

## CHAPTER 2: SPECIES CONCEPTS AND TAXONOMIC EVIDENCE

### 2.1 Species concepts

#### 2.1.1 Introduction

The species is the fundamental category of taxonomic hierarchy and the building blocks of classification (Stuessy, 1990). It is an artifact of human thought to create order in diversity. Species are defined by species concepts (Mayr, 2002). Many different concepts exist because the variation of life seen in nature is diverse and complex and the philosophical views of taxonomists differ, so much so, that not one concept or definition is satisfactory and unanimously accepted by all (Donoghue, 1985). A brief review of selected species concepts is therefore necessary before one can decide what concept or combination of concepts will be valuable in classifying a specific group under study. Especially in the case of the Plantae, the species concepts for other kingdoms do not hold (Wheeler & Meier, 2000) and combinations of species concepts often provide the most user-friendly classification systems (Lebatha *et al.*, 2006).

#### 2.1.2 Morphological Species Concept

The morphological species concept is also known as the morphospecies, classical phenetic species [phenetic refers to characters of an organism that can be observed and measured (Ridley, 2004b)] or Linnaean species concepts (Mayden, 1997). This concept defines a species as a group of organisms whose morphological and phenetic characters differ from that of other groups of organisms.

The degree of morphological variation is therefore used to determine whether certain individuals belong to the same or a different species (Mayr, 1982). Although the morphological species concept does not examine the species in reproductive terms, Stuessy (1972) and Hull (1970) state that the morphological discontinuities recognized between species do reflect biological limits of isolation, commonality of

interbreeding and genetic divergence due to the connection between character cohesion and dispersal mechanisms.

The morphological species concept could be misleading, as it may lead to the recognition of new species when polymorphic diversity within a species is encountered, or the recognition of a single species when morphologically very similar species are encountered or when two populations have only recently evolved from a common ancestor (Ridley, 2004a & b). It does not treat species as historical entities that form lineages, which means that the definition of a species will change as the species changes through time and descent (Cladridge *et al.*, 1997). Cladridge *et al.* (1997) are of opinion that the morphological species concept is not a concept but rather a method of description.

### **2.1.3 Ecological Species Concept**

Organisms are adapted to the resources they exploit and the habitats they occupy (Ridley, 2004b). The ecological species concept emphasizes ecologically based natural selection in the maintenance of species (De Queiroz, 1998) and defines a species as a clusters of organisms utilizing different ecological niches, as formulated by Van Valen (1976): “A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range”.

Only species that occupy sufficiently different niches can coexist, and should their niches be the same or nearly so, the superior competitor could drive the inferior competitor to extinction (Ridley, 2004b). Coyne & Orr (2004) find this problematic and argue that the species forced to extinction was not a species at all. They also state that some groups can coexist as distinct entities in sympatry without gene flow, even if their adaptive zones are identical.

Andersson (1990), however, finds it justifiable to use habitat differences as a criterion to decide whether or not to give taxonomic recognition to a morphotype for which phenetic criteria are not conclusive, as Retief *et al.* (2008) found with *Euclea sekhukhuniensis* Retief, Siebert & A.E. van Wyk, which was previously thought to be

a hybrid between two different species which occupied different habitat types. The subsequent new species was an ecologically adapted taxon which evolved through natural selection in an ecotone.

#### **2.1.4 Biological Species Concept**

The biological species concept states that species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr, 2002). This concept rests on the hypothesis of cohesion (a group of interbreeding populations) and reproductive isolation (individuals seek and recognize one another for mating and so prevent gene flow between different populations) (Stuessy, 1990; Mayden, 1997). Interbreeding is therefore of prime importance in evolution, and breeding determines whether morphological or ecological divergence can occur. Organisms remain similar because they interbreed often enough and distinct morphological units arise that are maintained by barriers that prevent interbreeding with other related organisms (Donoghue, 1985).

The biological species concept is only applicable to sexually reproducing organisms (Mayr, 2002) and poses difficulties in the determination of interbreeding among populations, the real extent of gene flow among populations and in determining reproductive barriers (Stuessy, 1990). It is not applicable to the species of flowering plants that show interspecific hybridization or to asexual and allopatric forms (Gornall, 1997; Stuessy, 1990).

Stuessy (1990) is of the opinion that the biological species concept is not needed for practical taxonomy, but for evolutionary taxonomy from which evolutionary hypotheses can be developed and to stimulate workers dealing with preserved specimens to consider and discuss broader evolutionary implications of the relationships they see and document.

It has been suggested that the biological species concept should be revised as reproductive isolation is an epiphenomenon of secondary interest (Wu, 2001), but this idea is rejected on the basis that our current knowledge of the genetics of speciation is still insufficient (Rundle *et al.*, 2001).

### **2.1.5 Phenetic Species Concept**

Phenetics describes the relationships between organisms based on overall similarities and differences, without weighting the characters that are considered to be derived from a common ancestor. The resulting groups or clusters can then be defined as a species (Stuessy, 1990).

The phenetic species concept defines a species as a group of organisms that are phenetically similar and distinct from other groups of organisms (Mayden, 1997; Ridley, 2004b). It treats species as classes and not lineages and should the species change through descent, then the species have to be revised (Mayden, 1997).

Phenetics links closely with numerical taxonomy. Numerical taxonomy mathematically analyses the variation in a large number of characters in a group of organisms. Numerical taxonomists therefore define a species as a set of organisms of phenetic distinctness. This approach is problematic as several methods may be used to recognize phenetic clusters and these methods can result in different clusters, necessitating an arbitrary choice between different procedures (Ridley, 2004b).

Ridley (2004b) is of the opinion that the biological, phenetic and ecological species concepts are related, because individuals that are adapted to similar niches are most likely to be phenetically similar, because they share phenetic characters that are used to exploit the ecological resource. Individuals that interbreed are also likely to be phenetically similar.

### **2.1.6 Phylogenetic Species Concept**

Phylogenetics is the study of the stages in the evolutionary history of organisms. An outgrowth of this, and the general need among researchers for a lineage definition of a species that is process free, has led to the development of the phylogenetic species concept (Mayden, 1997; Coyne & Orr, 2004). At least four phylogenetic species concepts are currently recognized, that is, the Hennigian Species Concept, the Autapomorphic Species Concept, the Genealogical Species Concept and the

Phylogenetic Species Concept, each placing emphasis on a different aspect of the phylogenetic theory (Davis, 1995).

The most accepted version is the phylogenetic species concept of Cracraft (1983), where species are defined as a group of organisms which are diagnosably distinct and which have a genealogical pattern of ancestry and descent. Diagnosably distinct groups are recognized on the basis of one or more diagnostic characters. These diagnostic characters are mainly morphological, but any attributes of the organism, e.g. DNA sequences, can be used (Cracraft, 1989; Coyne & Orr, 2004). This is problematic as it would imply that, for example, every population with a slight difference in colour, or a single nucleotide difference in the DNA sequence, is a different species, which would increase the number of species recognized tremendously and illogically (Coyne & Orr, 2004).

Unlike the Autapomorphic version which argues that the species should be monophyletic and recognized on the basis of apomorphic characters, Cracraft (1989) argues that the phylogenetic species recognized will be monophyletic, unless there is an error, and that it is not necessary for the diagnostic characters to be apomorphic since species may be distinct from other species and yet not possess characters that can be hypothesized as derived. Cracraft (1989) is of the opinion that it provides a theoretically coherent ontology for systematic and evolutionary biology.

### **2.1.7 Evolutionary Species Concept**

The most theoretically significant of the species concepts that accommodates all types of organisms according to Mayden (1997), is the evolutionary species concept, as defined by Wiley (1978). Wiley's (1978) evolutionary species concept defines a species as a single lineage which maintains its identity from other lineages and has its own evolutionary tendencies.

The concept does not consider species as classes, nor does it focus on species as ecological entities. It does not require knowledge of changes in a specific mate recognition system nor are there thresholds for particular attributes needed for the existence of a species. Reproductive isolation is considered a derived attribute from

plesiomorphic status of reproductive compatibility and reproductive success is uninformative (Mayden, 1997).

The concept is therefore capable of dealing with species as spatial, temporal, genetic, epigenetic, ecological, physiological, phenetic and behavioural entities (Coyne & Orr, 2004).

The above overview of the different species concepts is only brief, giving the general idea of the concepts as well as the main pros and cons, but there are various authors who have published numerous papers that give lengthy discussions about the application of each concept (e.g. Andersson, 1990; De Queiroz & Donoghue, 1990; Nixon & Wheeler, 1990; Andersson, 1992; Bremer & Eriksson, 1992; Davis & Nixon, 1992; Funk, 1992; Grant, 1992; Lidén, 1992; Baum & Donoghue, 1995; Lucknow, 1995; Mallet, 1995; McDade, 1995; Olmstead, 1995; Wiens & Servedio, 2000; De Queiroz, 2007). As it is not the purpose of this chapter to give an in depth philosophical discussion of each concept, these articles will not be discussed further here.

Considering these concepts, however, one may raise the question as to which species concept is currently used in the Nyctaginaceae.

### **2.1.8 Species Concepts currently used in the Nyctaginaceae**

The species concept currently used is the morphological species concept. Morphological characters are used to distinguish between the different genera and species, and to divide the genera into different tribes (Bogle, 1974; Bittrich & Kühn, 1993; Zomlefer, 1994; Judd *et al.*, 2002). There are, however, great controversies regarding the delimitation of species based on morphology. For instance, Fosberg (1978) states that *Boerhavia senso lato* is very different in habit from other genera in the family, but closer inspection reveals four groups that can be recognized as distinct genera, namely, *Anulocaulis*, *Commicarpus*, *Cyphomeris* and *Boerhavia senso stricto*.

Many species within the family are pollinated by hawkmoths (Levin *et al.*, 2001) and Spellenberg (2000) reports self-pollination in *Boerhavia* and some *Mirabilis* species.

Woodson (1961) speculates that interspecific hybridization may take place between species. Since this hypothesis has not yet been tested and the extent to which species interbreed or not interbreed is not known, the biological species concept can therefore not be applied.

Phylogenetic studies have only recently been conducted for the Nyctaginaceae (Levin, 2000; Douglas & Manos, 2007). The small number of genera and the small sampling sizes of the genera were not sufficient to make definite conclusions, but rather provided a general idea of what the relationships between genera might be (Levin, 2000; Douglas & Manos, 2007). Recently analyses, however, were sufficient to reclassify the family into monophyletic tribes (Douglas & Spellenberg, 2010), but further phylogenetic research is still necessary before the phylogenetic species concept can be applied.

## **2.2 Taxonomic evidence (useful characters)**

### **2.2.1 Introduction**

Taxonomists use a wide array of data to compile a classification system and any data derived from any part of the organism during any stage of its development which shows differences between species, may be considered to be of taxonomic significance (Judd *et al.*, 2008; Stace, 1980). These data are derived from various disciplines in plant biology, such as morphology, anatomy, palynology and molecular biology (Woodland, 1997). A brief review of the types of taxonomic evidence that are meaningful for the classification of a target group is necessary before one can decide what method or combination of methods will be valuable in generating diagnostic characters for a given group.

### **2.2.2 Morphology**

Morphology is the external form or appearance of a plant and plays a fundamental role in practically all biological disciplines (Woodland, 1997; Judd *et al.*, 2008). Morphology was the first taxonomic evidence used in classification systems and its significance was already evident in ancient, artificial classifications. Morphology

provides the characters mostly used in classification keys and descriptions (Stuessy, 1990) e.g. *Oxalis ericifolia* Oberlander & Dryer differs from other *Oxalis* species in having massive papillate protrusions on the adaxial leaflet epidermis, a wine-red androecium, broadly swollen peduncular articulations and a short petal claw (Oberlander *et al.*, 2009). *Senecio umbricola* Cron & B.Nord. differs from other *Senecios* in having a rhizomatous habit, lyrate pinnatisect leaves which are green above and purple below, and white rays (Cron & Nordenstam, 2009).

Morphological characters have the advantage of being easily seen and both vegetative and reproductive characters are used (Stuessy, 1990). Vegetative characters, however, tend to be more plastic or variable than reproductive characters, but are particularly used in groups where reproductive characters are unhelpful e.g. Poaceae (Stace, 1980; Stuessy, 1990).

Morphological characters that are considered in the Nyctaginaceae are numerous. They include the growth forms that vary from annual and perennial herbs, to shrubs and trees, to climbers or lianas. Leaves are either opposite, alternate or fascicled, linear to ovate or rounded, with the margins entire to sinuate. Thorns are present on the branches in some genera. The flowers are apetalous and the calyx can either be inconspicuous or large and colourful, simulating a corolla, while the involucre bracts simulate a calyx. The androecium varies from one to many stamens with the filaments usually connate at the base. The gynoecium consists of only one carpel. The fruit is an achene or a nutlet that is enclosed in an anthocarp. The anthocarp can be either fleshy, coriaceous or hard with wings, ribs, or lobes, which in most genera are covered in sticky glands or warts (Bogle, 1974; Bittrich & Kühn, 1993; Spellenberg, 2004).

### **2.2.3 Anatomy**

Anatomy is concerned with the internal structure of plants (Judd *et al.*, 2008) and Stace (1980) warns that these characters should not be neglected as they are just as valuable as morphological ones e.g. the palm genus *Tahina spectabilis* J. Dransf & Rakotoarinivo differs anatomically from other coryphoid palms in having non-vascular fibres which are solitary and free in the mesophyll and confined to the abaxial half of the lamina (Dransfield *et al.*, 2008). Woodland (1997) stated that cells



and tissues provide many clues to the natural grouping of plants and the identification of unknown specimens.

Anatomical data useful for taxonomy includes both the internal features and the surface of an organ, as seen by light microscopy, scanning electron microscopy (SEM) and transmission electron microscopy (TEM). Features observed with the SEM are referred to as micromorphological characters and those with the TEM as ultrastructural (Judd *et al.*, 2008). TEM studies, however, do not reveal characters of taxonomic usefulness except in groups such as algae, fungi and bacteria (Woodland, 1997).

Taxonomic evidence in general can be provided by secondary xylem and the presence or absence of specialized cells which contain crystals, latex, resins, mucilage and essential oils, as well as the form and distribution of laticifers and secretory canals or cavities. The number of leaf traces and gaps in the nodes varies and leaves are anatomically very variable organs which can provide numerous systematically significant characters. The cuticle may possess deposits of papillae, striae or rods of diagnostic distribution and the epidermal cell size, shape, contents, wall thickness, number of cell layers and the presence of papillae varies. The subsidiary cells of stomata differ, resulting in different stomatal types. The distribution and shape of mesophyll cells and the presence or absence of intercellular spaces may provide useful clues. Other useful characters include trichome morphology and distribution, patterns of vascular traces in flowers, and the position of floral primordia and their sequence of initiation. Developmental studies assist with the understanding of homologies (Dickison, 2000; Judd *et al.*, 2008).

Stem and root anatomy in the Nyctaginaceae are anomalous in that the primary vascular bundles develop in successive rings of collateral vascular bundles. Stomata vary in the distribution and nature of the surrounding cells (anomyocytic, paracytic, actinocytic or with a single subsidiary cell) and epicuticular wax crystals are absent or present. Hairs are either glandular or non-glandular. The mesophyll is centric, dorsiventral or isobilateral with Kranz structures known in some genera. Crystalline granules are often present in the epidermal cells and calcium oxalate is deposited in

the form of raphides, crystals and styloids (Metcalf & Chalk, 1950; Bogle, 1974; Bittrich & Kühn, 1993).

#### **2.2.4 Palynology**

The scanning electron microscope is used to obtain information on external features of pollen grains and the transmission electron microscope for internal features of pollen grains. Pollen grains may be used at all levels of the taxonomic hierarchy and emphasis is placed on comparative features such as apertures and wall structure. Data for taxonomic use is derived from the aggregation of pollen grains, the shape of the grain, the aperture number, shape and position, the external wall layer and internal protoplasm (Stuessy, 1990). For instance, the large number of apertures makes the pollen of Polygalaceae distinct from the closely related families, the Leguminosae, Surainaceae and Quillajaceae. Within the Polygalaceae, the genus *Heterosamara* has kidney-shaped pollen, suggesting that a species with such pollen, such as *Polygala wattersii* Hance is best placed in *Heterosamara* (Banks *et al.*, 2008).

Genera within the Nyctaginaceae have a wide range of pollen morphology with the most useful characters being the size of the pollen grains (22 to 210  $\mu\text{m}$  in diameter); the shape of the grain (spheroidal, prolate or oblate); the aperture number, shape and position (3 to 18 colpate, 12 or more pantoporate with pores sometimes covered by a pore plate) and the exine thickness and pattern (spinulose, tubuliferous or reticulate; spinules vary in size and distribution) (Nowicke, 1970; Bogle, 1974).

#### **2.2.5 Molecular data**

Each nucleotide in the DNA and RNA of cells can vary and therefore supply characters that can be used to infer evolutionary relationships among organisms (Doyle, 1993; Judd *et al.*, 2008). Variation in the genome can be observed directly by DNA sequencing or indirectly by polymorphisms (Doyle, 1993). Plant cells contain mitochondria, chloroplast and nuclear genomes, all of which can provide systematic information (Judd *et al.*, 2008).

### 2.2.5.1 Mitochondrial genome

In the mitochondrial genome the genes evolve slowly and rearrangements occur so often within individual plants that they do not characterize or differentiate species or groups of species. These genes are most useful for assessing ancient events such as the origin of the angiosperms or the phylogeny of large groups such as the seed plants. Commonly used genes include those that encode for the subunits of ATP synthase (*atp1* and *atpA*) and maturase (*matR*) (Judd *et al.*, 2008).

### 2.2.5.2 Chloroplast genome

The chloroplast genome is stable within cells and within species. The loss and gain of genes or their introns are common enough to be worth looking for, but rare enough to be stable indicators of evolutionary change (Judd *et al.*, 2008).

The *rbcL* gene encodes for the larger subunit of the photosynthetic enzyme Rubisco. It is often chosen because it is universal among plants, fairly long and presents no problems with alignment. It has, however, limitations in that it has a slow rate of change and the protein it encodes for is highly conserved and greatly constrained at the amino acid level. This makes the *rbcL* gene not particularly useful for inferring relationships within and between closely related genera (Judd *et al.*, 2008).

Chloroplast genes that can be used to infer phylogeny of closely related species include the *ndhF* (the gene that codes for subunit F of NADP dehydrogenase), the genes that encode the  $\alpha$  and  $\beta$  subunit of RNA polymerase II (*rpoA* and *rpoC2*), a muter gene in the intron that separates the coding region of *trnK* (*matK*), the gene that encodes for the  $\beta$  subunit of ATP synthase (*atpB*) and spacer regions (noncoding sequences between genes) and introns in the genome itself (Judd *et al.*, 2008).

### 2.2.5.3 Nuclear genome

Within the nuclear genome, the order of the genes is presumed to be stable, both within species and between species. Genes that encode for ribosomal RNA, especially 18S and 26S, are used to infer relationships among large groups of plants. The ITS

regions are used to determine relationships among species and introns are used to determine relationships among similar species or populations. Phytochrome genes (genes that encode for the proteins that respond to light signals and control plant growth, development and photosynthesis) are also popular genes to infer relationships (Judd *et al.*, 2008).

Other techniques include microsatellites, Random Amplified Polymorphic DNA (RAPD), Restriction Site Analysis, Restriction Fragment Length Polymorphisms (RFLP), Amplified Fragment Length Polymorphism (AFLP) and genome mapping (Judd *et al.*, 2008).

Various authors (Lipscomb, 2003; Seberg, 2003), however, warn that DNA sequences and nucleotides are simply characters which should be used together with other data in analysis and not as an identification tag for a species.

Molecular studies done on the Nyctaginaceae have used the internal transcribed spacer ITS -1 and ITS -2 region of the nuclear genome as well as the 5.8S region of the nuclear ribosomal DNA (Levin, 2000; Douglas & Manos, 2007). Chloroplast genome regions include the 5' *accD* coding region, the intergenic region between the *rbcL* and *accD* genes and the *ndhF*, *rps16* and *rpl16* region (Levin, 2000; Douglas & Manos, 2007). Levin (2000) found that the ITS region evolves faster and is phylogenetically more informative than the region between the *rbcL* and *accD* or the 5' *accD* region. Douglas & Manos (2007) found that the 5.8S region is highly conservative which infers its value as a character to use in systematics.

### **2.2.6 Ecology**

Ecology helps the taxonomist to understand the distribution of taxa and the composition of floras, the genetic and phylogenetic relationships between taxa and the variation that occurs in populations and their evolutionary adaptations (Radford *et al.*, 1974).

Ecological characters include habitat which are classified according to edaphic and vegetation relations: biotic, abiotic, spatial and temporal factors which are an

indication of the relationship between the plant and its environment and adaptive features of the plant, which can give an idea of the origin of the community, migration patterns into the area, evolutionary trends within the population and past and present trends in the climate (Radford *et al.*, 1974). Ecological characters can also limit a species to a specific distribution range. For instance, *Ocimum motjaneanum* McCallum & Balkwill is a serpentine endemic known from only four localities in Swaziland (McCallum & Balkwill, 2004).

The Nyctaginaceae occur at altitudes of 0 – 3000m (Bohlin, 1988; Stannard, 1988; Thulin, 1990; Thulin, 1993; Whitehouse, 1996) in coastal regions, montane vegetation, semi-desert and desert habitats (Spellenberg, 1993; Bittrich & Kühn, 1993; Spellenberg & Poole, 2003). These representatives grow in soils derived from calcareous, gypseous and igneous rocks and on sandy substrates (Smith, 1976; Thulin, 1990; Le Duc, 1995; Whitehouse, 1996). In southern Africa, the Nyctaginaceae occur from 0 – 1800m above sea level in coastal dune forests and thickets, forests, grasslands, savanna and in arid regions; often along water courses and rivers in sandy, rocky or stony and calcareous soils (Stannard, 1988; Coates Palgrave, 2002).

### **2.2.7 Biogeography**

Biogeography is the science to study, analyse and explain the patterns of distribution of organisms as well as the changes that have taken place in the past and are taking place today (Cox & Moore, 2005; Judd *et al.*, 2008). This understanding helps to interpret the origin, migration and evolution of species and floras (Radford *et al.*, 1974).

Each taxon has a certain pattern of distribution or a geographical range which is a diagnostic character of a taxon (Van Wyk & Smith, 2001) and forms part of the definition of a species. Distribution information of individual species enables the identification of areas of endemism [defined as the situation in which a species is restricted to a particular geographical region (Allaby, 1996)]. This is important in conservation planning (Nielsen, 1999) when centres of endemism are considered [Centre of Endemism is defined as an area which is rich in species or contain a large number of species endemic to that region (Van Wyk & Smith, 2001)]. For instance,

the unique habitat formed by the Sneeuwberg Mountains in the Eastern Cape results in 33 species that are endemic to that area (Clarke *et al.*, 2009). Species distribution data also underlies activities such as drug discovery, ecotourism, the trade in natural resources, pest control and crop improvement by using the genetic diversity of wild relatives, to name but a few (Cracraft, 2002).

When the distribution of all the species of a genus is drawn on a map, there are one or more areas with a high concentration of species, which is known as the centre of diversity or centre of genetic diversity. The centre of diversity is also considered to be the centre of origin, that is, the region where a group of organisms is believed to have originated (Stace, 1980; Allaby, 1996). The major patterns of evolution and migration can be determined when the characteristics of a taxon in its centre of diversity are studied relative to the characteristics progressively further from the centre, often leading to the uncovering of the ways in which a taxon has adapted to the different environments which it encountered during its migration. This information aids in determining the taxonomic relationships and delimitations of biotypes found within a taxon (Stace, 1980). Related taxa have or had, due to their common ancestry, a common or interrelated geographic distribution. When the distribution of a large number of taxa is analysed, certain geographical patterns may be found to recur consistently and they are known as floristic elements. Knowledge of these floristic elements helps to explain the pathways of migration into a region and this may aid in taxonomic decisions when there are uncertainties (Stace, 1980).

Distribution ranges which correlate with differences or similarities in structural features can also be used to determine the relationships between taxa (Radford *et al.*, 1974).

The Nyctaginaceae are mainly distributed in the tropical and subtropical areas of the New World (Bittrich & Kühn, 1993; Jordaan, 2000), with some genera extending into the temperate regions (Thulin, 1994). Only *Boerhavia*, *Commicarpus*, *Phaeoptilum*, *Pisonia* and *Mirabilis* occur in the Old World (Bittrich & Kühn, 1993). In the Americas the family has two centres of distribution, namely, tropical and subtropical South America and the Antilles, and the southwestern United States of America and northern Mexico in North America (Bittrich & Kühn, 1993; Douglas & Manos, 2007).

*Commicarpus* is an African genus and occurs throughout the continent except for the extreme north and south and the wet rainforest areas of the west (Meikle, 1978). Northeastern tropical Africa and southern Arabia are the centre of diversity for this genus (Thulin, 1990). The monotypic *Phaeoptilum spinosum* is endemic to southern Africa and occurs throughout the dry western parts of Namibia and Northern Cape (Craven & Marais, 1992; Bittrich & Kühn, 1993; Jordaan, 2000), although there are reports that it also occurs in tropical Africa (Riley, 1963; Leistner, 2005). In southern Africa, Namibia is the centre of diversity for the family.