apex	
5: Crenate: rounded at the apex	

Pappus scale series:

Table 8: Pappus scale series

Series	
1: Uniseriate: single whorl of scales at fruit apex	
2: Biseriate: two layers/whorls of scales at apex of fruit. One outermost and one inner	

Discussion:

All *Berkheya* species studied possess pappus scales, which is a notable and useful feature as they show variation between species. Surface structures of the achenes, such as twin hairs and surface cells, are quantitative and also were also shown to be taxonomically informative. The features of the species of each of the five Clades are described and discussed below. The phylogeny (Figure 4) was split into five images, each representing one clade Images of corresponding achenes were added to each clade and labelled alphabetically from A to U.

Clade 1.

Upon grouping the species into the clades identified by the ITS data, it was found that the majority of the fruits of Clade 1 (Figure 14) have no twin hairs, except for *B. circiifolia* and *B subulata*, which are found in subclades 1a and b respectively (see plates 1A – 1L). The characters of these achenes corresponded with the subclades found in the phylogenies, as the species found in subclade 1a all have glabrous cells (*B. circiifolia* has visible swollen cell at the base of the twin hairs) on the surface of the fruit, while species of subclades 1b and 1c have more flattened cells. Achenes of all species of Clade 1 are ribbed, as were some species of Clade 3 and Clade 4. The pappus scales of these species are variable as *B. circiifolia*, *B. bipinnatifida*, *B. subulata* and *B. draco* are papillate, while the rest have smooth scales (the former two species are in sublade 1a while *B. subulata* and *B. draco* are in subclade 1b). Premorse pappus scales seem to be the structure typical of species in subclade 1c, with the exception in this case being *B. speciosa*. Clade 1 species have between 10 and 20 uniserate pappus scales. From this it may be noted that in the first clade, both the surface structure and the scales are informative.

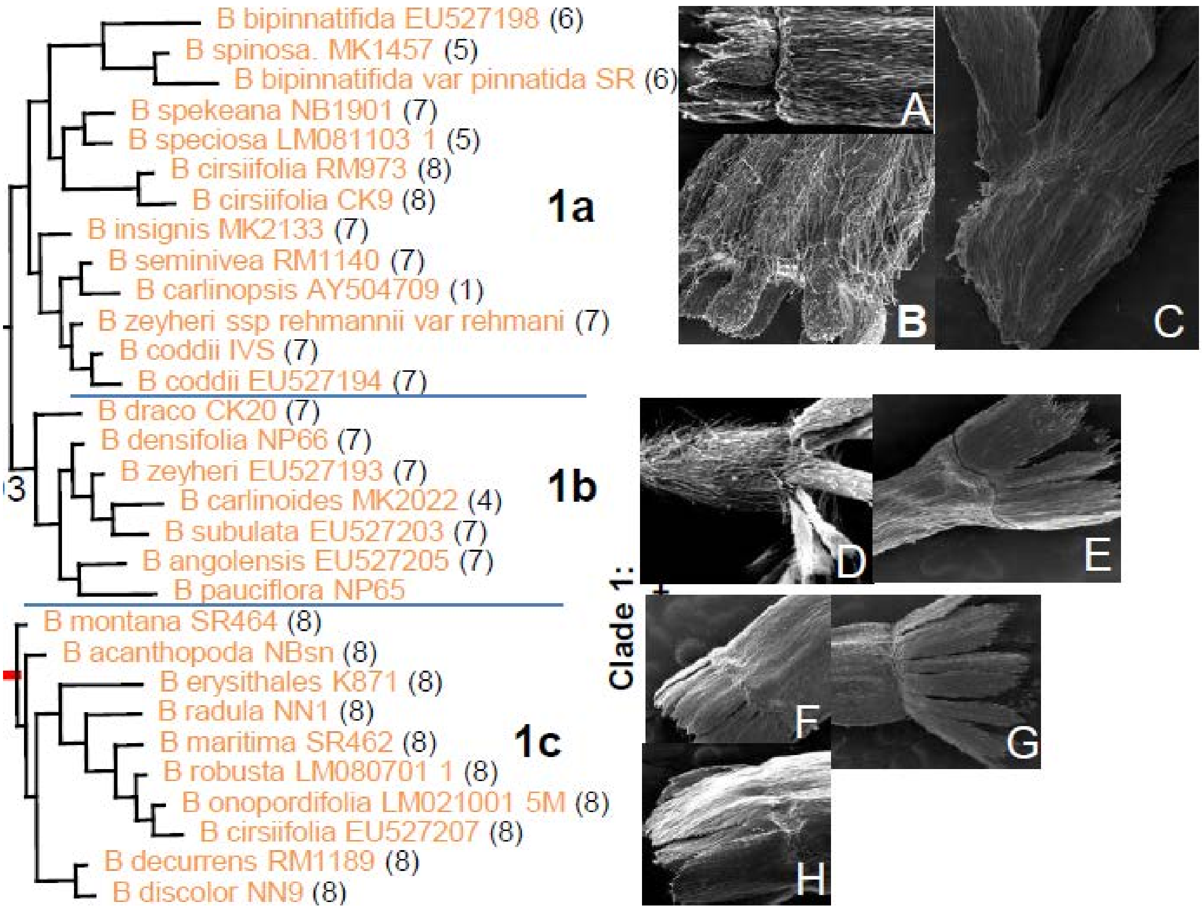


Figure 14: Clade 1 of ITS BI phylogeny with achene samples of species in this clade shown. **A**: *B. cirsiifolia*, **B**: *B. speciosa* **C**: *B. speciosa*, **D**: *B. subulata*, **E**: *B. draco*, **F**: *B. acanthopoda*, **G**: *B. deccurens*

Clade 2

Clade 2 species (Plates 2A – 2B; Figure 15) all have long dense and twisted twin hairs with the exception of *B. setifera*. *B. rhapontica* possesses swollen cells at the base of the twin hairs. Pappus scales within this clade were found to have a consistent structure with all species having 20 scales except for *B. setifera* which has 8. The difference in morphology of *B. setifera* is most notable within the clade. This species is also a little anomalous for this clade, as it is distributed further north than the remaining species of the clade.

Figure 15: Clade 2 of ITS BI phylogeny with achene samples of species in this clade shown. **I**: *B. setifera*, **J**: *B. echinacea*

Clade 3

Species in Clade 3 (Plates 3A-3F; Figure 16) are characterised by twin hairs which are present in all species, and where visible, basal cells are swollen in all species except for *B. cardopatifolia*. These twin hairs are characteristically short and sparse in *B. onobromoides*, *B. cardopatifolia* and *B heterophylla* (all of clade 3a). Achenes of *Cuspida* are shown to have long, twisted and dense twin hairs, which is not found in the other species of this clade. Similar to *B. pinnatifida*, *Cuspida* achenes have short, mildly acuminate scales which are highly papillate. This is arguably a feature restricted to *Cuspida* and may be used to further support the separation of *Cuspida* into a subclade separate from the other species of Clade 3.

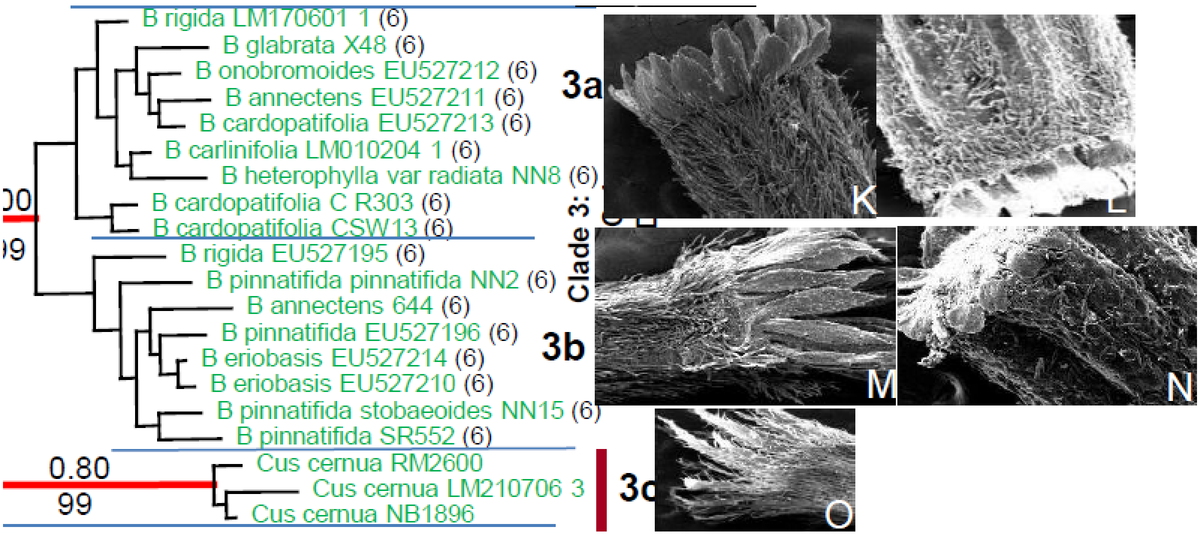


Figure 16: Clade 3 of ITS BI phylogeny with achene samples of species in this clade shown. **K**: *B. carlinifolia*, **L**: *B. onobromoides*, **M**: *B. pinnatifida*, **N**: *B. heterophylla*, **O**: *C. cernua*

Clade 4

Clade 4 (Plates 4A-4E; Figure 17) species show a general achene structure which is uniform; all taxa examined possess long, twisted and dense twin hairs. In addition, pappus scales have the same structure throughout, with all scales being acuminate and varying in the length. The longest are found in *B. canescens* and *B. cuneata* (observed from an immature achene). All scales in this clade are papillate. *B. cruciata*, which occurs in the same subclade as *Cullumia* and *B. angusta*, seems to exhibit a varied structure which includes a very dense cover of visibly swollen cells at the base of the twin hairs. Karis (2006) highlighted glabrous achenes as a feature common between *B. cruciata* and *Cullumia* species. This may thus be a character which helps define the species of subclade 4b in addition to other characters common to *B. cruciata* and *Cullumia* species. The ability to make clear comparisons between *B. angusta* and *Cullumia* is complicated by the fact that collections of *B. angusta* are rare, so it is therefore difficult to accurately assess the structure of these fruit and thus compare them to current findings.

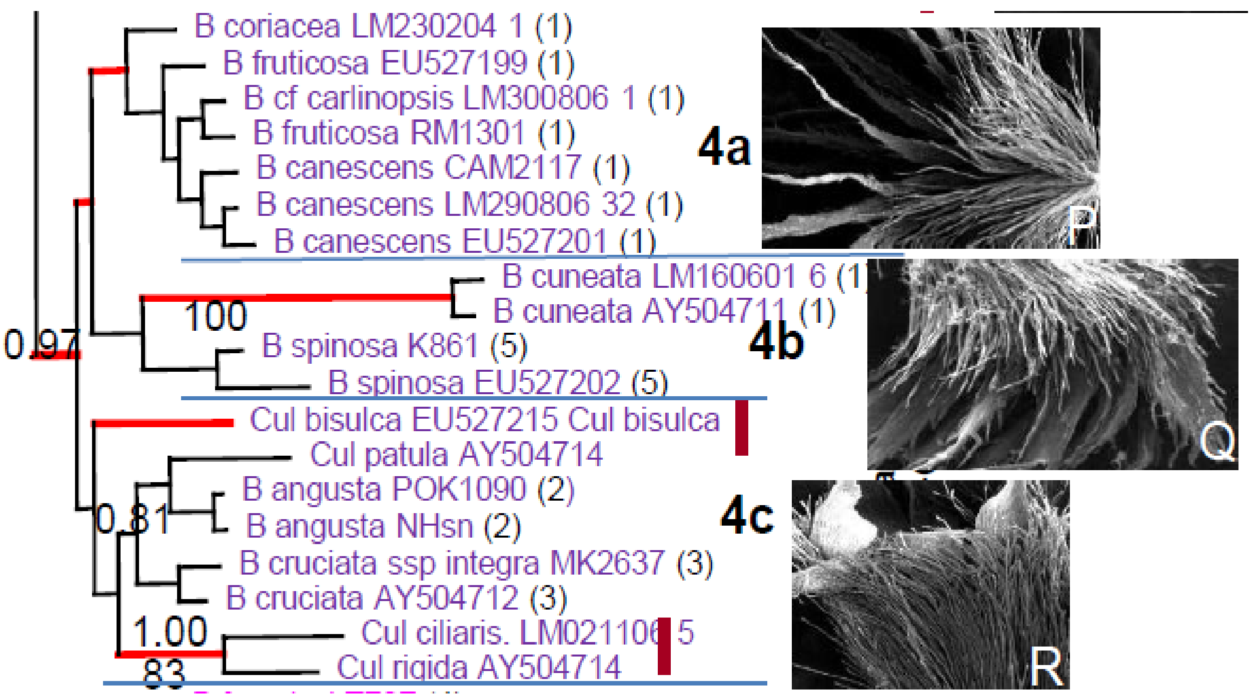


Figure 17: Clade 4 of ITS BI phylogeny with achene samples of species in this clade shown. **P**: *B. canescens*, **Q**: *B. cuneata*, **R**: *B. cruciata*

Clade 5

Species of Clade 5 (Plates 5A-5C, Figure 18) exhibit an almost identical or uniform achene structure in all species examined. Fruits possessed long, twisted and dense twin hairs while the scales exhibit papillate, mildly accuminate scales which all have deeply serrated margins, giving them a spinescent morphology. The availability of a *Didelta* species for achene morphology would have allowed for further analyses into the overlap in structure within the clade and its subclades. Three species were sampled from this clade, with only a single species, *B. spinosissima*, being from subclade 5b. Although the achenes of this species showed the most morphological variation, shown in the scale structure an number, compared to the other species analysed within this clade, more sampling (as those done by Roessler 1959) would be needed to gain a better understanding of the morphology of the achenes of species within this clade.

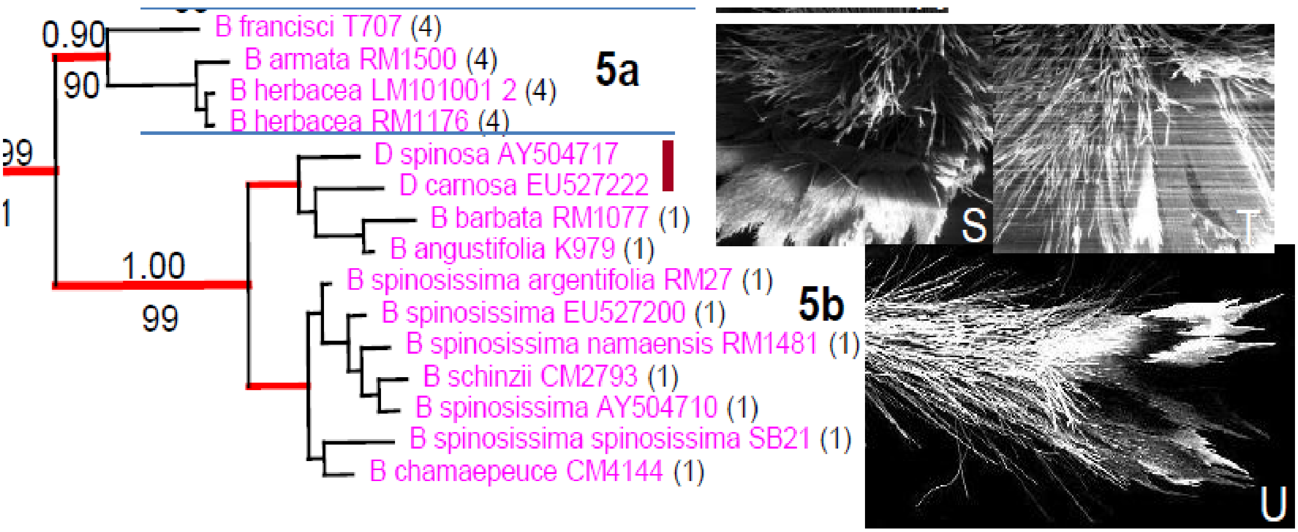


Figure 18: Clade 5 of ITS BI phylogeny with achene samples of species in this clade shown.
S: *B. herbacea*, **T**: *B. armata*, **U**: *B. spinisissima*

Although Clades 4 and 5 have *Cullumia* and *Didelta* embedded within them, mature flower heads were not found on available herbarium specimens, which unfortunately meant that achenes of these could not be examined and described here.

Synthesis: the value of achene morphology in *Berkheya* and allies.

Data in Table 4 indicate that the morphology of achenes within different clades, and even subclades is uniform. Common traits were successfully identified in the structure of achenes within clades, showing that specific combinations of morphological characters may be associated with each clade, which can be compared to existing phylogenetic data (As shown in Figure 19). Clade 1 species typically have no twin hairs, which is characteristic of this clade, as all other clades possessed twin hairs of various structures. Clade 3 showed a characteristic feature of twin hairs with swollen basal cells, which were also shown by *Cuspida*, which falls into this clade. Species of Clade 4 and Clade 5 on the other hand have dense twin hairs, but most characteristic were the pappus scales, which were highly acuminate and typically long in Clade 4, while clade 5 possessed distinctly mildly acuminate scales for all sampled taxa. An understanding of the species distributions within the clades on a molecular level coupled with insight into the morphological characters of these species allows for a comparison of datasets which allows for a robust analysis of this data, thus creating a clearer understanding of the systematic within the group. This chapter has thus successfully illustrated the importance of achene data as a phylogenetic indicator.

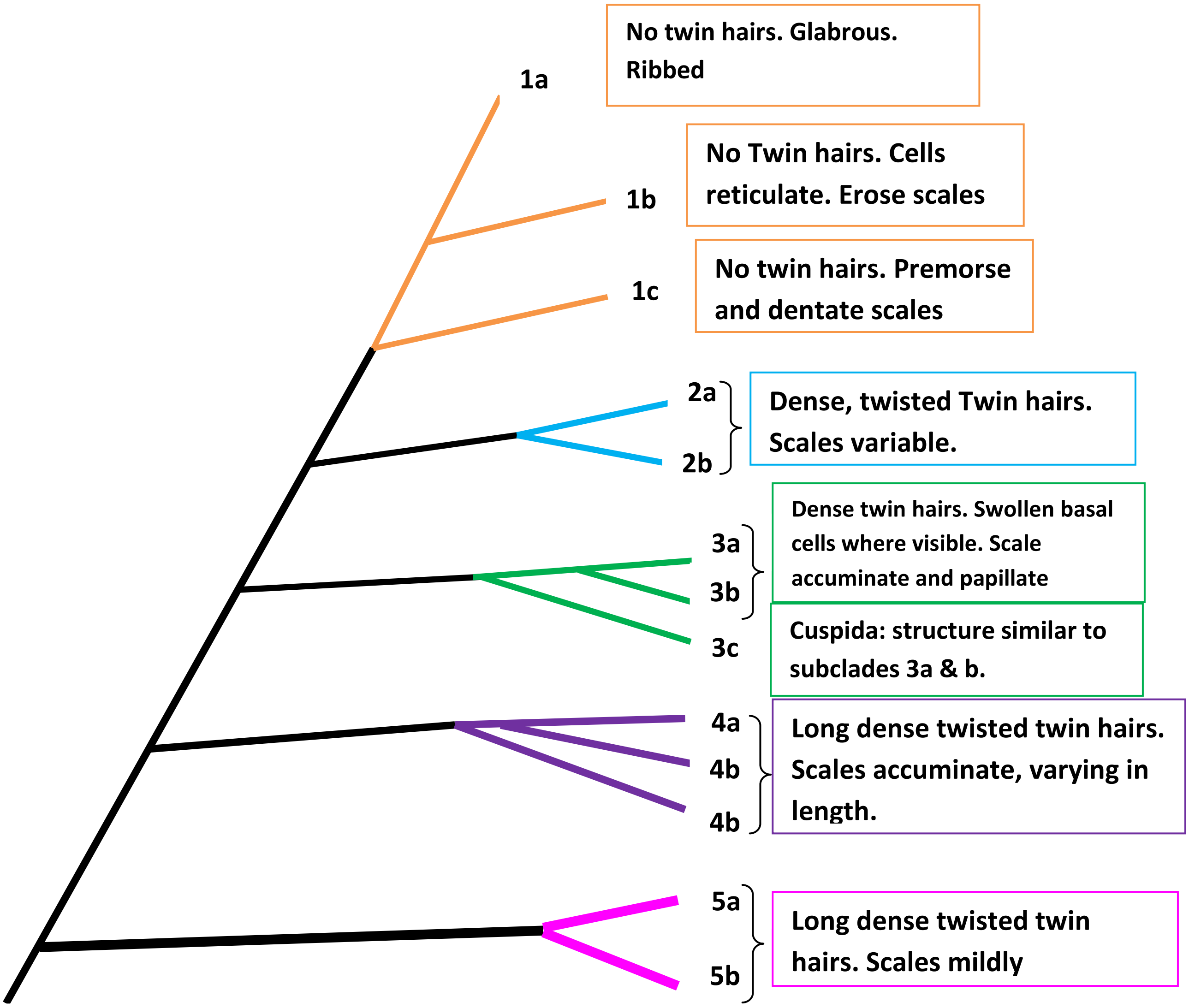


Figure 19: Line diagram summarizing achene morphological features within each clades as per ITS BI data.

Results presented here illustrate the importance of achene morphology in supporting the relationships within *Berkheya* and its sister genera, as elucidated by ITS sequence data. Clear consistencies were found in morphological data within clades (Figure 19). Figure 19 illustrates how the understanding of these characters aids in the confirmation of known species groupings, as shown in the clades of *Berkheya* data and its allies. The relative ease of the close inspection of scanning electron micrographs at high resolutions, and where necessary, the use of light microscopy, further increases the credibility of this data, and thus the potential for increased use of this type of data in future studies. A closer look into these fruits and their characters, coupled with increased numbers of species sampled, would allow for a more robust result in this respect. Achenes should thus be investigated further in future studies, ideally in conjunction with other morphological features such as pollen, floret and other capitulum characters as has been suggested in previous studies.

Chapter 4: General Conclusions

Individual and combined analyses of ITS and *psbA-trnH* data has provided a clear demonstration of the paraphyly of the genus *Berkheya*. The large number of taxa sampled in this study confirms the conclusions of previous studies (based on very small sample sizes) which noted the possible paraphyly of *Berkheya* (Funk and Chan, 2008; Karis, 2006). The addition of further genera known to be linked to *Berkheya* and its allies such as *Heterorachis,* as well as further phylogenetic analyses of plastid data in particular is needed as there is some evidence of incongruence (notably, involving the placement of *Cullumia*), possibly as a consequence of past hybridisation. Greater sample sizes are expected to improve the signal within the data and it is anticipated that this data will confirm congruence with the ITS findings.

Humphreys and Linder (2009) place a preference on monophyly as it provides both predictable and stable attributes within described genera. They state that taxa should be monophyletic and classification be constructed in a way that is illustrated clearly in phylogenies, and therefore show a preference for the recognition of larger monophyletic groups to generic rank. For this reason we find that consideration should be given to sinking *Didelta, Cullumia* and *Cuspida* into *Berkheya*. If this is carried out, then all taxa will become *Berkheya* species as the publication of the genus *Berkheya* (1784) preceeds those of its sister genera. As an alternative, Clade 5, which includes *Didelta,* could be defined as a separate genus which would result in *Berkheya* species within this clade then being renamed as *Didelta*. These two options would, according to our findings, create monophyletic, named clades, and thus decrease the amount of discrepancies shown in classifications of Gorteriinae.

The agreement between the molecular data and Roesler's (1959) Series-level taxonomy further strengthens the confidence in the use of morphological data, as well as the value and validity of Roessler's original classification. Species found in Series Fruticosae, Angustae, Cruciatae and Armatae are shown to constitute the winter rainfall clades of the ITS phylogeny, while Series Subulatae and Decurrentes taxa form the Summer rainfall clades, with Series Rigidae occurring entirely in the year-round rainfall clade. Very few species were found to deviate from Roesler's classification, which suggests only minor revision of this classification is needed, such as *B. bipinnatifida* and *B. spinosa*, which are found in Roessler's Series Speciosae. And taxa of monotypic series Cruciatae and Angustae, which are associated with *Cullumia* and *Didelta* illustrate the need for such a revision.

The examination of achene morphology provided further support to the molecular findings, including support for the inclusion into *Berkheya* of some of the segregate genera. The use of morphological data in Chapter 3 illustrates the importance of achene characters as being potentially phylogenetically useful, as these data showed the clades and even subclades retrieved by the ITS data to each be morphologically homogeneous. These data allowed the identification of common traits in the achenes of taxa occurring in the same clades, thus showing that specific combinations of morphological characters may thus be associated with each clade, which can be used as to support results shown in molecular data.

Unfortunately, this study is limited by a lack of a comprehensive parallel plastid data set, and the expansion of the *psbA-trnH* is a research priority. However, the comprehensive ITS data set provides valuable insights into the taxonomy and biogeography of the genus, and thus forms a sound base for further research into this fascinating group of plants.

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APPENDIX A

ITS Alignment:

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Hir_echinus_DQ444719             TCGAACCCTGCATAGCAGAA-CGACCCGCGAACASGTAAC-CACAACCGGGTGTCAAGGG
Gor_sp_EF556363                  TCGAACCCTGCATAGCAGAA-CGACCCGCGAACACGTACC-CACAACCGGGTGTCAAGGG
B_spinosa_MK1457                 TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_bipinnatifida_var_pinnatida_SR TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_bipinnatifida_EU527198         TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_spekeana_NB1901                TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_speciosa_LM081103_1            TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_carlinoides_MK2022             TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_insignis_MK2133                ????????TGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_seminivea_RM1140               TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_coddii_IVS                     TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_subulata_EU527203              TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_carlinopsis_AY504709           TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_angolensis_EU527205            TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_zeyheri_ssp_rehmannii_var_rehm TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_zeyheri_EU527193               TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_densifolia_NP66                TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_coddii_EU527194                TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_onopordifolia_LM021001_5M      TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_acanthopoda_NBsn               TCGAACCCTGCACAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATCGAGG-
B_cirsiifolia_RM973              TCGAACCCTGCATAGCAGAA-CGACCCGTGAACACGTAAC-TACAACCGGGCATTGAGG-
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B_zeyheri_ssp_rehmannii_var_rehm CGGAAATTGGTTTTCCGTGCTTGCGGCGCGGTTATCCGAAATAGGAGTCCCC-TTCGGTG
B_zeyheri_EU527193               CGGAAATTGGTTTTCCGTGCTTGCGGCGCGGTCATCCGAAATAGGAGTCCCC-TTCGGTG
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B_spekeana_NB1901                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
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B_carlinoides_MK2022             GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_insignis_MK2133                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_seminivea_RM1140               GCAAGGGAAGC-CTCG-TCATAGACCCCAAC?CGTCGTCTTGCGAC-GAT-GCTTCG
B_coddii_IVS                     GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_subulata_EU527203              GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_carlinopsis_AY504709           GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_angolensis_EU527205            GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_zeyheri_ssp_rehmannii_var_rehm GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_zeyheri_EU527193               GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_densifolia_NP66                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_coddii_EU527194                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_onopordifolia_LM021001_5M      GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_acanthopoda_NBsn               GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTCG-
B_cirsiifolia_RM973              GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_cirsiifolia_CK9                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTTGCGAC-GAT-GCTTCG
B_cirsiifolia_EU527207           GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_robusta_LM080701_1             GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_maritima_SR462                 GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_radula_NN1                     GCAAGGGAAGC-CTCG-TCATAGACCCTAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_decurrens_RM1189               GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_discolor_NN9                   GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-TCTTCG
B_draco_CK20                     GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGTGAC-GAT-GCTTCG
B_erysithales_K871               GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
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B_pannosa_EU527209               GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGTGAC-GAC-GCTTCG
B_ferox_var_glandulosa_1340      GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTCTCGCGAT-GAT-GCTTCG
B_cf_rhapontica_LM020406_37a_B_r GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGTGAC-GAC-GCTTCG
B_rhapontica_ssp_rhapontica_POK1 GCAAGGGAAGC-CTCG-TCATAGACCCCAAAGTGTCGTCTCGTGAC-GAC-GCTTCG
B_rhapontica_EU527207            GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGTGAC-GAC-GCTTCG
B_carduoides_NB1924_B_carduoides GCAAGGGAAGC-CTCG-TCATAGACCCCAAGGTGTCGTCTTGTGAT-GAC-GCTTCG
B_setifera_NN20                  GCTAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCTCGAC-GAC-GCTTCG
B_setifera_EU527208              GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCTCGAC-GAC-GCTTCG
B_echinacea_169                  GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCTCGAC-GAC-GCTTCG
B_echinacea_ssp_polyacantha_179  ???????????-????????????????????????????????????????????-
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B_onobromoides_EU527212          GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_annectens_EU527211             GCAAGGGAGGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGGC-GAC-GCTTCG
B_cardopatifolia_EU527213        GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTTGCGAC-GAT-GCTTCG
B_carlinifolia_LM010204_1        GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_heterophylla_var_radiata_NN8   GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_cardopatifolia_C_R303          GCAAGGGAAGC-CTCG-TAATAGACCCTA???TGTCGTCTCGCGAC-GAT-GCTTCG
B_cardopatifolia_CSW13           GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_glabrata_X48                   GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCTCGAC-GAT-GCTTCG
B_rigida_LM170601_1              GCAAGGGAAGC-CTCG-TAATAGACCCTAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_annectens_644                  GCAAGGAAAGG-CTCG-TCA-AGACCCCAACGTGTCGTCTCGCGAC-GAT-ACTTCG
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B_pinnatifida_stobaeoides_NN15   GCAAGGAAAGG-CTCG-TCATAGACCCTAACGTGTCGTCTTGTGAC-GAT-ACTTCG
B_pinnatifida_SR552              GTAAGGAAAGG-CTCG-TCATAGACCCTAACGTGTCGTCTCGTTAC-GAT-ACTTCG
B_eriobasis_EU527214             GCAAGGAAAGG-CTCG-TCATAGACCCTAACGTGTCGTCTCGCGAC-GAT-ACTTCG
B_eriobasis_EU527210             GCAAGGAAAGG-CTCG-TCATAGACCCTAACGTGTCGTCTCGCGAC-GAT-ACTTCG
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Cus_cernua_LM210706_3            CCAAGGGAAAC-CTCT-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GGTTCC
Cus_cernua_NB1896                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
Cus_cernua_RM2600                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGTGTCGTCTCGCGAC-GAT-GCTTCG
B_francisci_T707                 GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTCGTCTC?????-???-??????
B_cf_carlinopsis_LM300806_1      GCAAGGGAAGC-CTCA-TCATAGACCCCAAC?CGTTGTCTCGCGAC-GAT-GCTTCG
B_fruticosa_RM1301               GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTTGTCTCCCGAC-GAT-GCTTCG
B_fruticosa_EU527199             GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTTGTCTCGCGAC-GAT-GCTTCG
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B_spinosa_K861                   GCAAGGGAAGC-CTCT-TCATAGACCCCAACGCGTCGTCTCAAGAC-GAC-GCTTCG
B_spinosa_EU527202               GCAAGGGAAGC-CTCTATCATAGACCCCAACGCGTCGTCTCACGACTGACTGCTT--
B_coriacea_LM230204_1            CCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_angusta_POK1090                GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_angusta_NHsn                   GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_cruciata_ssp_integra_MK2637    GCAAGGGAAGC-CTCA-TCATAGACCCTAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_cruciata_AY504712              GCAAGGGAAGC-CTCA-TCATAGACCCTAACGCGTCGTCTCGCGAC-GAT-GCTTCG
B_sp_LM021106_5                  GCAAGGGAAGC-CTCA-TCATAGACCCCAACGTGTCGTCTCGTGAC-GAT-GCTTCG
B_pauciflora_NP65                GCAAGGGAAGC-CTCG-TCATAGACCCCAACGCGTCGTTTCGCGAC-GAT-GCTTCG
Cul_rigida_AY504714              GCAAGGGAAGC-CTCA-TCATAGACCCCAACGCGTCGTCTCGCGAC-GAT-GCTTCG
Cul_patula_AY504714              GCAAGGGAAGC-CTCA-TCATAGACCCCTACGCGTCGTCTCACTAC-TAT-CCTTCG
B_herbacea_LM101001_2            GCAAGGGAAGC-CTCA-TCATAGACCCCAACGTGTCGTCTCTCGAC-GAT-GCTTCG
B_herbacea_RM1176                GCAAGGGAAGC-CTCA-TCATAGACCCCAACGTGTCGTCTCTCGAC-GAT-GCTTCG
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B_spinosissima_namaensis_RM1481  GCAAGGGAATC-CTCG-TCATAGACCCCAACG??TCGTCTCTTGAC-GAT-GCTTCG
B_spinosissima_argentifolia_RM27 GCAAGGGAATC-CTCG-TCATAGACCCCAACGCGTCGTCTCTTGAC-GAT-GCTTCG
B_spinosissima_EU527200          GCAAGGGAATC-CTCG-TCATAGACCCCAACGCGTCGTCTCTTGAC-GAT-GCTTCG
B_spinosissima_AY504710          GCAAGGGAATC-CTCG-TCATAGACCCCAACGCGTCGTCTCTTGAC-GAT-GCTTCG
B_chamaepeuce_CM4144             GCAAGGGAATC-CTCG-TCATAGACCCCAAYGCRTCGTCTCTTGAC-GAT-GCTTCG
B_barbata_RM1077                 GCAAGGGAATC-CTCG-TCATAGACCCCAACGCGTCGTCTCTTGAC-GAT-GCTTCG
B_angustifolia_K979              GCAAGGGAATC-CTCG-TCATAGACCCCAACGCGTCGTCTCTTGAC-GAT-GCTTCG
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psbA-trnH alignment:

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Hirpicium_echinus_RM861          GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATACGAGTTTTTGAACTAA
Gorteria_diffusa                 ???????CATCTACAAATGGATAAGACTTTGGTCTGATTGTATACGAGTTTTTGAACTAA
Didelta_spinosa_LM160704_4       ????????ATCTACAA-TGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_armata_RM1500           GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_armata_RM1206           ????????????????????????????????TCTGATTGTATA?GAGTTTTTGAACTAA
Berkheya_barbata_RM1077          ????????????????????????????????????????????????????????????
Berkheya_carduoides_NB1924       GAAGCTCCATCTACAAATGGATAAGACTTTGGTCCGATTGTATAGGAGTTTTTGAACTAA
Berkheya_carlinifolia_LM_010204  GAAGCTCCCTCTTCAAATGGATAAGACTTTGGTCCGATTGTATAGGAGTTTTTGAACTAA
Berkheya_cf_carlinopsis_LM300806 GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_cirsiifolia_RM973       ??????????????????????????????????????TGTATAGGAGTTTTTGAACTAA
Berkheya_canescens_LM290806_32_e GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_cruciata_ssp_integra_MK GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_cuneata_LM160601_6      GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_discolor_NN9            GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_decurrens_SR473_etc     GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_fruticosa_RM1301        GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_bipinnatifida_ssp_bipin GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_herbacea_RM1176         GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_heterophylla_var_hetero ???GCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_heterophylla_var_radiat GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_codii_IVS               GGGGCGCTCCTCACAAA-GGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_insignis_MK2133         GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_multijuga_LM030103_35   ????????????????????????????????????????????????????????????
Berkheya_pinnatifida_ssp_ingrata GAAGCTCCATCTACAAAAGGATAAGACTTTGGTCCGATTGTATAGGAGTTTTTGAACTAA
Berkheya_pinnatifida_ssp_pinnati GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_buphthalmoides_C_R241_e GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_rigida_LM170601_1       GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_montana_SR464_etc       GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_rosulata_LM030103_24    ???????????????????????????????????GATTGTATAGGAGTTTTTGAACTAA
Berkheya_schinzii_CM2793         GAAGCTCCATCTACAAATGGATAAGACTTTGGTC?GATTGTATAGGAGTTTTTGAACTAA
Berkheya_seminivea_RM1140        GAAGCTCCAT?TACAAATGGATAAGACTTTGGTTTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_decurrens_RM1189_etc    GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_speciosa_SR565          GAAGCTCCATCTACAAATGGATAAGACTTTGGTTTGATTGTATAGGAGTTTTTGAACTAA
Berkheya_sp_LM0201001_2          GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAAATAA
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Berkheya_acanthopoda_NBsn_etc    GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA
Cullumia_setosa_var_setosa_RM107 GAAGCTCCATCTACAAATGGATAAAACTTTGGTTTGATTGTATAGGAGTTTTTGAACTAA
Cuspidia_cernua_NB1896           GAAGCTCCATCTACAAATGGATAAGACTTTGGTCTGATTGTATAGGAGTTTTTGAACTAA

Hirpicium_echinus_RM861          AAAAGGAGCAATAGCTTCCCTCTTGTTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Gorteria_diffusa                 AAAAGGAGCAATAGCTTCCATCTTGTTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Didelta_spinosa_LM160704_4       AAAAGGAGCAATAGCTTCCCTCTTGATA-----AAACAAGAGGGCATTATTGCTCCTTTT
Berkheya_armata_RM1500           AAAAGGAGCAATAGCTTCCCTCTTGATA-----AAACAAGAGGGCGTTATTGCTCCTTTT
Berkheya_armata_RM1206           AAAAGGA?CAATAGCTTCCCTCTTGATA-----AAACAAGAGGGCGTTATTGCTCCTTTT
Berkheya_barbata_RM1077          ????????????????????????????????????????????????????????????
Berkheya_carduoides_NB1924       AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_carlinifolia_LM_010204  AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_cf_carlinopsis_LM300806 AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_cirsiifolia_RM973       AAAAGGAGCAATAGCTTC??TCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_canescens_LM290806_32_e AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_cruciata_ssp_integra_MK AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_cuneata_LM160601_6      AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTTTTGCTCCTTTT
Berkheya_discolor_NN9            AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_decurrens_SR473_etc     AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_fruticosa_RM1301        AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_bipinnatifida_ssp_bipin AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_herbacea_RM1176         AAAAGGAGCAATAGCTTCCCTCTTGATA-----AAACAAGAGGGCGTTATTGCTCCTTTT
Berkheya_heterophylla_var_hetero AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_heterophylla_var_radiat AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_codii_IVS               AAAAGGAGCAATAGCTTCCCTCTTATTT----TATCAAAGAGGGCGTTATTGCTCCTTTT
Berkheya_insignis_MK2133         AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
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Berkheya_pinnatifida_ssp_pinnati AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_buphthalmoides_C_R241_e AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_rigida_LM170601_1       AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_montana_SR464_etc       AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_rosulata_LM030103_24    AAAAGGAGCAAAAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_schinzii_CM2793         AAAAGGAGCAATAGCTTCCCTCTTGTTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_seminivea_RM1140        AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_decurrens_RM1189_etc    AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
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Berkheya_sp_NN11                 AAAAGGAGCAATAGCTTTTCCCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_rhapontica_ssp_aristosa AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Berkheya_acanthopoda_NBsn_etc    AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Cullumia_setosa_var_setosa_RM107 AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT
Cuspidia_cernua_NB1896           AAAAGGAGCAATAGCTTCCCTCTTATTT-----TATCAAGAGGGCGTTATTGCTCCTTTT

Hirpicium_echinus_RM861          TTTTATTTAGT-----ACTCTTTTCCTTACATAGTTTCTTTAAAAATAAGAAGGGCTTTT
Gorteria_diffusa                 TTTTATTTAGT-----ACTATTTGACTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Didelta_spinosa_LM160704_4       TTTTATTTAGT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_armata_RM1500           TTTTATTTAGT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_armata_RM1206           TTTTATTTAGT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_barbata_RM1077          ????????????????ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_carduoides_NB1924       TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_carlinifolia_LM_010204  TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_cf_carlinopsis_LM300806 TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_cirsiifolia_RM973       TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_canescens_LM290806_32_e TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_cruciata_ssp_integra_MK TTTTATTTAAT-----ATTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_cuneata_LM160601_6      TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_discolor_NN9            TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_decurrens_SR473_etc     TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_fruticosa_RM1301        TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
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Berkheya_codii_IVS               TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_insignis_MK2133         TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_multijuga_LM030103_35   TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_pinnatifida_ssp_ingrata TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_pinnatifida_ssp_pinnati TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_buphthalmoides_C_R241_e TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_rigida_LM170601_1       TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_montana_SR464_etc       TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_rosulata_LM030103_24    TTTTATTTAAT-----AC??TTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_schinzii_CM2793         TTTTATTTAGT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
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Berkheya_seminivea_RM1140        TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_decurrens_RM1189_etc    TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_speciosa_SR565          TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_sp_LM0201001_2          TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_sp_NN11                 TTTTATTAAAT-----ACTATTTGCTTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_rhapontica_ssp_aristosa TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Berkheya_acanthopoda_NBsn_etc    TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Cullumia_setosa_var_setosa_RM107 TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT
Cuspidia_cernua_NB1896           TTTTATTTAAT-----ACTATTTGCCTTACATAGTTTCTTTAAAAATAACAAGGGCTTTT

Hirpicium_echinus_RM861          TATAGTTTGGTTCAATTAGCGTGTTTTATCTTTGTATTAATTGATATT------------
Gorteria_diffusa                 TATAGTTTGGTTCGATT-------------------------------------------
Didelta_spinosa_LM160704_4       TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATTTTCTCT
Berkheya_armata_RM1500           TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_armata_RM1206           TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_barbata_RM1077          TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATTTTCTCT
Berkheya_carduoides_NB1924       TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_carlinifolia_LM_010204  TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_cf_carlinopsis_LM300806 TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_cirsiifolia_RM973       TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_canescens_LM290806_32_e TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_cruciata_ssp_integra_MK TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_cuneata_LM160601_6      TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_discolor_NN9            TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_decurrens_SR473_etc     TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_fruticosa_RM1301        TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_bipinnatifida_ssp_bipin TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_herbacea_RM1176         TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_heterophylla_var_hetero TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_heterophylla_var_radiat TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_codii_IVS               TATAGTTTGGTTCGATTAGCGTGTTTTCCCTTTGTATTAATTTATATTATAATT------
Berkheya_insignis_MK2133         TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_multijuga_LM030103_35   TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_pinnatifida_ssp_ingrata TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_pinnatifida_ssp_pinnati TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_buphthalmoides_C_R241_e TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_rigida_LM170601_1       TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_montana_SR464_etc       TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
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Berkheya_rosulata_LM030103_24    TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_schinzii_CM2793         TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_seminivea_RM1140        TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_decurrens_RM1189_etc    TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_speciosa_SR565          TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_sp_LM0201001_2          TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_sp_NN11                 TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------
Berkheya_rhapontica_ssp_aristosa TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Berkheya_acanthopoda_NBsn_etc    TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Cullumia_setosa_var_setosa_RM107 TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATTATAATT------
Cuspidia_cernua_NB1896           TATAGTTTGGTTCGATTAGCGTGTTTTCTCTTTGTATTAATTTATATT------------

Hirpicium_echinus_RM861          ----------------------CTAATTAGAATATTATA-GGTTTATATATCCTTTT---
Gorteria_diffusa                 ---------------------------TAGAATATTATAAGGTTTATATATCCTTTT---
Didelta_spinosa_LM160704_4       TTGTATTAATTTATATTATAATCATAT---------ATA-GGTTTATATATTCTTTTCCG
Berkheya_armata_RM1500           -----------------ATA-T--------------ATA-GGTTTATATATCCTTTTCCG
Berkheya_armata_RM1206           -----------------ATA-T--------------ATA-GGTTTATATATCCTTTTCCG
Berkheya_barbata_RM1077          TTGTATTAATTTATATTATAATTATAT---------ATA-GGTTTATATATCCTTTTCCG
Berkheya_carduoides_NB1924       -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_carlinifolia_LM_010204  -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_cf_carlinopsis_LM300806 -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_cirsiifolia_RM973       -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_canescens_LM290806_32_e -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_cruciata_ssp_integra_MK -----------------ATAATC-------------AGA-GGCTTATATATCCTTTT---
Berkheya_cuneata_LM160601_6      -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_discolor_NN9            -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_decurrens_SR473_etc     -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_fruticosa_RM1301        -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_bipinnatifida_ssp_bipin -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_herbacea_RM1176         -----------------ATA-T--------------ATA-GGTTTATATATCCTTTTCCG
Berkheya_heterophylla_var_hetero -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_heterophylla_var_radiat -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_codii_IVS               -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_insignis_MK2133         -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_multijuga_LM030103_35   -----------------ATAATC-------------ATA-GGTTTATATATCCTTTT---
Berkheya_pinnatifida_ssp_ingrata -----------------ATAATC-------------AGA-GGCTTATATATCCTTTT---
Berkheya_pinnatifida_ssp_pinnati -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
Berkheya_buphthalmoides_C_R241_e -----------------ATAATC-------------ATA-GGCTTATATATCCTTTT---
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Berkheya_rigida_LM170601_1       -----------------ATAATC------------ATA-GGCTTATATATCCTTTT---
Berkheya_montana_SR464_etc       -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_rosulata_LM030103_24    -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_schinzii_CM2793         -----------------ATA-T-------------ATA-GGTTTATATATTCTTTTCCG
Berkheya_seminivea_RM1140        -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_decurrens_RM1189_etc    -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_speciosa_SR565          -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_sp_LM0201001_2          -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_sp_NN11                 -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_rhapontica_ssp_aristosa -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Berkheya_acanthopoda_NBsn_etc    -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Cullumia_setosa_var_setosa_RM107 -----------------ATAATC------------ATA-GGTTTATATATCCTTTT---
Cuspidia_cernua_NB1896           -----------------ATAATC------------ATA-GGCTTATATATCCTTTT---

Hirpicium_echinus_RM861          ----------------CCCAATCTTTTATGAAGTTTATTTATAATTCAATTTCAATCTA
Gorteria_diffusa                 ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTCAATCTA
Didelta_spinosa_LM160704_4       ATTTAAATATCCTTTTCCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTCAATCTA
Berkheya_armata_RM1500           ATTTATATATCCTTTTCCCAATCTTTTATGAAATTTATTTCCAATTCAATTTCAATCTA
Berkheya_armata_RM1206           ATTTATATATCCTTTTCCCAATCTTTTATGAAATTTATTTCCAATTCAATTTCAATCTA
Berkheya_barbata_RM1077          ATTTAAATATCCTTTTCCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTCAATCTA
Berkheya_carduoides_NB1924       ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_carlinifolia_LM_010204  ----------------CCCAATTTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_cf_carlinopsis_LM300806 ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_cirsiifolia_RM973       ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_canescens_LM290806_32_e ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_cruciata_ssp_integra_MK ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_cuneata_LM160601_6      ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_discolor_NN9            ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_decurrens_SR473_etc     ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_fruticosa_RM1301        ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_bipinnatifida_ssp_bipin ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_herbacea_RM1176         ATTTATATATCCTTTTCCCAATCTTTTATGAAATTTATTTCCAATTCAATTTCAATCTA
Berkheya_heterophylla_var_hetero ----------------CCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_heterophylla_var_radiat ----------------CCCAATTTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_codii_IVS               ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_insignis_MK2133         ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_multijuga_LM030103_35   ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_pinnatifida_ssp_ingrata ----------------CCCAATTTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
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Berkheya_pinnatifida_ssp_pinnati ----------------CCCAATTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_buphthalmoides_C_R241_e ----------------CCCAATTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_rigida_LM170601_1       ----------------CCCAATTTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA
Berkheya_montana_SR464_etc       ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_rosulata_LM030103_24    ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_schinzii_CM2793         ATTTAAATATCCTTTTCCCAATCTTTTATGAAGTTTATTTCCAATTCAATTTCAATCTA
Berkheya_seminivea_RM1140        ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_decurrens_RM1189_etc    ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_speciosa_SR565          ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_sp_LM0201001_2          ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_sp_NN11                 ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_rhapontica_ssp_aristosa ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Berkheya_acanthopoda_NBsn_etc    ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Cullumia_setosa_var_setosa_RM107 ----------------CCCAATCTTTTATGAACTTTATTTCCAATTCAATTTGAATCTA
Cuspidia_cernua_NB1896           ----------------CC-----TTTTATGAAGTTTATTTCCAATTCAATTTGAATCTA

Hirpicium_echinus_RM861          AAATAGATTGAAATGATAA------------------TTTTGCTTATTTATTATTATTAC
Gorteria_diffusa                 AAATAGATAAAAATGATAA------------------TTTTGCTTAT------TTATTAC
Didelta_spinosa_LM160704_4       AAATAGATAAAAATTAGAA------------------TTTTCCTTAT------TTATTAC
Berkheya_armata_RM1500           AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_armata_RM1206           AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_barbata_RM1077          AAATAGATAAAAATTAGAA------------------TTTTCCTTAT------TTATTAC
Berkheya_carduoides_NB1924       AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_carlinifolia_LM_010204  AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_cf_carlinopsis_LM300806 AAATAGATAAAAATTAGAA------------------TTTTGCTTAT------TTATTAC
Berkheya_cirsiifolia_RM973       AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_canescens_LM290806_32_e AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_cruciata_ssp_integra_MK AAATAGATAAAAATTAGAA------------------TTTTGCTTAT------TTATTAC
Berkheya_cuneata_LM160601_6      AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_discolor_NN9            AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_decurrens_SR473_etc     AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_fruticosa_RM1301        AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_bipinnatifida_ssp_bipin AAATAGATAAAAATTCTAA------------------TTTTGCTTTT------TTATTAC
Berkheya_herbacea_RM1176         AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_heterophylla_var_hetero AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_heterophylla_var_radiat AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_codii_IVS               AAATAGATAAAAATTCTAA-----------------ATTTTGCTTAT------TTATTAC
Berkheya_insignis_MK2133         AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
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Berkheya_multijuga_LM030103_35   AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_pinnatifida_ssp_ingrata AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_pinnatifida_ssp_pinnati AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_buphthalmoides_C_R241_e AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_rigida_LM170601_1       AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_montana_SR464_etc       AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_rosulata_LM030103_24    AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_schinzii_CM2793         AAATAGATAAAAATTATAAAATAGATAAAAATTATAATTTTCCTTAT------TTATTAC
Berkheya_seminivea_RM1140        AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_decurrens_RM1189_etc    AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_speciosa_SR565          AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Berkheya_sp_LM0201001_2          AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_sp_NN11                 AAATAGATAAAAATTTTAA------------------TTTTGATTAT------TTATTAC
Berkheya_rhapontica_ssp_aristosa AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Berkheya_acanthopoda_NBsn_etc    AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC
Cullumia_setosa_var_setosa_RM107 AAATAGATAAAAATTATAA------------------TTTTGCTTAT------TTATTAC
Cuspidia_cernua_NB1896           AAATAGATAAAAATTCTAA------------------TTTTGCTTAT------TTATTAC

Hirpicium_echinus_RM861          TTTAATTTCAGAAATAAGAAAGAAAAA-TA-G---AATATTTTTT----C-ATGTTAATG
Gorteria_diffusa                 TTTTATTTCAGAAATAAGAAAGAAAAA-TATGATCTTTTTTTTTTTT--C-TTGTTAATG
Didelta_spinosa_LM160704_4       TTTGATTTCAGAAAAAAGAAAGA-----TATGCTCTTTTTTTTTTTT--C-?GGT?AAGG
Berkheya_armata_RM1500           TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTT--C-ATGTTAATG
Berkheya_armata_RM1206           TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTT--C-ATGTTAATG
Berkheya_barbata_RM1077          TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTTT-C??????????
Berkheya_carduoides_NB1924       TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_carlinifolia_LM_010204  TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
Berkheya_cf_carlinopsis_LM300806 TTTGATTTCAGAAAAAAGAAAGAAAAATATGCTCTTTTTT--------C-ATGTTAATG
Berkheya_cirsiifolia_RM973       TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTTT-CCAGGTTAATG
Berkheya_canescens_LM290806_32_e TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTT-------C-ATGTTAATG
Berkheya_cruciata_ssp_integra_MK TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTT-------C-ATGTTAATG
Berkheya_cuneata_LM160601_6      TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTT-------C-ATGTTAATG
Berkheya_discolor_NN9            TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-AGGTTAATA
Berkheya_decurrens_SR473_etc     TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTT-----C-ATGTTAATA
Berkheya_fruticosa_RM1301        TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTT-------C-ATGTTAATG
Berkheya_bipinnatifida_ssp_bipin TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_herbacea_RM1176         TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTT--C-ATGTTAATG
Berkheya_heterophylla_var_hetero TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTT-------C-ATGTTAATG
Berkheya_heterophylla_var_radiat TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
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Berkheya_codii_IVS               TTTGATTTCAAAAAAAAGAAAGAAAAAA-AGGCTCCTTTTTTTTTC---CT-GGTTAATC
Berkheya_insignis_MK2133         TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTT---C-ATGTTAATA
Berkheya_multijuga_LM030103_35   TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTT----C-ATGTTAATG
Berkheya_pinnatifida_ssp_ingrata TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
Berkheya_pinnatifida_ssp_pinnati TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
Berkheya_buphthalmoides_C_R241_e TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
Berkheya_rigida_LM170601_1       TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGC--TTTT----------C-ATGTTAATG
Berkheya_montana_SR464_etc       TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_rosulata_LM030103_24    TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTTTTC-ATGTTAATG
Berkheya_schinzii_CM2793         TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTTTTC-ATGTTAATG
Berkheya_seminivea_RM1140        TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_decurrens_RM1189_etc    TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_speciosa_SR565          TTTGATTTCAGAAAAAAGAAAGAAAAA-AATACTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_sp_LM0201001_2          TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_sp_NN11                 TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTTTTT-C-ATGTTAATG
Berkheya_rhapontica_ssp_aristosa TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTTTT----C-ATGTTAATA
Berkheya_acanthopoda_NBsn_etc    TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Cullumia_setosa_var_setosa_RM107 TTTGATTTCAGAAAAAAGAAAGAAAAA-AATGCTCTTTTTTTTTT----C-ATGTTAATA
Cuspidia_cernua_NB1896           TTTGATTTCAGAAAAAAGAAAGAAAAA-TATGCTCTTTTTTTT------C-ATGTTAATG

Hirpicium_echinus_RM861          GAAAAATATAGTA--------------ATACTAGATAATACTAGATAATAGGAGAGGGGC
Gorteria_diffusa                 GAAAAATATAGTATTACAAATATAGTAATACTAGATAATACTAGATAATAGTAAAGGGGC
Didelta_spinosa_LM160704_4       GAAAAATAT?G?A--------------ATACTAGATAATACTAGATACTAGTAAAGGGGC
Berkheya_armata_RM1500           GAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_armata_RM1206           GAAAAATATA?TA--------------ATACTAAATAATACTAAATACTA?TAGAGGGGG
Berkheya_barbata_RM1077          ?????????????--------------?????????????????????????????????
Berkheya_carduoides_NB1924       CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_carlinifolia_LM_010204  CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_cf_carlinopsis_LM300806 CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_cirsiifolia_RM973       CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAAAGGGGC
Berkheya_canescens_LM290806_32_e CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_cruciata_ssp_integra_MK CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_cuneata_LM160601_6      CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_discolor_NN9            CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_decurrens_SR473_etc     CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_fruticosa_RM1301        CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_bipinnatifida_ssp_bipin CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_herbacea_RM1176         GAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
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Berkheya_heterophylla_var_hetero CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_heterophylla_var_radiat CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_codii_IVS               CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_insignis_MK2133         CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_multijuga_LM030103_35   CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_pinnatifida_ssp_ingrata CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_pinnatifida_ssp_pinnati CAAAAATATAGTA--------------ATACTAGATAATACTAGATA?????????????
Berkheya_buphthalmoides_C_R241_e CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_rigida_LM170601_1       CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_montana_SR464_etc       CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_rosulata_LM030103_24    CAAAAATAT????--------------?????????????????????????????????
Berkheya_schinzii_CM2793         GAAAAATAT?GTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_seminivea_RM1140        CAAAAATATA?TA--------------ATA?TAGATAATA?TA?ATA?????????????
Berkheya_decurrens_RM1189_etc    CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_speciosa_SR565          CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_sp_LM0201001_2          CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_sp_NN11                 CAAAAATATAGTA--------------ATCCTA?ATAATACTA?ATTCTAGAAAAGGGGC
Berkheya_rhapontica_ssp_aristosa CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Berkheya_acanthopoda_NBsn_etc    CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Cullumia_setosa_var_setosa_RM107 CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC
Cuspidia_cernua_NB1896           CAAAAATATAGTA--------------ATACTAGATAATACTAGATACTAGTAGAGGGGC

Hirpicium_echinus_RM861          GGATGTAGTCAAGYGGAT?????
Gorteria_diffusa                 GGATGTAGCCAAGTGGATCA???
Didelta_spinosa_LM160704_4       GGATGTACCCAAGGG?ATCA?GG
Berkheya_armata_RM1500           GGATGTAGCCAAGTGGATCAAG?
Berkheya_armata_RM1206           GGATGTAGCCAAGGGGAT-AAGG
Berkheya_barbata_RM1077          ???????????????????????
Berkheya_carduoides_NB1924       GGATGTAGCCAAGTGGATCAAGG
Berkheya_carlinifolia_LM_010204  GGATGTAGCCAAGTGGATCAAGG
Berkheya_cf_carlinopsis_LM300806 GGATGTAGCCAAGTGGATCAAGG
Berkheya_cirsiifolia_RM973       GGATGTACCCAAGTGGATCAAGG
Berkheya_canescens_LM290806_32_e GGATGTAGCCAAGTGGATCAAGG
Berkheya_cruciata_ssp_integra_MK GGATGTAGCCAAGTGGATCAAGG
Berkheya_cuneata_LM160601_6      GGATGTAGCCAAGTGGATCAAGG
Berkheya_discolor_NN9            GGATGTAGCCAAGGGGATCAAGG
Berkheya_decurrens_SR473_etc     GGATGTAGCCAAGTGGATCAAGG
Berkheya_fruticosa_RM1301        GGATGTAGCCAAGTGGATCAAGG
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Berkheya_bipinnatifida_ssp_bipin GGATGTAGCCAAGTGGATCAAGG
Berkheya_herbacea_RM1176         GGATGTAGCCAAGTGGATCAAGG
Berkheya_heterophylla_var_hetero GGATGTAGCCAAGTGGATCAAGG
Berkheya_heterophylla_var_radiat GGATGTAGCCAAGTGGATCAAGG
Berkheya_codii_IVS               GGATGTGCCCAAGGGCATCAAGG
Berkheya_insignis_MK2133         GGATGTAGCCAAGTGGATCAAGG
Berkheya_multijuga_LM030103_35   GGATGTAGCCAAGTGGATCAAGG
Berkheya_pinnatifida_ssp_ingrata GGATGTAGCCAAGTGGATCAAGG
Berkheya_pinnatifida_ssp_pinnati ???????????????????????
Berkheya_buphthalmoides_C_R241_e GGATGTAGCCAAGTGGATCAAGG
Berkheya_rigida_LM170601_1       GGATGTAGCCGAGTGGATCAAGG
Berkheya_montana_SR464_etc       GGATGTAGCCAAGTGGATCAAGG
Berkheya_rosulata_LM030103_24    ???????????????????????
Berkheya_schinzii_CM2793         GGA????????????????????
Berkheya_seminivea_RM1140        ???????????????????????
Berkheya_decurrens_RM1189_etc    GGATGTAGCCAAGTGGATCAAGG
Berkheya_speciosa_SR565          GGATGTAGCCAAGTGGATCAAGG
Berkheya_sp_LM0201001_2          GGATGTAGCCAAGTGGATCAAGG
Berkheya_sp_NN11                 GGATGTAGCCAAGGGGATCAAGG
Berkheya_rhapontica_ssp_aristosa GGATGTAGCCAAGTGGATCAAGG
Berkheya_acanthopoda_NBsn_etc    GGATGTAGCCAAGGGGATCAAGG
Cullumia_setosa_var_setosa_RM107 GGATGTAGCCAAGTG????????
Cuspidia_cernua_NB1896           GGATGTAGCCAAGTGGATCAAGG
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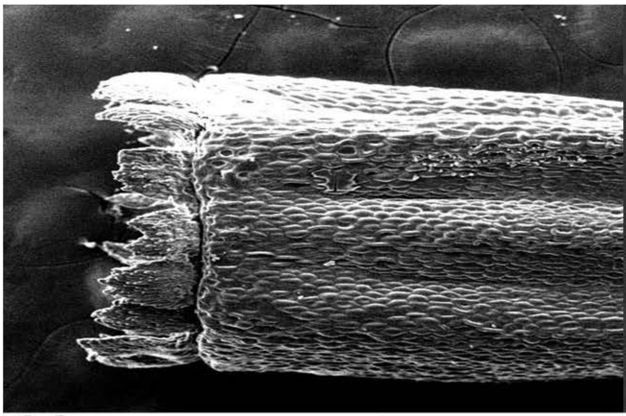
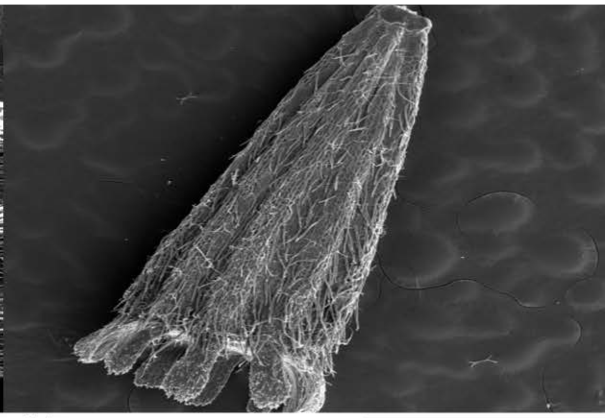
APPENDIX B: Achene plates showing achenes represented in morphological study in Chapter 3. Achenes shown with species names and numbered according to the clades which they belong tp.

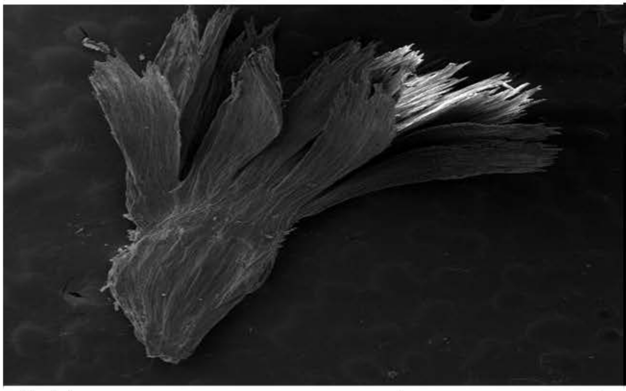
Clade 1:



1A B. circiifolia

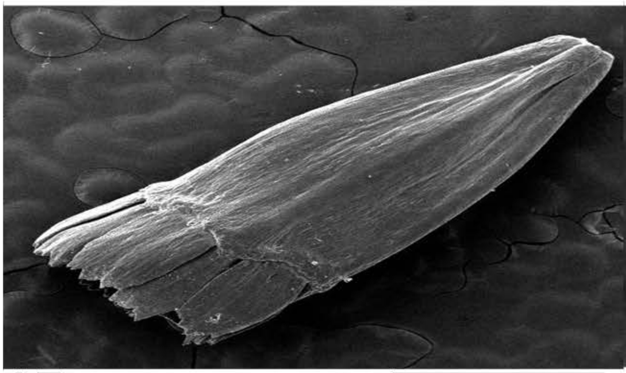


1B B. bipinnatifida

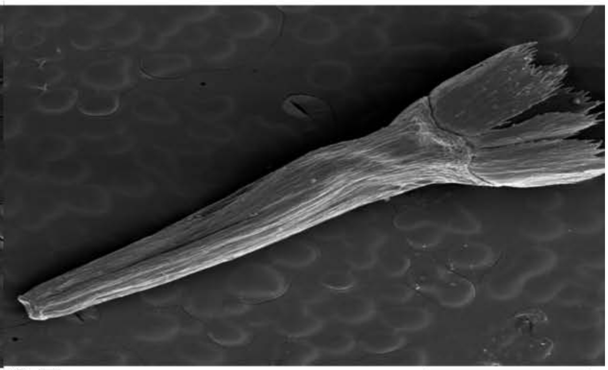


1C B. speciosa

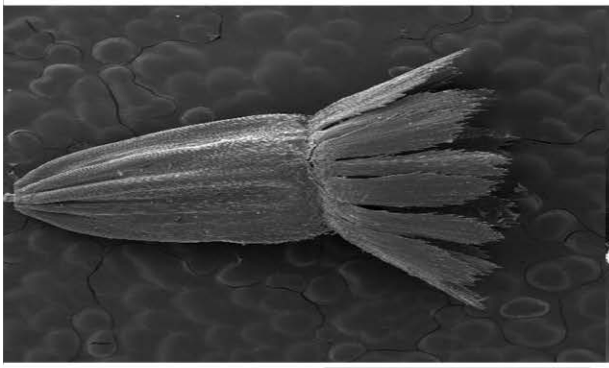
1D B. subulata



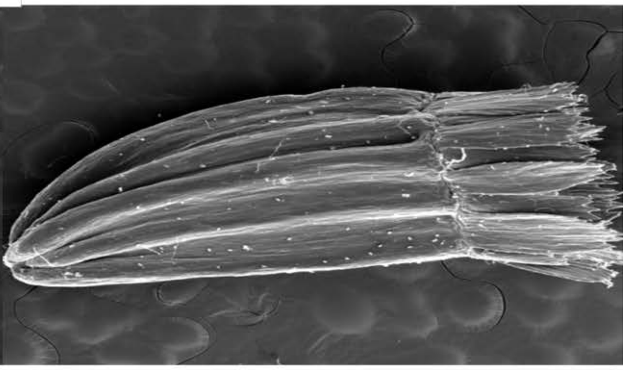
1E B. acanthopoda



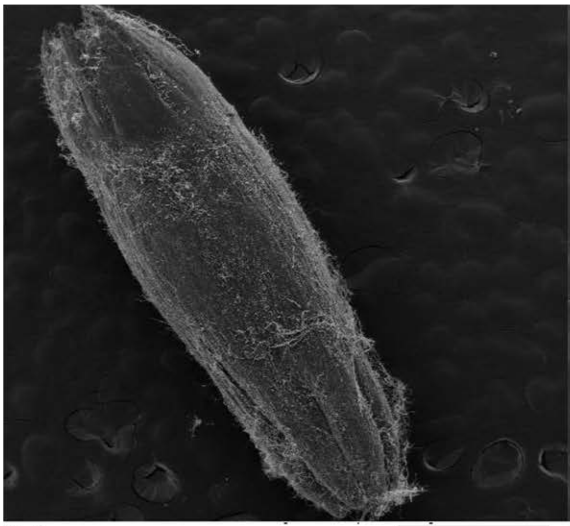
1F B.draco



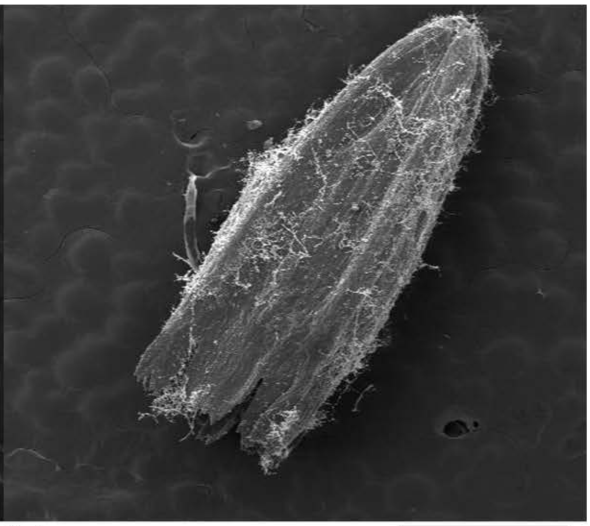
1G B. erysthales



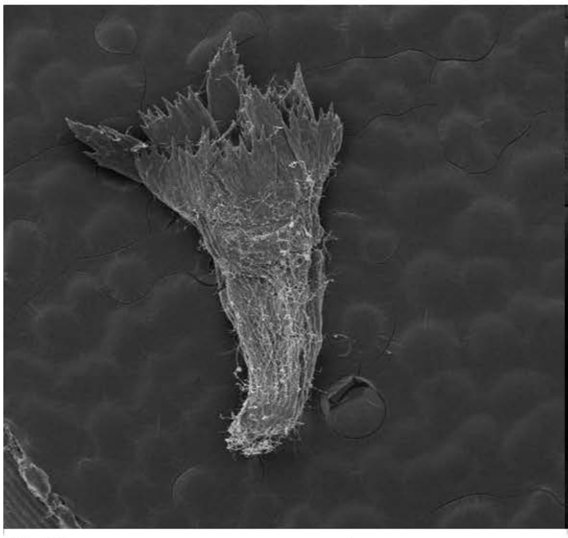
1H B. maritima



1I B. onopordifolia



1J B. robusta

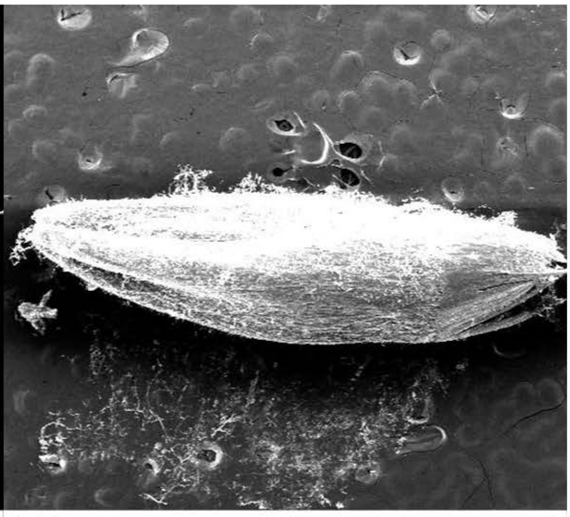


1K B. discolor

1L B. decurrens

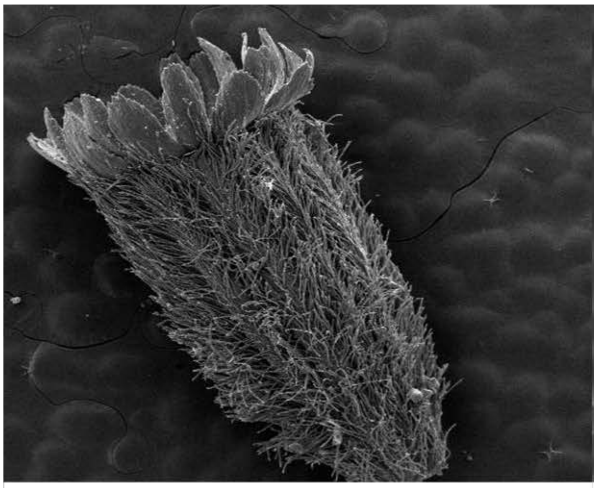
Clade 2:

2A B. echinacea

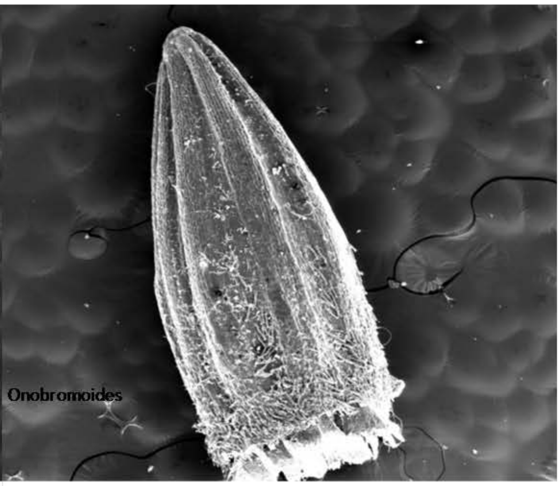


2B B. setifera

Clade 3:

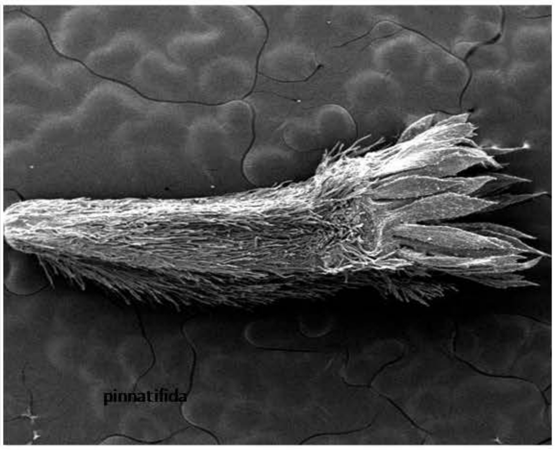


3A B. carlinifolia

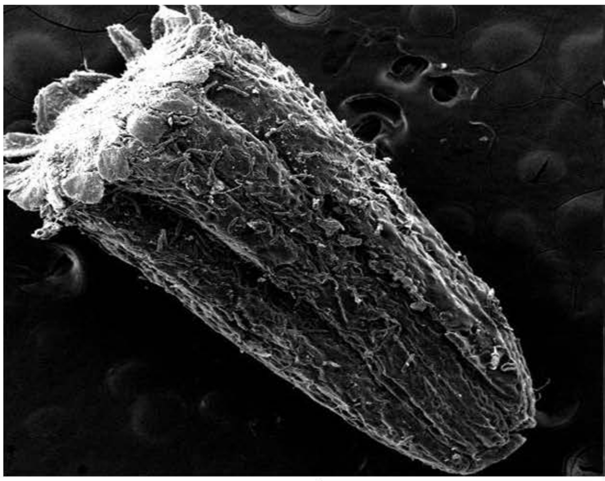


3B B.onobromoides

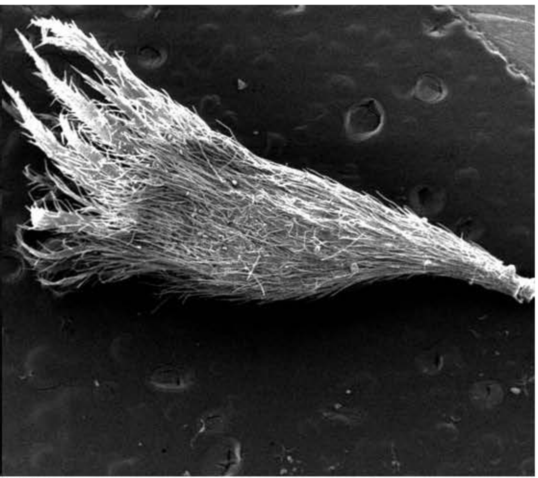
3C B. cardopatifolia



3D B. pinnatifida

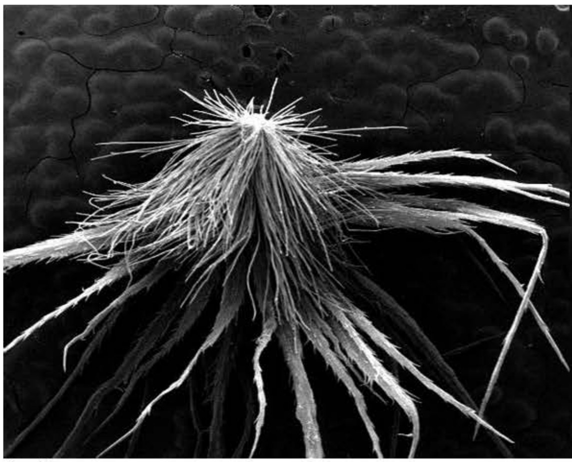


3E B. heterophylla



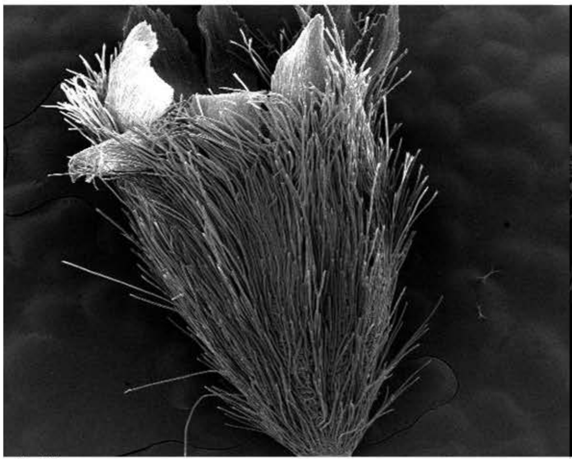
3F Cuspida cernua

Clade 4:



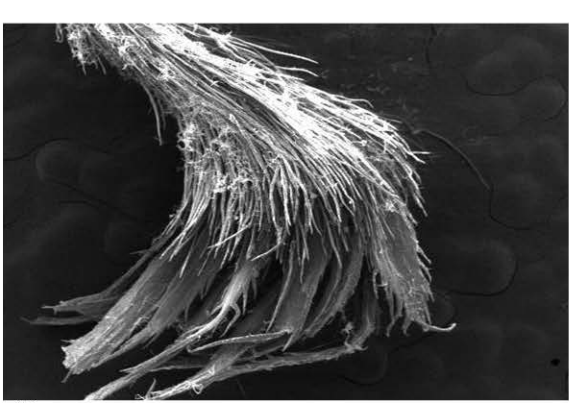
4A B. canescens

4B B. fruticosa



4C B. cruciata

4D B. coriacea



4E B. cuneata

Clade 5:

5A B. herbacea

5B B. armata

5c B. spinosissima