Chapter 1
General Introduction

Why is all nature not in confusion, instead of the species being, as we see them, well defined?

Darwin 1872: 161

Systematic biology, with its four major themes: diversity, phylogeny, biogeography and classification, forms the foundation for all other disciplines of biology (Cracraft, 2002). The earliest phase of systematics, the phase of exploration and discovery, involved the naming of plants and animals, i.e. taxonomy, and their classification into hierarchical groups - which in many instances did not reflect any shared evolutionary history (Jones & Luchsinger, 1987). Subsequently a greater interest in the role of evolution in determining the form and distribution of the diverse life on earth has developed, i.e. the study of both pattern and process.

Pattern is the "apparent orderliness of life" (as exhibited by relative degrees of similarity of organisms) and process is the mechanisms by which the pattern is generated (Eldredge & Cracraft, 1980). Evolution and speciation are two of the mechanisms in this process, where evolution is recognised as genetic change through time, and speciation, the process by which species are formed (Judd *et al.*, 1999). Evolution is descent with modification (Darwin, 1872), a dualistic process where the modification occurs within the pattern and process of descent (Knox, 1998).

An interest in developing classification systems reflecting the pattern resulting from the evolutionary processes arose in the early nineteenth century, with the first phylogenetic classification of plants that of Eichler (1883), although Haeckel had included drawing of genealogical trees in publications as early as 1866 (Stace, 1989). Darwin's and Wallace's evolutionary theories published around this time and the rediscovery of Mendel's laws of inheritance in 1905 were instrumental in promoting the development of phylogenetic classifications (Stace, 1989). Some of the noteworthy ones are Bessey (*Outlines of Plant Phyla*, 1911), Hutchinson (1926; 1973), Dahlgren (1975), Cronquist (latest version 1981) and Takhatjan (latest version 1981).

The publication of Hennig's '*Phylogenetic Systematics'* in 1966 in English laid the foundation for the modern field of phylogenetics or cladistics (Humphries & Funk, 1984), which aims to produce phylogenetic classifications objectively, in contrast to the subjective approaches of previous taxonomists. Phylogenetics has become so widely practised that it forms the basis of most evolutionary and biogeographical studies, but has also been an area that has generated unprecedented debate, controversy and argument. Most recently, cladistic patterns have been used in measuring biodiversity to prioritise areas for conservation (see Humphries *et al.*, 1995

for a review).

Conservation of the earth's biodiversity has become a priority in the scientific world, due to the realization of current and projected rates of destruction of ecosystems (Huntley, 1989). Central to this goal are questions about diversity: What is a species?; How many species are there?; Where are they distributed?; and How have these distributions changed over time?. Modern systematics therefore aims to inventory the species on earth, to discover the evolutionary history of life on earth and thereby understand relationships between species and groups of species, and to use this understanding to create predictive information systems (Cracraft, 2002; McNeely, 2002).

What is a species?

The question 'What is a species?' is therefore fundamental in the study of biodiversity and systematics. Much discussion on the nature of species has occurred over the years and numerous species concepts have been proposed. Three basic species concepts distil out the essence of most of the versions put forward: the morphological species concept, the biological species concept (Dobzhansky, 1935; Mayr, 1940) and the internodal species concept of Hennig (1966).

The morphological species concept is based on similarity between organisms, at the-macro-morphological level and/or in terms of gene structure. This includes both the classical taxonomic approach and that of pattern cladists, where shared sets of independent characters are used as a defining criterion, not as a diagnostic one (Kornet, 1993). The morphological species concept is equivalent to the traditional taxonomic approach and the phenetic species concept of Sneath & Sokal (1973) (Crisp & Chandler, 1996).

The biological species concept of Dobzhansky (1935) and Mayr (1940) is based on an innate interbreeding ability, where isolation plays a key role in delimiting species. Paterson (1978, 1980) redefined this concept in terms of a specific mate recognition system (SMRS) in his 'Recognition concept'. Van Valen (1976) focussed on ecology rather than reproduction, proposing an ecological species concept, where each species has its own unique ecological niche. However, similarity in properties (the morphological species concept) does not partition organisms into mutually exclusive species, and the biological species concept is restricted to organisms living at a particular time and place and lacks transitivity (Kornet, 1993).

Hennig's (1966: 64) concept of species delimitation (in time) by "two successive processes of species cleavage" has been referred to as the 'internodal species concept' (Nixon & Wheeler, 1990) and further refined to stipulate that "individual organisms are conspecific in virtue of their common membership of a part of the genealogical network between two

permanent splitting events or between a permanent split and an extinction event" (Kornet, 1993: 408).

The internodal species concept meets many of our intuitions about species, including the requirement for mutual exclusivity amongst groups of organisms that are morphologically distinguishable and show innate interbreeding isolation (Kornet, 1993). In addition, species are considered as historical entities, existing over a period of time. This formalisation of Hennig's internodal species is the 'Composite Species Concept' of Kornet (1993). The composite species concept therefore combines the views of species as a lineage and as a taxon (Crisp & Chandler, 1996).

A composite species is defined as "the set of all organisms belonging to an originator internodon, and all organisms belonging to any of its descendant internodons, excluding further originator internodons and their descendant internodons" (Kornet & McAllister, 1993: 78). An originator internodon is an internodon in which a character state (quality Q) achieves fixation and majority fixation is used for greatest diagnosability (Kornet & McAllister, 1993). Character states are (single or multiple) genetic properties that find a phenotypic expression. Application of the composite species concept is outlined in Kornet & McAllister (1993), in which a morphologically-defined quality Q is used to maximise practicality. A cladogram is then seen as a map of the sequence of character-state fixations in branches of the genealogical network. Segments of the cladogram do not correspond to species but to speciation events and indicate composite species (as opposed to "clado-species" which assume dichotomous speciation). It is recognised that the sequence in which the character changes/fixations occur cannot (usually) be known.

The implications of the composite species concept are that species are historically continuous and non-overlapping entities, are recognisable and do not interbreed (Kornet & McAllister, 1993). Since speciation is considered to usually occur by branching off, not by splitting dichotomously as supposed by Hennig (1966, Figure 6), some species may, and should be, paraphyletic. Hence, species need not all be monophyletic and therefore every species need not have an autapomorphy (unique derived character) distinguishing it. Instead, species will have unique sets or combinations of characters distinguishing them. This will be the case unless the ancestral species goes extinct, or sufficient time has elapsed for the original/parent species to evolve (i.e. develop a new quality Q).

The phylogenetic species concept (Nelsen & Platnick 1981; Cracraft, 1983; Nixon & Wheeler, 1990) is considered to be an operational application of the composite species concept (for organisms in the recent time slice), where unique combinations of character states are used for diagnosing species (Kornet & McAllister, 1993). Nelson and Platnick (1981:12) defined the phylogenetic species as "the smallest diagnosable cluster of self-perpetuating organisms that

have unique sets of characters". Speciation is therefore the point at which a lineage acquires an apomorphy, i.e. when a new characer is fixed (Nixon & Wheeler, 1992). As Crisp & Chandler (1996: 815) point out, this is true "even of species diagnosed by a plesiomorphy, because at some point earlier in history, every plesiomorphy was an apomorphy". Brooks & McLennan (2002) recognise two versions of the phylogenetic species concept based on how they subdivide a phylogenetic tree and how they deal with ancestral species - whether or not lineage splitting must be accompanied by character evolution (i.e. whether or not terminal branches that lack autapomorphies are distinguishable from their common ancestor). They also point out that the composite species concept differs from the phylogenetic species concept by recognising distinct species at the point of origin and fixation of each apomorphic trait, thereby ruling out the process of anagenesis in speciation - i.e. evolutionary change within a species lineage.

Despite the extensive debate concerning species concepts, there has been a distinct lack of clear communication of species concepts adhered to by biological monographers or the methods used, especially in botanical work (Luckow, 1995; McDade, 1995). Some workers (e.g. Sidwell, 1999 in *Brillantaisia* P.Beauv.) have adopted a pluralistic approach to species delimitation, applying the phylogenetic species concept of Nelson & Platnick (1981) to the majority of species in a genus, but resorting to numerical phenetics to investigate the variation in the widespread and variable species. This is an alternative approach, "essential for completing the task of producing a useful monograph" (Sidwell, 1999).

What is a genus?

In applying the binomial nomenclatural system of Linnaeus, the genus is the other essential category. In contrast to species, many early naturalists/taxonomists (including Lamarck and Bentham) did not consider genera to be natural entities, but rather arbitrary and intended to assist memorizing of names (Stevens, 2002). This convenience approach is reflected even in modern taxonomy, where genera are considered by some to represent a level of unifying features above the species; where perceptions make it beneficial to assign a distinct name (Jeffrey, 1987). However with the increased role of phylogenetics in elucidating evolutionary relationships, the category genus has been seen to signify a "group of species more closely related to one another than any are to other species" (Funk, 1985: 78). Synapomorphies diagnose these monophyletic groups and are hypotheses of homology, i.e. unique group membership characters inherited from a common ancestor (Farris, 1974).

Many traditionally circumscribed genera are paraphyletic or polyphyletic groups, defined by characters not shared by monophyletic groups. They are defined by plesiomorphies and often by characters indicating what they are not, rather than what they are (Eldredge and Cracraft, 1980). The concept of genus as a composite concept - i.e. including both monophyletic and paraphyletic entities is accepted by some (e.g. Clayton, 1983), while others advance the view

that genera should be strictly monophyletic (e.g. Stevens, 1985), arguing that the distribution of derived characters, rather than overall similarity, should be predicted by generic classification. This does not mean that the generic name is not predictive, in fact a system of classification which reflects evolutionary history as accurately as possible should have predictive value; the name should therefore communicate as much as possible about a plant (Schrire and Lewis, 1996).

Numerical approaches to systematics

The development and increased use of numerical approaches to systematics has ensued from a desire to develop methods that are objective, explicit, and repeatable, both in evaluation of taxonomic relationships and in the perception of taxa (Sneath & Sokal, 1973; Bremer & Wanntorp, 1978). It is generally acknowledged, however, that numerical techniques as used in classification and reconstructing evolution are not entirely objective as they involve numerous subjective decisions, including which measure of similarity or dissimilarity to use, weighting, what algorithms and programs to use, choice of characters, selection of sister-groups and/or outgroups (Robinson, 1986; Gower, 1988). Nevertheless, they are more transparent with testable hypotheses than traditional classification methods, where the thought processes of the taxonomist were seldom explicit.

The two main numerical approaches used are phenetics and cladistics. Phenetics makes use of as many characters as possible, usually morphological, anatomical or biochemical and equally weighted, to investigate overall similarity of organisms and thereby infer relatedness (Sneath, 1988). There are therefore no implications of relationship by ancestry (Sneath & Sokal, 1973). It is perceived that a large number of characters is required to produce a stable classification, originally advised as sixty or more (Sokal & Sneath, 1963), but later as many as is feasible, to avoid anomalous characters greatly affecting the outcome (Sneath & Sokal, 1973).

Cluster Analysis and ordination techniques are the most commonly used methods in evaluating variation amongst taxa. Cluster analysis is useful in separating organisms into groups that may be used in a classification as it imposes a hierarchical structure on the data, and has been widely used to examine geographical patterns of variation (Thorpe, 1983). The Unweighted Pair-Group Method using Arithmetic Averages (UPGMA) is the most preferred method for cluster analysis as it is space-conservative and shows the highest cophenetic correlation, regardless of the structure of the data (Sneath & Sokal, 1973). The cophenetic correlation is comparable to stress on an ordination (Sneath & Sokal, 1973), however it is not a direct measure of the degree to which the classification describes the distribution of character states (Farris, 1969).

Principal Components Analysis (PCA) is one of the most widely used ordination techniques,

advantageous in that it makes use of all the information contained in the similarity matrix to determine the component axes (Chandler & Crisp, 1998). However, PCA assumes normality of data, and so is not good for skewed data sets, at least without transformation, and cannot be used when missing values are present (Legendre & Legendre, 2003). Principal Coordinates Analysis (PCO) is recommended for data sets combining quantitative and qualitative characters (Legendre & Legendre, 2003). PCO is a form of multidimensional scaling, concerned with "the construction of a configuration of points in Euclidean space which reflects, in some sense, the relationships between a set of operational taxonomic units (OTUs) as implied by their observed proximities *whether these are Euclidean or not*" (Dunn & Everitt, 1982).

In contrast to phenetics, cladistics investigates relationships between species as inferred by ancestry (Hennig, 1966; Sneath, 1988) or by descent (Kornet, 1993), representing them by the phylogenetic branching patterns or cladograms. The relationships are expressed in topological units (number of nodes or internodes), or numbers of inferred evolutionary changes (Sneath, 1988). Cladistic principles for phylogenetic reconstruction are now commonly accepted and extensively used, although cladistic classification is still debated (de Queiroz & Gauthier, 1992; Bremer, 1994a; Brummit, 2002; Forey, 2002). The principle of parsimony, which selects the shortest route (least number of steps) as a reasonable explanation of evolution (Farris, 1983), is frequently used. Character compatability methods have been shown to perform better when there are large differences between the rates of evolutionary change in characters, whereas when rates are even, parsimony is shown to be superior (Felsenstein, 1981).

The outgroup method of rooting the tree, as described by Farris (1972; 1982) and as clarified and revised by Nixon & Carpenter (1993), is the currently accepted procedure to determine the direction of character transformations. Polarity should not be established before analysis (Nixon & Carpenter, 1993), neither using the principle that "common equals primitive", which has been shown to be untrue in many instances, nor using ingroup commonality to infer polarities (Watrous & Wheeler, 1981). The probability of finding the tree with the correct topology increases with increased "stemminess" (widely spaced internodes and short terminal branches), whereas a pectinate tree with less branching/dichotomy and more long branches that tend to become paired, tends to result in incorrect topologies (Smith, 1994).

Characters used - morphological vs molecular

Characters are the basic units by which evolutionary transformation is observed and evolutionary history traced. A character is a group of states that are considered to be modifications or alternate forms of the same thing, derived from a corresponding state in a common ancestor, and are therefore homologous (Platnick, 1979; Swofford & Olsen, 1990). Morphological and anatomical characters were initially used in cladistic analyses, but with the

advent of molecular techniques, a new source of data (DNA and nucleic acid sequences) became available. It has been argued that molecular data is superior to morphological in that it provides a larger amount of information and is therefore more reliable (Hillis, 1987; Scotland *et al.*, 2003), but Lee (2004) has shown that the number of phylogenetically informative positions in a molecular data set may be comparable with that in a morphological data set. It has also been argued that molecular data sets are superior as one does not need to assume homology for different structures, but the use of sequence data in phylogenetic analysis requires positional homology, i.e. the nucleotides at a given position in the taxa under study should all trace their origin to a single position in a common ancestor, which usually requires insertion and deletion events to be postulated (Swofford & Olsen, 1990). One distinct advantage of using molecular rather than morphological data is that the difficulties of dealing with quantitative data in terms of creating discrete character states from continuous variation are not present when dealing with molecular data (Lee, 2004). However problems like inadvertently dealing with paralogous genes are a pitfall unique to using molecular data sets (Donoghue & Sanderson, 1992). Therefore, the view that phylogenies should be based on molecular data alone (Gottlieb, 1988; Systma *et al.*, 1991) is rebutted by many other authors (Donoghue & Sanderson, 1992).

Another hot issue for debate has been whether or not to combine different data sets in phylogenetic analyses. There has been a growing awareness that to rely on a single data set may result either in insufficient phylogenetic resolution or misleading inferences (Wendel & Doyle, 1998) and it has become common practice to combine a number of different data sets (e.g. Olmstead & Sweere, 1994; Flores-Villela *et al.*, 2000; Cannon & Manos, 2001). However, there is acknowledgement that different character sets may have different underlying evolutionary histories and therefore result in different phylogenetic reconstructions for the sampled taxa (Wendel & Doyle, 1998). Some of these differences may be due to reticulate evolution resulting from hybridization between species; lateral gene transfer (in bacterial evolution); microevolution of intraspecific populations, involving genetic differentiation of allopatric populations; homoplasy (phylogenetic similarity resulting from evolutionary convergence) and host transfer in host-parasite relationships (Legendre & Makarenkov, 2002). Phylogenetic trees or cladograms are based on the premise that there is a unique relationship between organisms and their common ancestor and cannot account for reticulate evolution which violates this cladogenic model. Both of the two approaches to dealing with different data sets (outlined below) base their method on the assumption that there is an underlying cladogenic process and neither takes reticulate evolution fully into account.

The two main approaches advanced for gaining an overall estimate of phylogeny based on two or more data sets are the consensus approach and the combined approach (de Queiroz, 1993). The consensus approach involves obtaining estimates of the phylogeny separately for each data set and then obtaining a consensus tree from them. In the combined approach, data sets are

combined from the beginning and a phylogenetic analysis performed based on the combined data set. Both methods have their advantages and limitations (de Quieroz, 1993), and despite considerable debate around the topic regarding the optimal usage of multiple data sets (Hillis, 1987; Kluge, 1989; Barret *et al.*, 1991; Swofford, 1991; Bull *et al.*, 1993; Nelson, 1993; de Queiroz *et al.*, 1995; Wiens, 1998; Levasseur & Lapointe, 2001), no clear consensus has emerged. The partition homogeneity test of Farris *et al.* (1995) has been developed to measure congruence of data sets and is often used as a guide as to whether or not they should be combined. However, it has been noted that validated tests that pinpoint the cause of heterogeneity among data sets are needed (de Queiroz *et al.*, 1995).

Various measures used to test the confidence limits of the nodes of cladograms have been developed. These include the number of characters supporting a node, where an increased number indicates greater confidence in the node (Hennig, 1979; Linder, 1991), but also the nature of these characters - whether they are homoplasious or not (Linder, 1991). The consistency index (CI) is commonly used to indicate the level of homoplasy in a tree (Judd *et al.*, 1999). The CI is the minimum amount of possible evolutionary change divided by the actual tree length. Although useful, the CI fails to take into account where on a cladogram a character transformation occurs, so the retention index (RI) is usually also used (Skelton & Smith, 2002). The RI is the maximum number of steps minus the observed number of steps (i.e. actual length) divided by the maximum number of steps minus the theoretical minimum number of steps. The RI is therefore a measure of the degree to which the various character transformations are retained by succeeding taxa up the cladogram (Skelton & Smith, 2002).

The bootstrapping approach of Felsenstein (1985) involves randomly resampling the data set and re-analysing the random samples, and is a measure of the robustness of a node. Although the bootstrap is widely used, it is a controversial method for estimating confidence limits due to its not meeting a number of theoretical statistical requirements and also because of debate around the issue of "whether or not an unknown parameter, such as a tree, can have probabilities (confidence limits) associated with it" (Sanderson, 1995). A more recently developed index of support, Bremer support, is a measure of how persistent the nodes in the most parsimonious trees are in successively less parsimonious trees (Bremer, 1994b). The Bremer support is the number of extra steps it takes to collapse a node - the greater the number of steps, the more robust it is. The value gives a relative indication of how unparsimonious it would be to propose alternative groupings involving *a priori* assumptions regarding homoplasy (Skelton & Smith, 2002).

Biogeography

Understanding evolutionary histories of populations and species involves looking at their current and past distribution patterns. Biogeography has been defined as the science that endeavours to describe and interpret the geographic distributions of organisms (Avise, 2004),

thereby attempting to understand the biological and physical processes (both ecological and evolutionary) that have shaped the spatial arrangements of the species and biotas on Earth (Cox & Moore, 1993). Therefore after the systematics of organisms has been addressed, biogeographers ask a simple question: what lives where, and why? (Nelson & Platnick, 1981; Parenti & Humphries, 2004). Distribution maps can provide answers to the first question, the second question (why?) requires analysis and a broad understanding of the history of regions, the ecological requirements and reproductive practices of species (Parenti & Humphries, 2004).

Very importantly, biogeography provides information for regional diversity studies, with a focus on biodiversity of ecosystems, habitats and hotspots, vital for conservation planning and implementation (Walter, 2004). Conservation efforts have also focussed on Centres of Diversity, Centres of Endemism, hotspots - where high levels of human impact coincide with areas of high (plant) species diversity (Myers *et al.*, 2000; Küper *et al.*, 2004), and identification and conservation of rare and endemic species.

Two processes are generally recognised as being instrumental in forming basic global biogeographic patterns - dispersal and vicariance (Parenti & Humphries 2004). Disjunctions of organisms may therefore be explained by dispersal across pre-existing barriers or by the appearance of barriers fragmenting ancestral species ranges, i.e. vicariance (Humphries & Parenti, 1986). The 'dispersalist' school has its roots in the Linnaean and Darwin-Wallace traditions, but the idea that organisms originated in one area and migrated to others was contested as early as 1805 by von Humboldt and Bonpland, convinced instead that the history of the earth was reflected in the distribution of organisms (Humphries & Parenti, 1986). This view was further developed by the pangeographer, Croizat (1952; 1958), who identified tectonic change as the major causal explanation for different areas containing different species. Disjunctions were therefore seen as the result of tectonic change and representing the ranges of former taxa (Humphries & Parenti, 1986).

Both views have been applied in interpreting the distribution of the African flora - with the role of long distance dispersal being used to explain the composition of afroalpine flora (Hedberg, 1969; White, 1983a; White 1993). The migration of the flora from central Africa to the Cape was favoured by Levyns (1964) versus the notion that the Cape Flora (or its precursor) covered a large continuous area of the African continent, became fragmented and remained in tropical Africa only in montane areas (Wild, 1964).

Werger (1978, 1983) notes that past changes in climate have been the main determining force in the current distribution of vegetation in Africa. During the Quaternary, a series of glacial and inter-glacial periods greatly influenced the climate of South Africa, which, during glacial periods, would have been much wetter and cooler with more frequent and more severe frosts

in the central, western and southern parts, whereas the tropics would have been drier and cooler. The interior plateau of South Africa would have been covered by an alpine grassland similar to that in the southern parts of the eastern escarpment and the arid Karoo would have been much further north (Werger, 1978). Thus, a westward movement of vegetation from the eastern escarpment across the central plateau region is proposed, leaving "islands" of anomalous vegetation types on the mountains and in wetter areas once the drying, warming effects of the inter-glacial had made their mark.

Conservation and Rarity

Systematics has a key role to play in conserving biological diversity, by the predictive power of natural classification and in helping to set priorities for conservation (Vane-Wright, 1996). A number of different approaches in setting priorities for conservation have been taken in the past, mainly based on patterns of species richness and/or levels of endemism in a region (e.g. Oliver *et al.*, 1983; Cowling *et al.*, 1992). Other methods take phylogenetic relationships into account, thereby gaining an understanding of the evolutionary component of biodiversity and helping us to identify and preserve evolutionary potential (Brooks *et al.*, 1992).

In addition to maximising habitat diversity, it has been proposed that conservation areas should maximise 'taxic diversity', in which the number of clades in a cladogram of a particular group is maximally conserved rather than the number of species (Vane-Wright *et al.*, 1991). Others (e.g. Faith, 1992) have proposed that character diversity, rather than phylogenetic spread, should be maximised.

Amongst the criteria used for the quantification of biodiversity are the numbers of endemic species and numbers of rare, vulnerable or endangered species (Beentje, 1996). The number of endemic species is an important contributing factor, when endemic implies a limited distribution range as in the Centres for Plant Diversity (CPD) project, where the term endemic has been applied as pertaining to a specific phytochorion (Beentje, 1994). Seven centres of plant diversity have been identified in southern Africa (the region south of the Kunene, Okavango and Limpopo Rivers), under the auspices of the IUCN's CPD project based on combined criteria of high species richness and high levels of endemism. All of these centres of diversity are under threat from large-scale habitat modification and so are referred to as 'hotspots' by Cowling & Hilton-Taylor (1994), who identify an eighth hotspot - the Wolkberg Centre of Matthews *et al.* (1993).

Rarity is also an important consideration in prioritising conservation areas and activites, but rarity listings are lacking for most plant families (Beentje, 1994). Rarity can be interpreted in many ways. In the context of community and population biology, rarity is usually understood in terms of restricted distribution and/or numbers in an area or region, i.e. low abundance and/or small ranges (Gaston, 1994). Habitat specificity, in addition to geographic range and

local population size, has also been used as a criterion for assessing species rarity (Rabinowitz, 1981, 1986).

At large scales, the concept of rarity is closely linked to that of endemism (Gaston, 1994), but the concepts are not interchangeable. According to Kruckeberg & Rabinowitz (1985), "the narrow or local endemic is the one that best fits the colloquial notion of rarity". Version 3.1 of the *IUCN Red List Categories and Criteria* (2001) no longer has 'Rare' as a category, but because abundance and range are negatively correlated with persistence, these taxa are more prone to extinction. Rare species may occur in areas that are not species-rich and so their identification and distribution are useful tools in prioritising conservation areas (e.g. in the Cape Floristic Region; Rebelo and Tansley, 1993).

Causes for rarity of individual species include the ability to exploit only a narrow range of environmental conditions or the availability of suitable conditions being highly restricted (Gaston, 1994). This introduces the concept of the ecological niche. In addition to ecological factors, the evolutionary history of the organism plays a role in determining its distribution and hence its status as rare. The perception of rarity may also be a taxonomic artefact due to recognition of a taxon at an inappropriate level in the hierarchy (Fiedler, 1986).

Systematics of Cineraria

Cineraria L. is a member of the largest tribe in the Asteraceae, Senecioneae Cass., comprising ca. 3 200 species in 120 genera in three subtribes (Bremer, 1994a). It occurs mainly in the temperate regions and higher elevations of the tropics (Barkley, 1985), yet is nevertheless cosmopolitan. It was previously thought that the Senecioneae (and *Senecio* in particular) were the ancestors of the entire family Asteraceae (Small, 1919), but subsequent cladistic analysis has placed the tribe within the apomorphic subfamily Asteroideae (Bremer, 1994a). The Senecioneae have been traditionally loosely characterised by an epaleate receptacle and a pappus of capillary bristles. A more narrowly circumscribed group is now recognised by a uniseriate (or sometimes biseriate) involucre, with or without an outer calyculus of smaller bracts (Bremer, 1987). *Cineraria* has balusterform (dilated) filament collars in its stamens, discrete stigmatic areas and a chromosome number of 10, and is therefore a senecioid member of the subtribe Senecioninae (Nordenstam, 1978; Bremer, 1994a).

Phylogenetic studies have hypothesised close relationships between *Cineraria* and *Pericallis* D.Don from the Canary Islands (Pelser *et al.*, 2001; Swenson & Manns, 2003), and with *Dendrosenecio* (Hauman ex Hedb.) B.Nord. from the mountains of tropical and equatorial Africa (Knox & Palmer, 1995). Nordenstam (1978) was the first to propose a possible common ancestor for *Cineraria* and *Pericallis*, a genus more senecioid than cacalioid, despite its chromosome number (x = 30) and non-yellow flower colour. Knox and Palmer (1995) noted that a large number of restriction sites separated *Dendrosenecio* from *Cineraria*, very

likely indicating that other more closely related genera may occur between them. The position of *Cineraria* in the Senecioneae in regard to putative sister groups is here more fully investigated.

Cineraria is distinguished mainly by its compressed cypselae (Hilliard, 1977) and palmate venation of its leaves (Bremer, 1994a). Its centre of diversity is in southern Africa, but it occurs from the Cape Peninsula to the highlands of Ethiopia throughout the eastern African Afromontane archipelago as described by White (1978, 1983b). One species, *C. abyssinica*, extends from Ethiopia into the highlands of Yemen and Saudi Arabia and *C. anampoza* is endemic to Madagascar. *Cineraria* is essentially an afromontane genus, but it descends to sea level in the south-western Cape, exhibiting an 'African track' distribution pattern (Linder *et al.*, 1992).

Cineraria has not previously been monographed and numerous taxonomic problems existed in the genus. Currently, 35 species are recognised (Chapter 6), whereas previously the genus included about 50 and a number of undescribed species existed. The variation in a number of species complexes or highly variable species required investigation, viz. *C. deltoidea*, *C. lobata*, *C. aspera, C. erosa* and *C. erodioides*, and a number of species were poorly known and/or did not appear to conform with key generic attributes: *C. dregeana, C. exilis*, *C. mitellifolia*, *C. hederifolia, C. pedunculosa, C. argillacea, C. othonnoides*, *C. microglossa*, *C. purpurata*. A number of manuscript names were in circulation and specimens not matching existing species descriptions remained unidentified in herbarium collections. Certain high altitude species (*C. sebaldii*, Cufodontis, 1968) or forms of species (*C. geifolia* from the Drakensberg, *sensu* Hilliard, 1977) were recognised, but have been shown to be part of the variation in other species. Clearly a revision of *Cineraria* was required with clarification of its generic circumscription. Phylogenetic analysis has assisted with understanding infrageneric structure and clarifying the position of *Cineraria* within the Senecioneae.

As noted, only one species in *Cineraria* is widespread throughout the eastern mountains of Africa and a few are widespread in South Africa. A number are known to be endemic to certain regions and a few have been categorised as rare, endangered or data deficient (Scott-Shaw, 1999; Pfab & Victor, 2002). *Cineraria* occurs in six of the seven centres of diversity identified by the CPD project of the IUCN in southern Africa and in seven of the eight hotspots (*sensu* Cowling & Hilton-Taylor, 1994). It does not occur in the Kaokoveld Centre (see Van Wyk & Smith, 2001 for map of boundaries), although it does occur on the bordering Serra da Chela Plateau near Huila in Angola and also on the more southerly Brandberg Massif in Namibia, which has a number of affinities with the Kaokoveld Centre (Van Wyk & Smith, 2001). *Cineraria* occurs mainly on the mountains in these centres, and many species appear to be associated with specific geological formations, within certain ranges of altitude and commonly on the southern and south-eastern aspects (Cron & Balkwill, 1997).

The aims of this project were therefore to investigate the phylogeny of *Cineraria* and use the phylogenetic estimation to clarify its generic circumscription and elucidate its position in the Senecioneae, to examine its species limits and revise the genus *Cineraria*, analyse its biogeography and identify rare and threatened species for conservation purposes.
The objectives associated with these aims were:

- To use the phylogenetic approach to delimit the genus *Cineraria* as an homologous entity, unified by diagnostic apomorphic characters, and to investigate possible infrageneric level classification.

- To further elucidate the position of *Cineraria* within the Senecioninae with regard to sister groups.

- To investigate variation within a number of polymorphic species or species complexes in *Cineraria* using the phenetic approach.

- To appraise the specific limits in *Cineraria* by applying the phylogenetic species concept (the practicable version of the composite species concept) and assess its applicability.

- To produce a monograph of the genus *Cineraria*.

- To investigate distribution patterns within *Cineraria* and to hypothesise a reconstruction of its biogeographic history.

- To investigate levels of rarity and endemism in *Cineraria*, to identify some of the factors contributing to rarity in *Cineraria* and to highlight implications for conservation.

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