

Taxonomic assessment of *O. furcillata* (Oxalidaceae)

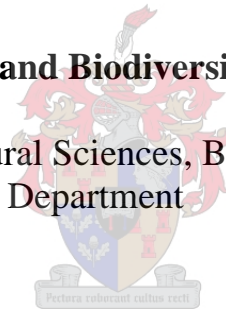
By

PULCHERIE BISSIENGOU

Assignment submitted in partial fulfilment of the requirements
for degree of Masters of Science in

Systematics and Biodiversity Science

In the faculty of Natural Sciences, Botany and Zoology
Department



**UNIVERSITY OF STELLENBOSCH
SOUTH AFRICA**

Supervisors: Dr. L.L. Dreyer and Dr. E. M. Marais

December 2005

DECLARATION

I, the undersigned, hereby declare that the work contained in this assignment is my own original work and has not previously in its entirety or part been submitted at any university for a degree.

.....

Pulcherie Bissiengou

.....

Date

Abstract

The family Oxalidaceae has a worldwide distribution, but is most common in tropical and subtropical regions. *Oxalis* L. is the largest genus of the family comprising ca. 800 of the 900 species. *Oxalis* species are annual or perennial herbs or rarely subshrubs or trees. The current study assesses on the taxonomic placement of *O. furcillata* Salter. Currently this species, comprising two varieties, *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* Salter, is placed in section *Foveolatae*. Members of this section have endospermous seeds and fleshy leaflets. However, both in terms of leaf morphological and seed characters the two varieties of this species appear to be misplaced within this section. In addition *O. furcillata* var. *caulescens* has a unique pollen type, different from both the typical variety and the rest of the section. Both lines of evidence thus suggest that *O. furcillata* var. *caulescens* may be misplaced within this section. The present study thus sets out to assess the placement of *O. furcillata* in general, and the placement of *O. furcillata* var. *caulescens* in particular. A multi-disciplinary approach was followed, which included analyses of macro-morphological (including LM and SEM analyses), biogeographical and palynological characters. The variability of quantitative characters was assessed using the STATISTICA 6.0 software package. Leaf dimensions, plant height, bulb length, petiole length and palynology showed sufficient differences between the two taxa to confirm the separate identity of these two varieties as separate species. *O. furcillata* var. *caulescens* was thus raised to specific status as *O. caulescens* (Salter) Bissiengou. The results suggest two different options in terms of the taxonomic placement of the species *O. furcillata* and *O. caulescens*. They can either remain in section *Foveolatae*, best placed near *O. senecta* and *O. densa* or may moved to the highly variable section *Latifoliolatae*. But retaining them within the section *Foveolatae* appeared to be the better alternative. The correct position will be established both through further morphological analyses and correlation to the *trnL*-F and ITS sequence-based phylogeny of the southern African members of *Oxalis*.

Opsomming

Die familie Oxalidaceae het 'n wêreld-wye verspreiding, maar kom veral in tropiese en subtropiese omgewings voor. *Oxalis* L. is die grootste genus in die familie, en sluit ongeveer 800 van die 900 spesies in. *Oxalis* spesies is eenjarige of meerjarige kruide, selde halfstruik of bome. Die huidige studie evalueer die taksonomiese plasing van *O. furcillata* Salter. Tans groepeer hierdie spesie, wat die twee variëteite *O. furcillata* var. *furcillata* en *O. furcillata* var. *caulescens* Salter insluit, binne die seksie *Foveolatae*. Lede van hierdie seksie het endosperm-houdende sade en sukkulente blare. Die twee variëteite van hierdie spesie skyn egter misplaas te wees binne hierdie seksie, beide in terme van blaarmorfologiese- en saad-kenmerke. Hiermee saam het *O. furcillata* var. *caulescens* ook 'n unieke stuifmeeltype, wat verskil van beide die stuifmeel van die tipiese variëteit en die res van die seksie. Beide hierdie kenmerke suggereer dus dat *O. furcillata* var. *caulescens* moontlik verkeerd geplaas is binne hierdie seksie. Die huidige studie het dus ten doel om die plasing van *O. furcillata* in die breë, en *O. furcillata* var. *caulescens* spesifiek, te evalueer. 'n Multidissiplinêre benadering is gevolg, wat 'n analise van makro-morfologiese (insluitend LM en SEM analyses), biogeografiese en palinologiese kenmerke ingesluit het. Die variasie van kwantitatiewe kenmerke is geassesseer deur gebruik te maak van die STATISTICA 6.0 sagteware-pakket. Blaardimensies, plant-hoogte, bol-lengte, petiool-lengte en palinologie het genoeg verskille tussen die twee taksa getoon om hierdie twee variëteite as aparte spesies, elk met eie identiteit, te beskou. *O. furcillata* var. *caulescens* is dus tot spesifieke status gehef as *O. caulescens* (Salter) Bissiengou. Die resultate stel ook twee verskillende moontlikhede voor ten opsigte van die taksonomiese plasing van die spesies *O. furcillata* en *O. caulescens*. Hulle kan of in die seksie *Foveolata* behou word, waar hulle die beste geplaas word naby *O. senecta* en *O. densa*, of hulle kan na die hoogs varieërende seksie *Latifoliolatae* geskuif word. Die beter alternatief tans is om hulle binne die seksie *Foveolatae* te behou. 'n Beter plasing sal eers gedoen kan word na afloop van verdere morfologiese analyses en korrelasies wat met die *trnL-F* en ITS basisvolgorde gebasseerde filogenie van suider Afrikaanse lede van *Oxalis* verkry kan word.

ACKNOWLEDGEMENTS

I wish to extend a special thank you to my supervisors, Doctors L. L. Dreyer and E. M Marais, for their commitment in ensuring that I completed my studies.

I thank my parents, friends and fellow students for their concerns and support during the good and bad times.

I am grateful to Frances Moore and Wilma Meatz for painstakingly proof reading the manuscript.

I would also like to thank the many staff at the International Office, Stellenbosch University for effectively liaising on my behalf with my sponsors, the Gabonese Government.

Finally, yet most importantly, I would like to give thanks to the Lord Jesus who helped me each step of the way during my stay here in Stellenbosch.

Contents

Abstract	i
Opsomming	ii
Acknowledgements	iii
Chapter 1 Introduction	1
Phylogenetic placement of the family Oxalidaceae	1
Phylogenetic relationships within Oxalidaceae	2
Literature review of <i>Oxalis</i> in southern Africa	3
Research problem	5
Justification of the study	6
Aims of the study	7
Key questions	7
Chapter 2 Materials and Methods	9
2.1 Specimens examined	9
2.2 Morphological studies	11
2.2.1 Macro-morphological studies	11
2.2.2 Statistical analysis	11
2.3 Palynological study	11
2.4 Biogeographical study	12
Chapter 3 Results	13
3.1 Morphological description of the two taxa	13
3.1.1 <i>Oxalis furcillata</i> var. <i>furcillata</i>	13
3.1.2 <i>Oxalis furcillata</i> var. <i>caulescens</i>	14
3.2 Statistical analysis	22
3.3 Palynological study	26
3.4 Geographical distribution	29
Chapter 4 Discussion and conclusions	30

4.1 Character analysis of the groups defined within section <i>Foveolatae</i>	30
4.1.1 Character analysis of species with well-exserted stems, group 1: (<i>O. convexula</i> and <i>O. attaquana</i>)	31
a. Vegetative characters of subterranean parts	31
b. Vegetative characters of the above-ground parts	31
c. Reproductive characters	32
Peduncles	32
Floral parts	32
d. Indumentum	32
4.1.2 Characters analysis of the stemless species, group 2: (<i>O. pulchella</i> , <i>O. foveolata</i> , <i>O. punctata</i> , <i>O. senecta</i> and <i>O. densa</i>)	34
Comparison between <i>O. pulchella</i> and <i>O. foveolata</i>	34
a. Vegetative characters of subterranean parts	34
b. Vegetative characters of the above-ground parts	34
c. Reproductive characters	35
Peduncle	35
Floral characters	35
d. Indumentum	35
Character analysis of the four varieties of <i>O. pulchella</i>	37
Character analysis of <i>O. punctata</i>	39
a. Vegetative characters of subterranean parts	39
b. Vegetative characters of the above-ground parts	39
c. Reproductive characters	39
Peduncle	39
Floral characters	39
d. Indumentum	39
Characters analysis of the three forms of <i>O. punctata</i>	40
Species of <i>O. senecta</i> and <i>O. densa</i>	41
a. Vegetative characters of subterranean parts	41
b. Vegetative characters of the above-ground parts	41
c. Reproductive characters	42
Peduncle	42

Floral parts	42
d. Indumentum	42
4.2 Discussion	44
4.2.1 Comparison between species, varieties and forma within section <i>Foveolatae</i> .	44
4.2.2 Comparison between <i>O. furcillata</i> var. <i>furcillata</i> and var. <i>caulescens</i>	46
Macro-morphology	46
Palynology	49
Geographical distribution and ecology	50
4.3 Conclusions	52
 Chapter 5 Taxonomic placement of <i>O. furcillata</i> and <i>O. caulescens</i>	54
5.1 Taxonomic demarcation of <i>O. furcillata</i>	54
5.1.1 Description	54
5.1.2 Diagnostic characters	55
5.1.3 Geographical distribution	55
5.1.4 Designation of forms	55
5.1.5 Key to the forms	56
Selected specimens studied	56
5.2 Taxonomic demarcation of <i>O. caulescens</i>	57
5.2.1 Description	57
5.2.2 Diagnostic characters	57
5.2.3 Geographical distribution and ecology	58
Selected specimens studied	59
5.3 Proposed taxonomic placement of <i>O. furcillata</i> and <i>O. caulescens</i>	59
References	65

Chapter I Introduction

Phylogenetic placement of the family Oxalidaceae

The family Oxalidaceae has a worldwide distribution, but is most common in tropical and subtropical regions. The classical systematic position of the Oxalidaceae was in the order Geraniales in the Rosidae (Cronquist 1981; Thorne 1983), along with families Geraniaceae, Limnanthaceae, Tropaeolaceae and Balsaminaceae. Other families that were included in this order are Lepidobotryaceae, Hypseocharitaceae and Biebersteiniaceae (Takhtajan 1980), Zygophyllaceae, Erythroxylaceae, Balanitaceae, Humiriaceae, Linaceae and Lepidobotryaceae (Dahlgren 1983).

The Chase *et al.* (1993) classification based on *rbcL* gene sequence data, places Oxalidaceae in the Rosid clade in two possible positions in two different heuristic searches. In the first search (Search I), where the genus *Hypseocharis* Remy was used as representative of the family Oxalidaceae, the family resolves into the Rosid II clade. In this search *Hypseocharis* resolved as sister taxon to members of the family Geraniaceae. This position agrees with previous classification systems proposed by Takhtajan (1980) and Cronquist (1981). For the second search (Search II), the family Oxalidaceae, represented by the genus *Oxalis* L., was grouped along with the Eucryphiaceae, Cunoniaceae, Tremandraceae and Cephalotaceae within the Rosid I clade. This classification differs from previous classifications in that the Oxalidaceae no longer resolves with families previously thought to be closely related. For example, members of the family Geraniaceae are now well-separated in the angiosperm phylogeny. Both searches I and II were confirmed by Price and Palmer (1993) in their search for the phylogenetic relationships of the Geraniaceae and Geraniales. They concluded that *Hypseocharis* is closer related to members of the Geraniaceae than to those of Oxalidaceae and at the same time they proposed the exclusion of the Oxalidaceae from the Geraniales.

Nandi *et al.* (1998) did a combined cladistic analysis of the Angiosperms using *rbcL* and non-molecular data sets. In their analyses only the trees based on *rbcL* and the combined data set are reasonably well-resolved, with bootstrap percentages greater than 50%, whereas the non-molecular trees show only eleven clades supported by bootstrap percentages greater than 50%. According to these analyses, Oxalidaceae and

Connaraceae are closely related families in the three phylogenetic trees retrieved on non-molecular, *rbcL*-based and combined data sets. They resolve within the Rosid I clade in the Cunonialean clade, which includes the Cunoniales (families Eucryphiaceae, Cephalotaceae, Tremandraceae and Elaeocarpaceae). In the non-molecular tree, these two families are placed in the Rosid I clade and appear to be distantly related to the family Zygophyllaceae. According to their analyses, Connaraceae and Oxalidaceae share the absence of ellagic acid and the presence of rapanone, a benzoquinone (Fieser & Chamberlain 1948; Hegnauer 1962-1994 as quoted by Nandi *et al.* 1998). These two families also share sieve tube plastids of the Pic-type (Behnke 1981 as quoted by Nandi *et al.* 1998), the absence of oxalate druses (Metcalf & Chalk 1950 as quoted by Nandi *et al.* 1998), a short exotestal palisade, endotestal crystals, fibrous exotegmen (Corner 1976 as quoted by Nandi *et al.* 1998) and exclusively uniseriate wood rays (Nandi *et al.* 1998).

The Angiosperm Phylogeny Group (APG 1998) combined morphological data and sequence data of the *rbcL*, *atpB* and 18S nuclear ribosomal DNA regions of many families of flowering plants. Their results placed Oxalidaceae into a new order, the Oxalidales within the Eurosids I clade, which is partially agrees with the second search of Chase *et al.* (1993), in that it groups Oxalidaceae with the families Cephalotaceae, Connaraceae, Cunoniaceae, Elaeocarpaceae and Tremandraceae. Recently, the APG II (2003) updated their classification of APG (1998) and supported the APG (1998) circumscription of the Oxalidales.

Savolainen *et al.* (2000), in their phylogeny of the eudicots based upon combined *atpB*, and *rbcL* sequence data, also placed the Oxalidaceae in the order Oxalidales in the Eurosids I clade. In this case the Oxalidales includes six families, namely Brunelliaceae, Cephalotaceae, Connaraceae, Cunoniaceae, Elaeocarpaceae and Oxalidaceae.

Phylogenetic relationships within Oxalidaceae

The number of genera included in the Oxalidaceae differs according to various authors. Boesewinkel (1985) included seven genera, namely: *Biophytum* DC. (70 species), *Oxalis* L. (ca. 800 species), *Averrhoa* L. (2 species) *Sarcotheca* Blume (11 species), *Dapania* Korth. (3 species), *Lepidobotrys* Engl. (1 species) and

Hypseocharis Remy (9 species). Knuth (1930) also added the genus *Eichleria* Progel with its two species to the list. Other authors such as Hutchinson (1959) transferred *Averrhoa* to the family Averrhoaceae in the order Rutales, and *Dapania* and *Sarcotheca* to the family Lepidobotryaceae in the Malpighiales. Chant (1978; 1993) reduced the genera in the Oxalidaceae to *Oxalis*, *Biophytum* and *Eichleria* and included *Sarcotheca* and *Averrhoa* in the Averrhoaceae. According to Dreyer (1996), the genera *Hypseocharis* and *Lepidobotrys* are poorly known and their affinities uncertain. Some authors place them in the monotypic families Hypseocharitaceae and Lepidobotryaceae. Most authors, according to Dreyer (1996), delimit the Oxalidaceae to include the genera *Oxalis*, *Biophytum*, *Dapania*, *Sarcotheca*, *Averrhoa*, *Hypseocharis* and *Lepidobotrys* (Veldkamp 1971; Robertson 1975; Lourteig 1979; Cronquist 1981; Boesewinkel 1985; Rama Devi & Narayana 1990).

The phylogenetic position of *Hypseocharis* has subsequently been resolved. Veldkamp (1971) suggested that the genus *Hypseocharis* represents a link between the Oxalidaceae and Geraniaceae. However, Boesewinkel (1988) provided evidence that *Hypseocharis* is more closely related to the Geraniaceae than to the Oxalidaceae. He demonstrated that *Hypseocharis* and members of the Geraniaceae share the presence of crassinucellate ovules, all have a scant endosperm along with fused styles and share similarities in the details of their seed wall anatomy. These characters are not present in the Oxalidaceae. The similarities between *Hypseocharis* and Geraniaceae are further demonstrated by the vascular bundles of the flower and the staminal arrangement, which *Hypseocharis* shares with *Monsonia* L. and *Sarcocaulon* (DC.) Sweet (Rama Devi 1991). Thus, based on morphological and anatomical data, *Hypseocharis* appears to be closer related to Geraniaceae rather than being intermediate between Oxalidaceae and Geraniaceae. This was confirmed by the molecular study by Price and Palmer (1993) in which *Hypseocharis* was found strongly linked to the Geraniaceae with a bootstrap support value of 100%. Consequently *Hypseocharis* is no longer considered a member of the Oxalidaceae.

Literature review of *Oxalis* in Southern Africa

Oxalis is the largest genus of the family Oxalidaceae, with the entire family comprising about 900 species of which about 800 species belong to this single, large

genus (Cronquist 1981). *Oxalis* species are annual or perennial herbs or rarely subshrubs or trees. Members of the genus often have subterranean structures that may consist of rhizomes, corms, tubers, tuberous roots or true bulbs, as is the case of all southern African species (Salter 1944). These structures are used for resource storage to facilitate dormancy during the dry seasons and for asexual reproduction. The above-ground stems range from absent, very short and inconspicuous to well-developed in some shrubby forms. The presence or absence of above-ground stems was used to delimit several of the species southern African (Salter 1944). *Oxalis* species have alternate leaves that are digitately or pinnately trifoliate. The leaflets are entire to obcordately-bilobed, even bifurcate. Peduncles that are subtended by leaves vary in length between species, and are often articulated near the base. The genus displays very limited flower morphological variation. Flowers are uniformly actinomorphic, funnel-shaped and pentamerous (Cronquist 1981). The limited floral variation can be ascribed to the breeding system of the genus. Oxalidaceae (*Oxalis*) is one of only a few angiosperm families (including Amaryllidaceae, Connaraceae, Linaceae, Lythraceae and Pontederiaceae) that display a tristylous breeding system (Ornduff 1974; Barrett *et al.* 1997). Tristylous taxa display three morphologically different floral morphs within a single species, namely long, medium and short morphs. Long morphs have long-styled flowers with two sets of anthers below the level of the stigma; mid-styled flowers have one set of anthers above the stigma and a second set below the stigma; and short-styled flowers have two sets of anthers above the stigma (Ornduff 1974; Barrett *et al.* 1997). All native South African *Oxalis* taxa are probably trimorphic, but more work on the state of expression of tristily among southern African taxa is needed (Salter 1944).

The genus *Oxalis* displays two centers of diversity, one in South Central America (including more than 500 species) and another in southern Africa, which is most species-rich within the Cape Floristic Region (Cowling and Hilton-Taylor 1997; Goldblatt and Manning 2000). The CFR region includes about 150 of the total of about 210 southern African *Oxalis* species (Goldblatt and Manning 2000). Within South Africa, *Oxalis* species display three centers of diversity (Oberlander *et al.* 2002). The largest center is positioned on the Cape peninsula, extending to the Kogelberg/Hottentot's Holland Mountain ranges to the east. A secondary center of diversity is situated in the Clanwilliam/ Nieuwoudtville region. This centre exhibits a

wide range of unique species, both within *Oxalis* and in other taxonomic groups (Schumann & Kirsten 1992; Rebelo 1995 as quoted by Oberlander *et al.* 2002). The third main center of *Oxalis* biodiversity is situated in the Kamiesberg region of the Northern Cape Province.

The most recent taxonomic revision of the southern African *Oxalis* species was published by Salter (1944). This was the most comprehensive revision of the southern African members of *Oxalis*. His work was based on morphological characters that he observed in British herbaria (Kew and the British Museum of the Natural History) as well as in living plants, both in their natural habitats and in cultivation in South Africa. He compiled a full description for all species known then, and paid a great deal of attention to the bulbs and important floral characters. The latter cannot readily be ascertained from dried specimens. The detailed examination resulted in an attempt to group the species according to their natural affinities. However, he admitted that his analysis of the species was entirely artificial and was intended purely as a means for identification. He placed large emphasis on the division between acaulescent (stemless) and caulescent (with exserted stem above-ground) species. He recognized many varieties and forma, which brought the total number of recognized taxa to *ca.* 270 (Dreyer 1996). The taxa were arranged into 11 sections, namely: *Corniculatae*, *Ionoxalis*, *Cernuae*, *Oppositae*, *Stictophyllae*, *Foveolatae*, *Sagittatae*, *Campanulatae*, *Latifoliolatae*, *Crassulatae*, and *Angustatae*. Sections *Corniculatae* and *Ionoxalis* are American sections represented by one naturalized species each in South Africa. The rest of the sections are endemic to southern Africa.

South African *Oxalis* species are sun-loving plants and occur on open plains and slopes. There are, however, some species that are confined to temporarily water-logged soils, while others prefer shady environments, *e.g.* *O. incarnata* L. (Salter 1944).

Research problem

In his taxonomic revision of the South African species of *Oxalis*, Salter (1944) assigned *O. furcillata* Salter to section *Foveolatae*. Members of this section are known to have fleshy leaflets that are mostly conduplicate. The section is also known for its endospermous seeds. However, according to Salter's (1944) description,

O. furcillata var. *furcillata* and *O. furcillata* var. *caulescens* Salter have exendospermous seeds. Salter (1944) also mentioned that neither of the two varieties possesses fleshy leaflets, rendering them different to other members of the section. He suggested that this taxon may thus be poorly placed within the section, but did not propose an alternative taxonomic placement.

Salter (1944) described *O. furcillata* var. *caulescens* as being different from the typical variety on the basis of possessing a well-exserted above-ground stem. He mentioned that *O. furcillata* var. *caulescens* shares characteristics with members of section *Angustatae* subsection *Sessilifoliae*, and suggested that an alternative placement may be considered in future.

Dreyer (1996), in her palynological review of *Oxalis* in Southern Africa, found a pollen type in *O. furcillata* var. *caulescens*, which differs from that of the typical variety and that of the rest of the section as well. The C10 pollen type of *O. furcillata* var. *caulescens* is incongruent with the general pattern of the tectum in section *Foveolatae* that ranges from C2 to C8. She also suggested that, although morphological features support an affinity of *O. furcillata* var. *caulescens* with taxa of the subsection *Sessilifoliae*, *O. furcillata* var. *caulescens* might be better placed with species in section *Campanulatae*, groups within section *Latifoliolatae*, section *Crassulae* or near individual species within *Angustatae* subsection *Multifoliolatae*. Due to the uncertain placement of *O. furcillata* var. *caulescens* in section *Foveolatae*, additional taxonomic studies are thus urgently needed.

Justification of this study

The South African members of *Oxalis* are seasonal geophytes, which appear to occur on nutrient-poor, nutrient-intermediate or comparatively rich soils. According to Goldblatt and Manning (2000), members of this genus favor lowland habitats in the Cape Floristic Region. In their ranking of the 20 largest genera of the Cape Flora, they placed *Oxalis* as the 7th largest Cape genus. The genus includes 94 endemic species in this region alone.

For such a large genus, the South African *Oxalis* species have received limited systematic attention in the past. Salter (1944) completed the most recent taxonomic revision of the genus in South Africa, but his work is outdated and shows some

limitations. Dreyer (1996) completed a palynological revision of the genus. Her results highlighted the need for more studies towards an improved systematic classification of the southern African members of *Oxalis*.

This study focuses on the taxonomic placement of *O. furcillata*. Currently this species (including both varieties) is placed in section *Foveolatae*, but according to Salter (1944) members of this section have endospermous seeds, while the seeds of both varieties of *O. furcillata* are exendospermous. Moreover, in terms of pollen type, *O. furcillata* var. *caulescens* seems to be misplaced within section *Foveolatae*. Both lines of evidence thus suggest that *O. furcillata* var. *caulescens* may be misplaced within the section. The present study sets out to assess the placement of *O. furcillata* in general, and the placement of *O. furcillata* var. *caulescens* in particular.

Aims of the study

The aim of this study is three-fold:

Firstly to assess the characteristics of members of section *Foveolatae* in order to:

- 1– Identify the diagnostic characters of *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*.
- 2– Use these diagnostic characters as a framework for the correct placement of one or both of these taxa within section *Foveolatae*.

Secondly, should it prove necessary (which is very likely, based on palynological data), an improved phylogenetic placement for *O. furcillata* var. *caulescens* will be sought, mainly within one of the following sections: *Campanulatae*, *Latifoliolatae*, *Crassulae* or *Angustae* subsection *Xanthotrichae*.

The third objective is to find the closest relatives of *O. furcillata* var. *caulescens* within the section into which it is finally placed.

Key questions

In order to achieve these aims, the following questions are asked:

1. What are the diagnostic characters of *O. furcillata* as a species, and of the two varieties of this species respectively?
2. Is *O. furcillata* correctly placed within section *Foveolatae*?
3. Are the two varieties of *O. furcillata* truly members of the same species, and correctly demarcated as they stand?
4. If not, should *O. furcillata* var. *caulescens* be raised to a specific rank, and what are the true taxonomic affinities and thus correct sectional placement of the newly delimited species?

Chapter 2 Materials and Methods

The first phase of this project focussed on distinguishing between the two varieties of *O. furcillata* in order to identify key diagnostic characters for each of the varieties. This part of the study was, in the first instance, based on morphological comparisons between herbarium specimens obtained on loan from the Compton (NBG), Bolus (BOL) and National Herbarium, Pretoria (PRE), as well as specimens from the herbarium of the University of Stellenbosch (STEU), South Africa (Table 2-1). These collections were supplemented by comparisons with living material collected in their natural localities during 2004 and 2005, living specimens of which are currently cultivated in the Botanical Gardens of the University of Stellenbosch (Table 2-1).

The second phase was based on morphological comparison between species, varieties and forma within section *Foveolatae* in order to evaluate the level of variation between different taxonomic ranks as described by Salter (1944).

2. 1 Specimens examined

A total of twenty-three specimens (Table 2-1) were studied, eleven of *O. furcillata* var. *furcillata* and twelve of *O. furcillata* var. *caulescens*. This list enabled me to study a wide representation of both taxa.

Table 2-1: List of specimens of *O. furcillata* var. *caulescens* and *O. furcillata* var. *furcillata* examined in the present study. Specimens used for palynological studies are marked with an asterisk (*).

<i>O. furcillata</i> var. <i>furcillata</i>			
Collector and Collector's number	Herbarium	Locality	Grid reference
Salter 2593	NBG	13 miles south of Steinkopf	2917 BC
Salter 2576*	BOL	Mesklip	2917 DD
Salter 5538	NBG	7 miles north of Concordia	2917 DB
Bayer 2236b*	NBG	Hondeklipbaai, Karkams	3017 BB
Beyer 3	NBG	Hester Malan Nature Reserve	2917 DB
Schleiben 9071	PRE & BOL	18 miles north east of Springbok	2917 DB
Leistner 2567	PRE	6 miles north east of Concordia	2917 DB
Van Wyk 5739	PRE	Hester Malan Nature Reserve	2917 DB
Dreyer 702*	STEU	Between Spektakel Pass and Springbok	2917 DA
Oberlander 149*	STEU	Farm Narab-Boerdery, Springbok	2917 DA
Oberlander 22*	STEU	Narab-Boerdery close to seasonal stream	2917 DA
<i>O. furcillata</i> var. <i>caulescens</i>			
Salter 6674*	BOL	16 miles north-east of Garies	3018 CA
Salter4607	NBG	6 miles south of Kamieskroon	3017 BD
Salter 1412*	NBG & BOL	7 miles south of Kamieskroon	3017 BD
Salter 1484*	NBG & BOL	Kamieskroon	3017 BB
Salter 854*	BOL	Kamieskroon	3017 BB
Salter 890	NBG & BOL	Springbok	2917 DB
Salter 4580*	NBG & BOL	2 miles north of Concordia	2917 DB
Salter 5571	BOL	13 miles south of Kamieskroon	3017 BD
Salter 2593	BOL	13 miles south of Steinkopf	2917 BC
Salter 4570	BOL	10 miles south of Kamieskroon	3017 BD
Salter 2559	BOL	14 miles south of Kamieskroon	3017 BD
Le Roux 3936*	PRE	Hester Malan Nature Reserve	2917 DB

2. 2 Morphological studies

The morphological assessment included the study of macro-morphological, biogeographical, palynological and anatomical characters, and a comparison of these between the two varieties of *O. furcillata*.

2. 2. 1 Macro-morphology

For the macro-morphological study both quantitative and qualitative characters were considered. Quantitative characters were studied by measuring different parts of the plant with the aid of ruler. Qualitative characters were studied by using both a stereomicroscope and scanning electron microscope (SEM) to study the detail of surface characters that were too small to investigate with the naked eye.

2. 2. 2 Statistical analysis

The variability of quantitative characters between the two taxa was determined by entering measurement data for each taxon into the Microsoft Excel package. The data were then imported into the STATISTICA 6.0 software package, in which separate analyses were conducted for the two taxa. Box plots, in which ranges of values of selected variables (plant height, bulb length, peduncle length, petiole length, leaf width and leaf length) were plotted separately for the two taxa. The central tendency (mean) and variation statistics, that is, standard error (SE) and standard deviation (SD), were computed for each taxon, and the selected values are presented as the *Graph type* selected on the *2D Box Plot* in STATISTICA 6.0 software package.

2. 3 Palynological study

Palynological comparisons were executed by collecting pollen of both taxa from selected herbarium specimens (Table 2-1) with sufficient flowering material. Pollen grains were mounted onto brass stubs using double sided tape. The pollen grains were then sputter-coated with gold-palladium, and studied by using a Leo 1430 VP 7KV scanning electron microscope (SEM). Scanning electron micrographs of the pollen grains were taken at fixed magnifications to enable comparison of the two different taxa.

2. 4 Biogeographical study

For the biogeographical study the precise distributional range of each of the two varieties was assessed, based on both locality data obtained from herbarium specimens and a literature survey. The grid references for each locality were obtained from the Grid Reference Index (Leistner & Morris 1976), and were used to map the distribution pattern of each taxon.

Chapter 3 Results

3. 1 Morphological description of the two taxa

The morphological descriptions below were based on visual and stereo-microscope comparisons of herbarium material of *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*.

3. 1. 1 *O. furcillata* var. *furcillata*

Geophyte, 180–190 mm tall when in flower. **Bulbs** 30–35 mm long, lanceoloid, usually in clusters of 2–5 old bulbs, tunic black to brownish, bulbils sometimes arise from a lateral rhizome. **Rhizome** 40–70 mm long, erect, glabrous but hairy near apex. **Stems** usually absent, sometimes present, 12–80 mm (sometimes up to 200 mm) long with petioles arising from stem apex, puberulent with multi-cellular hairs. **Scales** brownish, alternate, ovate or widely ovate, apex acute, base cuneate or widely cuneate, ciliate with multi-cellular hairs, similar hairs also found abaxially along the mid-vein. **Leaves** clustered at the stem apex, whorled, lamina ternate, with three sessile leaflets; petioles 14–16 mm long, flattened, sometimes winged below the basal articulation in the outer, shorter leaves, terete, covered with long multicellular hairs; leaflets arising from apex of petiole, conduplicate, furcate with both apices narrowly obtuse, bases cuneate, margins entire, basal vein divided into two apically branched veins. **Peduncles** 30–35 (–52 mm) long, erect, glabrous. **Flowers** 4–12 per plant, solitary at the apex of a long peduncle. **Sepals** 5, all of equal size, 3.5–4 mm long, narrowly ovate, apex acuminate, base narrowly cuneate, abaxially hirsute with multi-cellular hairs, margin ciliate. **Petals** 5, white, widely obovate, broadly truncate, narrowly cuneate, glabrous. **Stamens** 10, arranged in two whorls, filaments pilose, interspersed with glandular hairs. **Styles** 1–3 mm (short morph), 4–5 mm (medium morph), 7–10 mm (long morph), pilose interspersed with glandular hairs. **Ovary** superior, elliptic, 1.5 mm long, covered with simple hairs, 3–4 ovules per locule. Mature seed exendospermous (Table 3.1).

3. 1. 2 *O. furcillata* var. *caulescens*

Geophyte, 80–90 mm tall when. **Bulbs** 10–15 mm long, ovoid, usually solitary, covered with brownish (sometimes darker) tunics, rarely two small bulbs clustered together, bulbils sometimes arise from a lateral rhizome. **Rhizomes** 40–50 mm long, minutely hairy near apex. **Stems** erect, 10–15 mm long with petioles arranged into loose whorls, minutely hairy. **Scales** brownish, alternate, ovate to widely ovate, acute, cuneate to widely cuneate, ciliate with multi-cellular hairs along the margins and similar hairs also found abaxially along the mid-vein. **Leaves** clustered, loosely whorled; petioles 40–60 mm long, terete, winged below the basal articulation, covered with long multicellular hairs; lamina ternate; leaflets sessile, arising from the apex of petiole, conduplicate, apex furcate and both apices obtuse, cuneate, margins lobed, ciliate with multicellular hairs. **Peduncles** 20–25 (–40) mm long, erect, glabrous. **Flowers** 1–2 per plant, solitary at the apex of a short peduncle. **Sepals** 5, 2 large and 3 smaller, 3.5–4 mm long, narrowly lanceolate to ovate, acuminate, narrowly cuneate, abaxially hirsute with multi-cellular hairs, ciliate. **Petals** 5, white, obovate, truncate, cuneate, glabrous. **Stamens** 10, arranged in two whorls, filaments covered with glandular hairs. **Styles** 1–2 mm (short morph), 4–5 mm (medium morph), 6–12 mm (long morph), pilose interspersed with glandular hairs, **Ovary** superior, elliptic, 1 mm long, covered with simple hairs, 3–4 ovules per locule. Mature seed exendospours (Table 3.1).

Table 3. 1 A list of morphological characters studied for *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*.

Characters	<i>O. furcillata</i> var. <i>furcillata</i>	<i>O. furcillata</i> var. <i>caulescens</i>
Growth form	Geophyte	Geophyte
Plant height when in flower	180–190 mm	80–90 mm
Bulb (solitary or clustered)	Usually in clusters of 2–5, rarely only one large, solitary bulb	Usually solitary, rarely two small bulbs clustered together
Presence of bulbils	Sometimes present, arising from a lateral rhizome	Sometimes present, arising from a lateral rhizome
Bulb length	30–35 mm	10–15 mm
Bulb shape	Widely lanceoloid	Ovoid
Tunic colour	Black to brownish	Mostly brownish, sometimes darker
Rhizome length	40–70 mm	40–50 mm
Rhizome indumentum	Glabrous, hairy near apex	Minutely hairy near apex
Stem	Usually absent, but sometimes present with petioles arising from stem apex	Present, with petioles arranged into loose whorls over a longer portion of stem
Stem length	When present 12–80 mm (sometimes up to 200 mm)	10–15 mm
Stem orientation	Erect	Erect
Stem indumentum	When stem is present, puberulent	Glandular hair along the apex of the stem
Number of leaflets	3	3
Leave arrangement	Whorled	Whorled
Leaflet venation	Basal vein divides into 2 branched veins	Basal vein divides into 2 branched veins
Lamina apex	Furcate and both apices are obtuse	Furcate and both apices are narrowly obtuse
Lamina base	Cuneate	Narrowly cuneate
Lamina margin	Conduplicate	Conduplicate
Bract colour	Brownish	Brownish
Bract arrangement	Alternate around the rhizome and stem	Alternate around the rhizome and stem
Bract shape	Ovate to widely ovate	Ovate to widely ovate
Bract apex	Acute	Acute
Bract base	Cuneate to widely cuneate	Cuneate to widely cuneate
Bract indumentum	Ciliate with multi-cellular hairs and hairs abaxially clustered along the midvein	Ciliate with multi-cellular hairs and hairs abaxially clustered along the mid-vein
Petiole length	14–16 mm	4–6 mm

Petiole base	Flattened, sometimes winged below basal articulation only in the shorter outer leaves	Terete, petiole winged below basal articulation
Petiole shape	Terete with an increase in diameter at the base	Terete with an increase in diameter at the base
Petiole indumentum	Long multi-cellular hairs	Multi-cellular hairs
Peduncle length	30–35 mm (sometimes up to 52 mm) long	20–25 mm long
Peduncle indumentum	Glabrous	Glabrous
Flowers per plant	4–12	1–2
Flower colour	White, turning yellow when dried	White, turning yellow when dried
Sepal number	5, all of equal size	5, 2 large and 3 smaller
Sepal length	3.5–4 mm	3.5– 4 mm
Sepal apex	Acuminate	Acuminate
Sepal base	Cuneate	Cuneate
Sepal shape	Narrowly ovate	Narrowly lanceolate to ovate
Sepal indumentum	Abaxially hirsute with multi-cellular hairs, margins ciliate	Abaxially hirsute with multi-cellular hairs, margins ciliate
Petal apex	Broadly truncate	Truncate
Petal base	Narrowly cuneate	Cuneate
Petal shape	Widely obovate	Obovate
Petal indumentum	Glabrous	Glabrous
Stamen type	Arranged into two separate whorls	Arranged into two separate whorls
Filaments number	10	10
Filament indumentum	Pilose, interspersed with glandular hairs	Minute glandular hairs sparsely distributed over entire filament
Stigmatic branches	5	5
Style indumentum	Pilose, interspersed with glandular hairs	Pilose, interspersed with glandular hairs
Ovary shape	Elliptic	Elliptic

A comparison of the morphological characters between *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* (Table 3.1) highlights some distinct morphological differences. Characters that vary consistently, and which can therefore be used to distinguish between the two taxa, include: general robustness of plants, plant height, bulb

type and length, rhizome length, petiole length, wings along the basal part of the petiole, leaf dimensions and the number of flowers per plant.

- 1- Robustness:** An obvious difference between the two varieties, visible on all herbarium material studied, is that the specimens of *O. furcillata* var. *furcillata* are more robust than those of *O. furcillata* var. *caulescens*. *O. furcillata* var. *furcillata* is a relatively large plant (180–190 mm tall), with numerous leaves. Individual plants may display some variation with some specimens having an obvious, medium-length stem and a small number of leaves (Figure 3.1 A), while in others the petioles are clustered terminally around a very long stem (Figure 3.1 B), and in still others stems are very short, almost lacking, but bear numerous leaves with very long petioles (Figure 3.1 C). Specimens of *O. furcillata* var. *caulescens* display less morphological variation, with all plants being smaller (80–90 mm high), with a short stem (10–15 mm), short petioles (4–6 mm long) and fewer leaves (Figure 3.2).
- 2- Plant height:** Plants of *O. furcillata* var. *furcillata* (Figure 3.1) are taller (180–190 mm high) than those of *O. furcillata* var. *caulescens*, which are about 80–90 mm high.
- 3- Bulb type:** *O. furcillata* var. *furcillata* has darker, compound bulbs whereas the bulbs of *O. furcillata* var. *caulescens* are solitary (rarely two together) with lighter brown tunics.
- 4- Bulb length and shape:** In *O. furcillata* var. *furcillata* the bulbs are widely lanceoloid and 30–35 mm long (Figure 3.1 A), whereas those of *O. furcillata* var. *caulescens* are ovoid and 10–15 mm long as depicted in Figure 3.2.
- 5- Rhizome length.** *O. furcillata* var. *furcillata* (Figure 3.1 A & C) has longer rhizomes (40–70 mm) than *O. furcillata* var. *caulescens* (40–50 mm), as shown in Figure 3.2.
- 6- Petiole length.** Laminae of *O. furcillata* var. *furcillata* are borne on long petioles (14–16 mm), which results in the plant having a tufted, "open umbrella" appearance (Figure 3.1 A). In comparison the petioles of *O. furcillata* var.

caulescens are much shorter (4–6 mm), so that the plant looks more compactly tufted (Figure 3.2).

- 7- Petiole structure.** The petioles of *O. furcillata* var. *furcillata* are sometimes winged (Figure 3.4 A) and flattened (Figure 3.4 B) below the basal articulation, whereas those of *O. furcillata* var. *caulescens* are always winged below the basal articulation (Figure 3.3).
- 8- Leaf number and leaflet dimensions.** Leaves of *O. furcillata* var. *furcillata* are numerous (Figure 3.1 E), with longer and broader leaflets than *O. furcillata* var. *caulescens*. The latter has fewer leaves, with shorter and narrower leaflets than in the typical variety (Figure 3.2).
- 9- Number of flowers per plant.** *O. furcillata* var. *furcillata* usually displays *ca.* 4–12 flowers per plant (Figure 3.1 C–D), whereas *O. furcillata* var. *caulescens* always only has 1–2 flowers per plant (Figure 3.2).

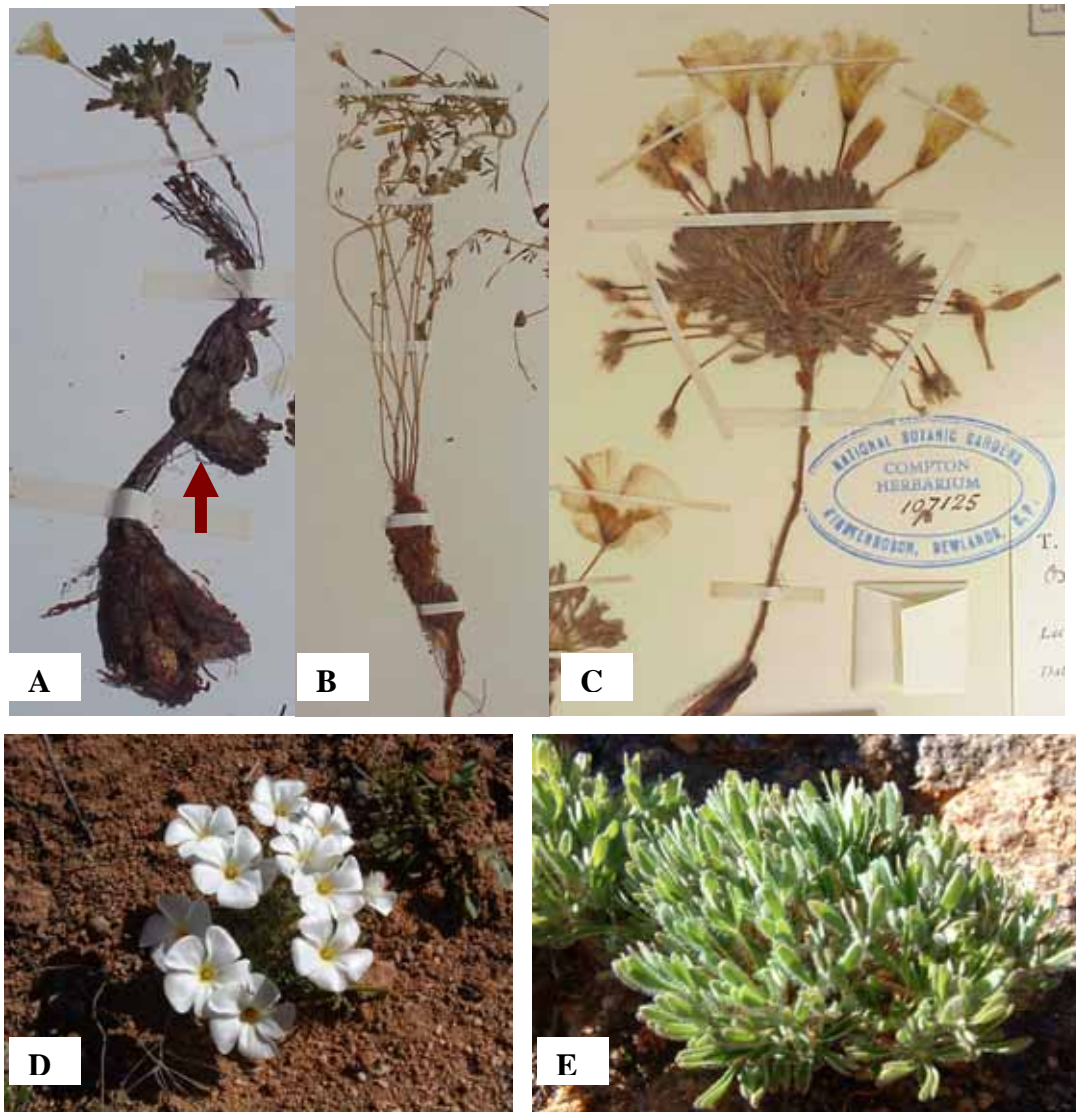


Figure 3. 1 Macro-morphology of *O. furcillata* var. *furcillata*. (A) arrow shows the presence of bulbils, *Oberlander 149* (STEU); (B) *Bayer 2236b* (NBG); (C) shows a robust plant with a very long rhizome, *Salter 2576* (NBG). D—E living plants showing numerous flowers, *Oberlander 22* (STEU) (D); and numerous leaves (E).

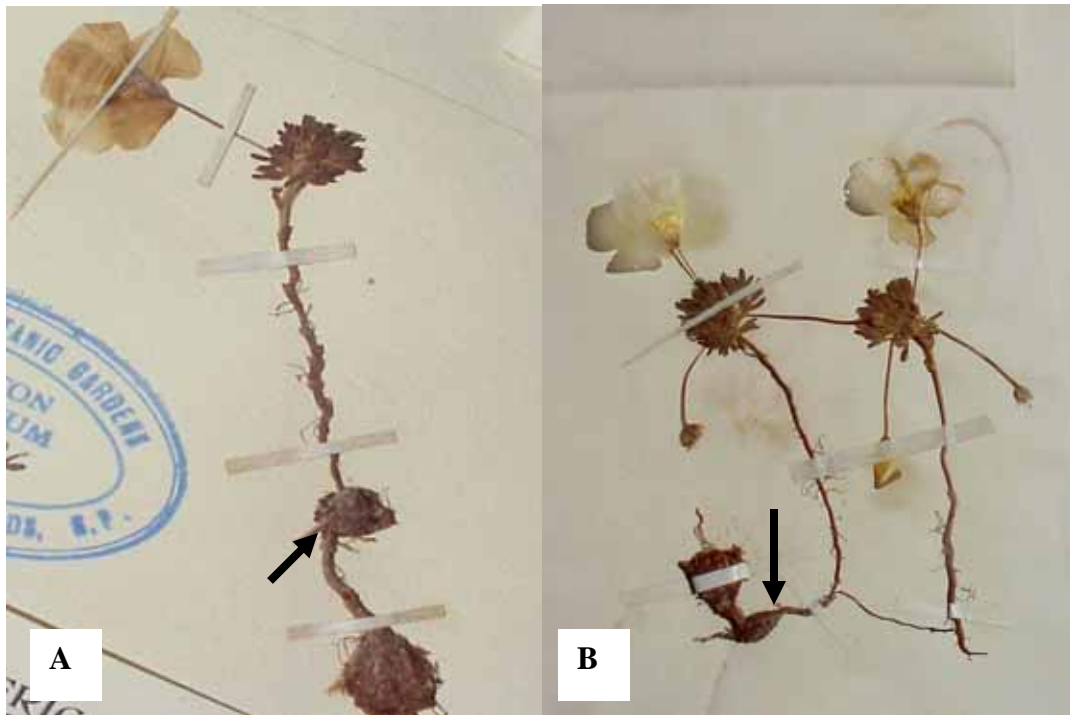


Figure 3. 2 Macro-morphology of *O. furcillata* var. *caulescens*: Salter 4570 (NBG) (A); Salter 5571 (NBG) (B); arrows indicate the bulbils.

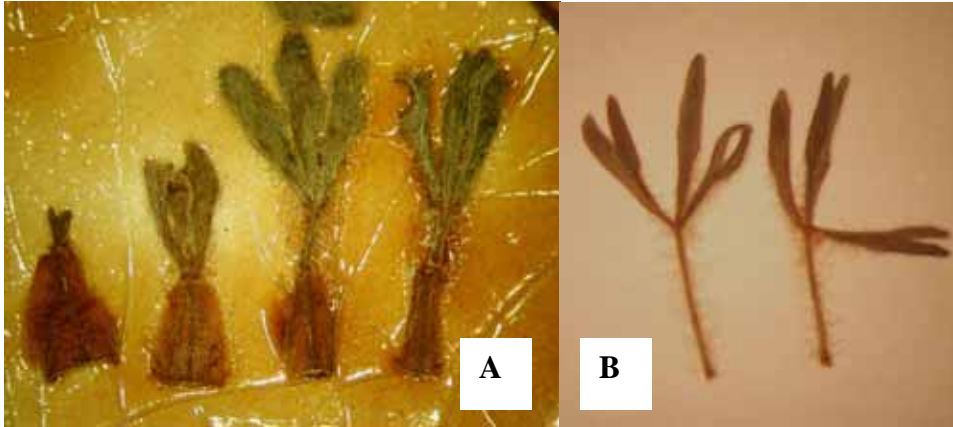


Figure 3. 3 Individual leaves of *O. furcillata* var. *caulescens*, showing the differences in petiole lengths and petiole structures below the basal articulations. (A) Reduced petioles of *O. furcillata* var. *caulescens* with distinct wings below the basal articulation of the petiole, *Salter 890* (NBG). (B) Long petioles of *O. furcillata* var. *caulescens* displaying no winged portion below the basal articulation, *Salter 1484* (NBG).



Figure 3. 4 Individual leaves of *O. furcillata* var. *furcillata*, showing the differences in petiole lengths and petiole structures below the basal articulations. (A) Reduced petioles of *O. furcillata* var. *furcillata* with distinct wings below the basal articulation of the petiole, *Beyer 3* (NBG). (B) very long petioles of *O. furcillata* var. *furcillata* that display a flattened portion below the basal articulation, *Beyer 3* (NBG).

3. 2 Statistical analysis

The morphological variability of quantitative characters of the two taxa was statistically assessed. These characters included plant height, bulb length, petiole length, leaflet length, leaf width and peduncle length. In these analyses *O. furcillata* var. *furcillata* is consistently given as taxon 1 and *O. furcillata* var. *caulescens* as taxon 2.

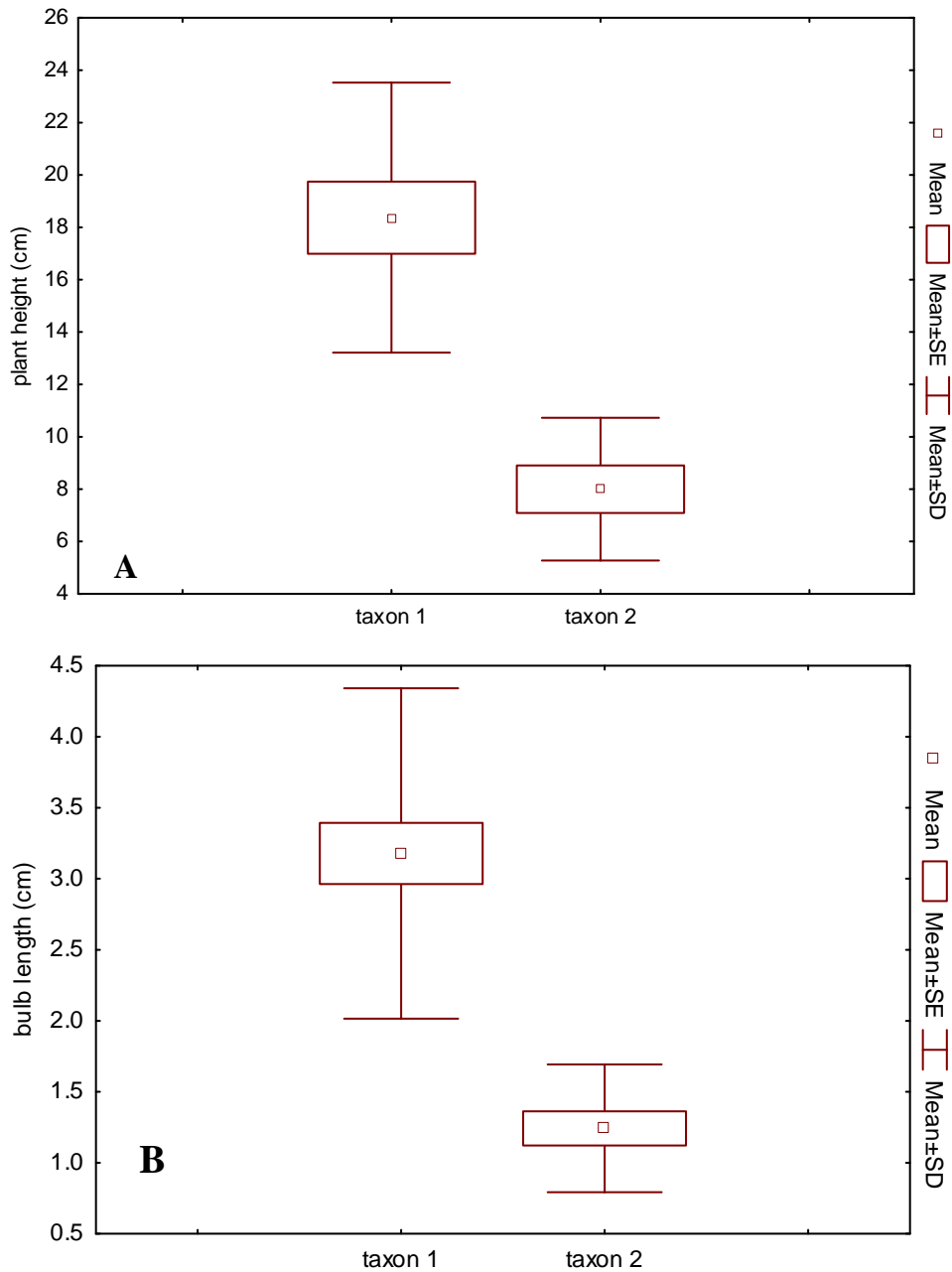


Figure 3. 5 (A): Box plot of comparative plant height of *O. furcillata* var. *furcillata* (taxon 1) and *O. furcillata* var. *caulescens* (taxon 2) based on herbarium specimen data only. (B): Box plot of comparative bulb length values are plotted for *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*. The mean and standard errors are indicated for each species. Plant height of *O. furcillata* var. *furcillata* is significantly longer (mean = 190 mm) than that of *O. furcillata* var. *caulescens* (mean = 90 mm). Bulb length of *O. furcillata* var. *furcillata* is also significantly longer (mean = 33 mm) than that of *O. furcillata* var. *caulescens* (mean = 13 mm).

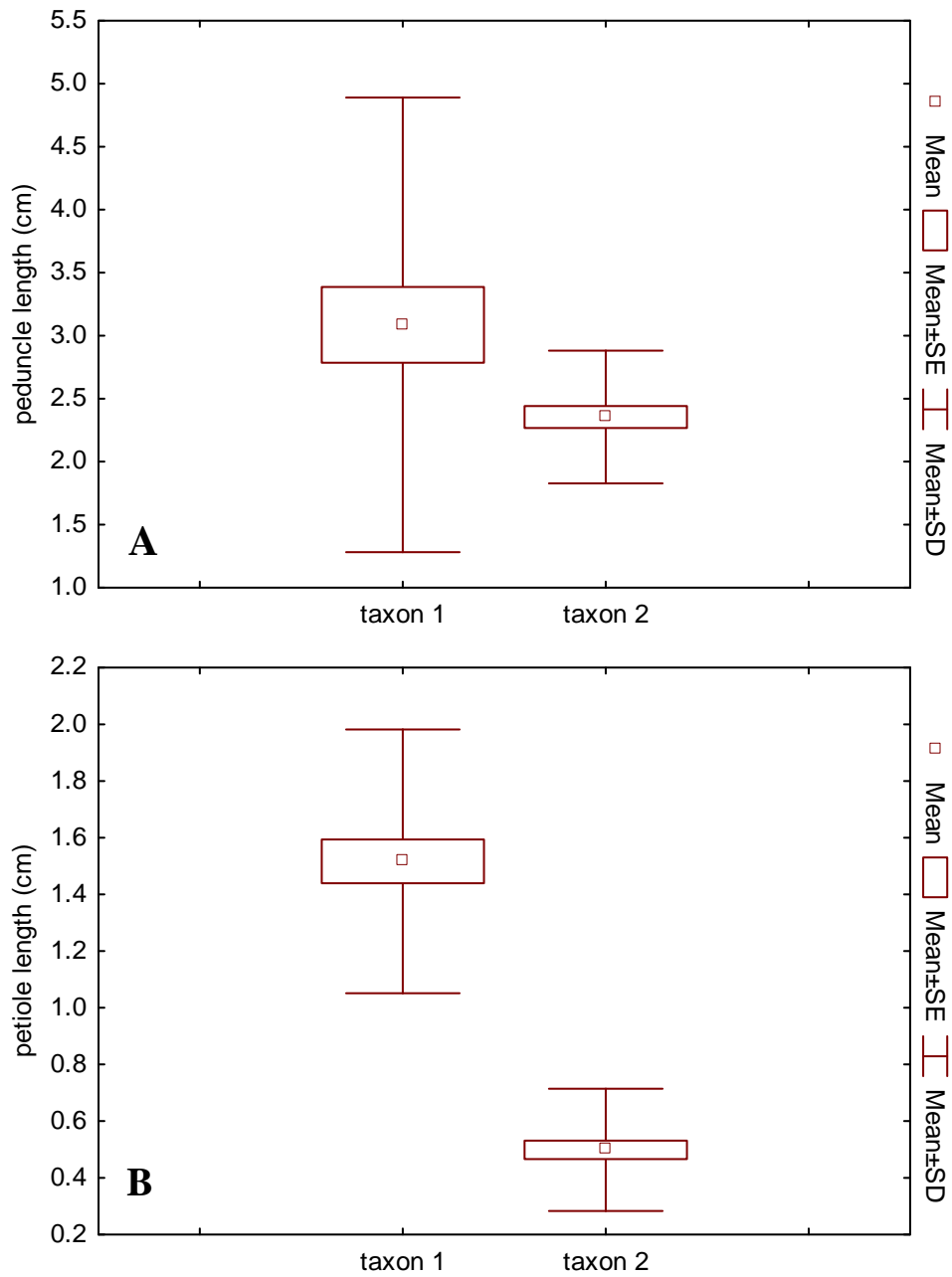


Figure 3. 6: A—B. Box plots of comparative peduncle length (A) and petiole lengths (B) of *O. furcillata* var. *furcillata* (taxon 1) and *O. furcillata* var. *caulescens* (taxon 2) based on herbarium specimen data only. The box plot for *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* based on petiole length shows that *O. furcillata* var. *furcillata* has longer petioles (mean = 15 mm) than *O. furcillata* var. *caulescens* (mean = 5 mm), and *O. furcillata* var. *furcillata* has longer peduncles (mean = 32 mm) than *O. furcillata* var. *caulescens* (mean = 25 mm).

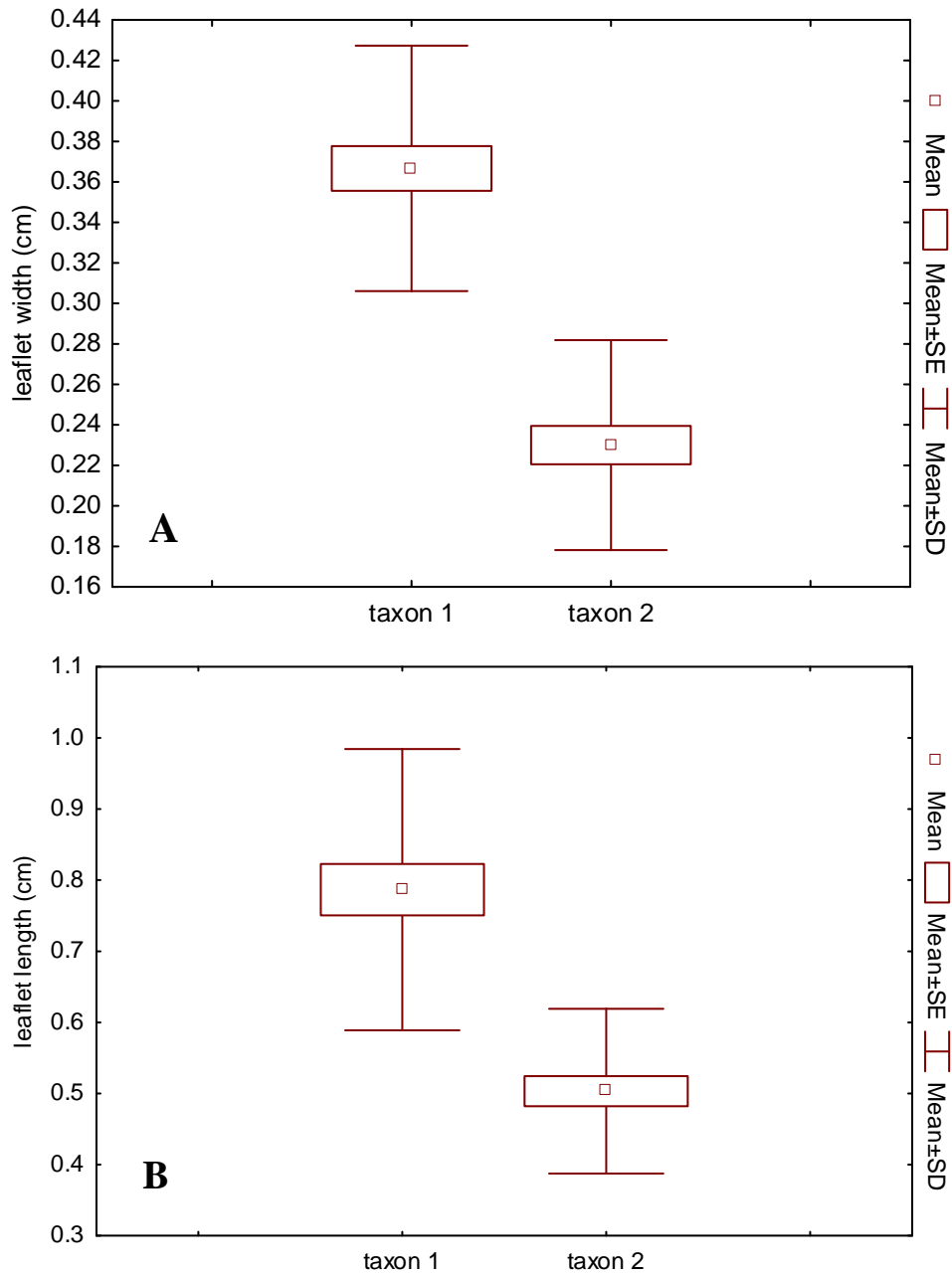


Figure 3. 7 A—B. Box plots of comparative leaflet width (A) and leaflet length (B) of *O. furcillata* var. *furcillata* (taxon 1) and *O. furcillata* var. *caulescens* (taxon 2) based on herbarium specimen data only. The box plot for *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* based on leaflet width shows that *O. furcillata* var. *furcillata* has wider leaflets (mean = 3.7 mm) than *O. furcillata* var. *caulescens* (mean = 2.3 mm), and *O. furcillata* var. *furcillata* also has longer leaflets (mean = 8 mm) than *O. furcillata* var. *caulescens* (mean = 5 mm).

3. 3 Palynological study

The current study confirmed the palynological results of Dreyer (1996). The pollen grains of both varieties are tricolpate, and are triangularly rounded in polar view and spherical in equatorial view. Colpi of the pollen grains of both varieties are elongated and covered with granular colpal membranes. The scanning electron micrographs (Figures 3.8 and 3.9) show that the structure of the tectum is different in the two varieties. Both taxa have pollen grains with a reticulate tectum, but in *O. furcillata* var. *furcillata* the tectum is micro-reticulate with rounded to oblong to slightly angular muri and there is a consistent lack of intraluminary bacula (Figure 3.8). Dreyer (1996) described this pollen type as C2. The tectum of the pollen grains of *O. furcillata* var. *caulescens* is finely reticulate with irregularly angular lumina and prominent intraluminary bacula clustered along the muri (Figure 3.9), which Dreyer (1996) referred to as pollen type C10.

The pollen grains of the two varieties of *O. furcillata* differ in terms of the following three characters:

1. **Tectum type:** Pollen type C2 found in *O. furcillata* var. *furcillata* has a micro-reticulate tectum, whereas the tectum of the C10 pollen type of *O. furcillata* var. *caulescens* is finely reticulate (Figures 3.8 and 3.9).
2. **Lumina shape:** The lumina are rounded to oblong to slightly angular in *O. furcillata* var. *furcillata*, while they are irregularly angular in *O. furcillata* var. *caulescens* (Figures 3.8 and 3.9).
3. **Intra-luminary bacula:** Mesocolpal intraluminary bacula are absent in the pollen grains of *O. furcillata* var. *furcillata* and present in the pollen grains of *O. furcillata* var. *caulescens* (Figures 3.8 and 3.9).

These three pollen characters can be added to the morphological characters discussed above to distinguish between *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*. Dreyer (1996) regarded these two pollen types as distinctly different, and this is partially supported by the preliminary molecular phylogeny of the genus based on *trnL-F* and ITS sequence data (Oberlander *pers. com.*). The majority of species with pollen type C10, group together in a well-resolved clade. This is embedded in larger clade where species bear mostly C2 type pollen (Oberlander *pers. com.*).

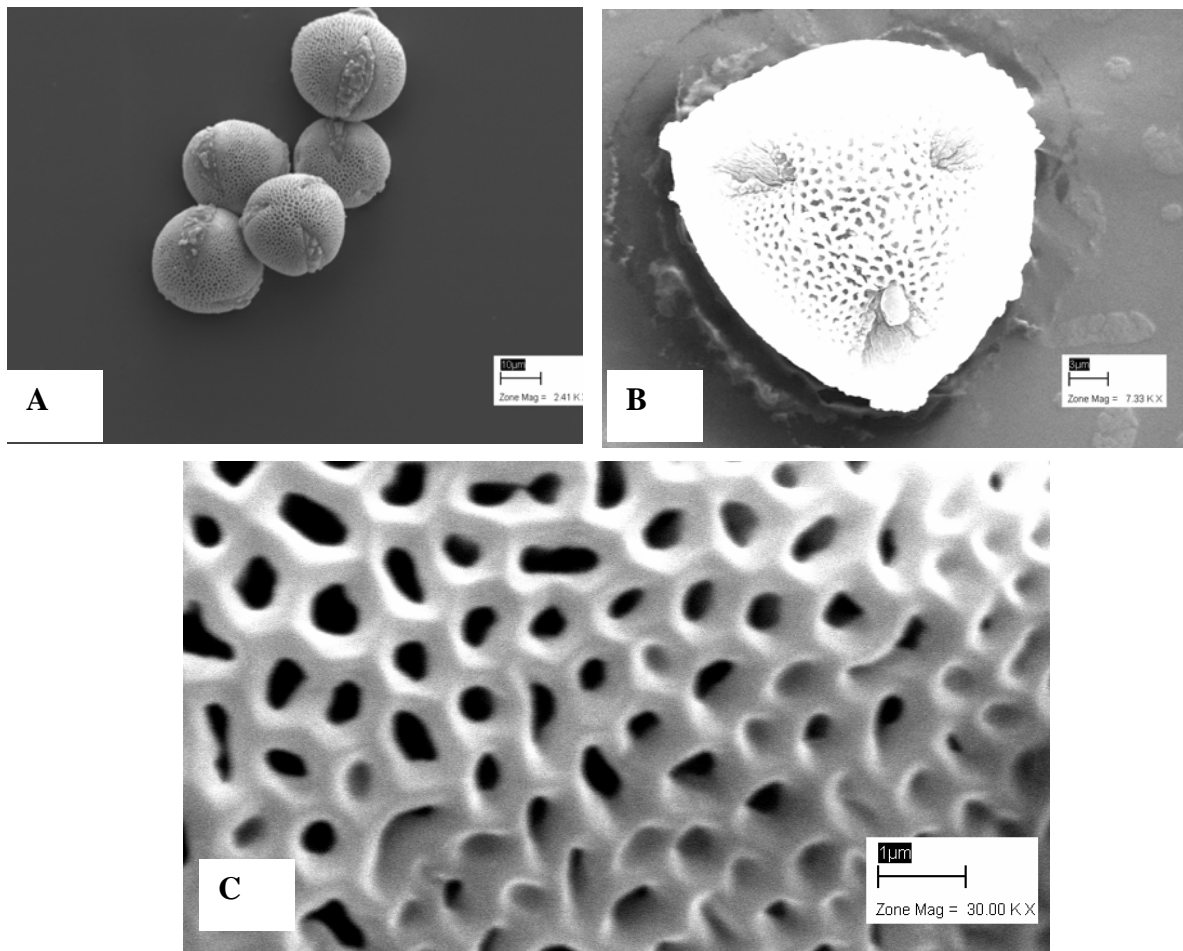


Figure 3. 8: A—C. Scanning electron micrographs of pollen grains of *O. furcillata* var. *furcillata*. (A) Pollen grains in equatorial and polar view, *Dreyer 702* (STEU); (B) pollen grain in polar view showing three colpi, *Bayer 2236b* (NBG); (C) Mesocolpial portion of the sexine showing a reticulate tectum with rounded to oblong to slightly angular muri, *Dreyer 702* (STEU). Note the absence of intraluminary bacula.

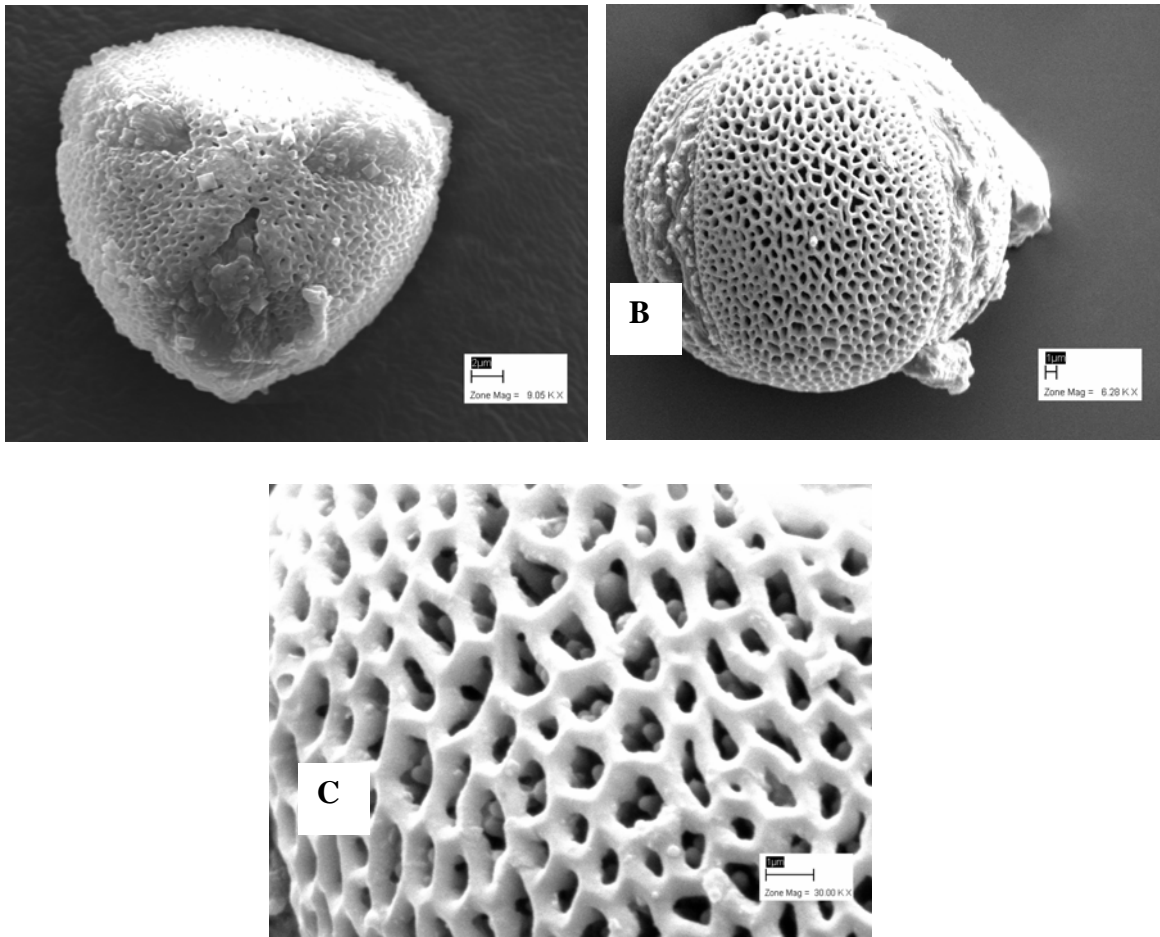


Figure 3. 9: A—C. Scanning electron micrographs of pollen grains of *O. furcillata* var. *caulescens*. (A) Pollen grain in polar view, *Salter 6674* (BOL); (B) pollen grain in equatorial view showing colpi, *Salter 1484* (BOL); (C) mesocolpial portion of sexine showing finely reticulate tectum with irregularly angular muri, *Le Roux 3936* (PRE). Note the presence of intraluminary bacula clustered along the muri.

3. 4 Geographical distribution

According to herbarium records, both *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* have small distributional ranges in the Northern Cape Province of South Africa (Figure 3.10) with the highest concentration in grid squares 2917 and 3017. In these grids the distributions of the two varieties overlap. Despite this, no intermediate forms have been found. The peak flowering time for both taxa is from June to July, although MO 228 was collected flowering as late as September.

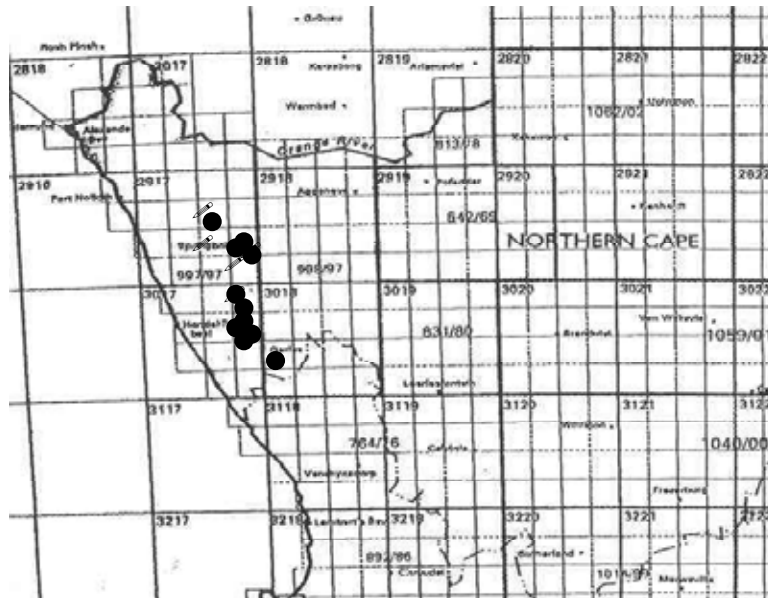


Figure 3.10: Geographical distributions of *O. furcillata* var. *furcillata* (!) and *O. furcillata* var. *caulescens* (#).

Chapter 4 Discussion and Conclusions

This chapter will first highlight the degree of morphological variation between selected taxa in section *Foveolatae* in order to evaluate the level of variation between different taxonomic ranks as described by Salter (1944). This information will then be used to compare *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* in order to assess the level of taxonomic relatedness of these two taxa.

4.1 Character analysis of the groups defined within section *Foveolatae*

Members of section *Foveolatae* resemble each other in terms of only a few morphological characters. Species can mostly only be distinguished from each other by particular character combinations. All members of the section have endospermous seeds, except for *O. furcillata* and its varieties that have exendospermous seeds. Salter (1944) divided the section into three main groups. The first group comprises two species, *O. convexula* Jacq. and *O. attaquana* Salter, and is characterized by having a well-exserted above-ground stem. The second group includes all the stemless taxa and comprises 22 species. Within this group *O. pulchella* Jacq includes five varieties and *O. punctata* L. f. three forms. The criteria used to select only some of the species for consideration in the current study will be discussed later in the detailed analysis of this group. The third group includes species with bifurcate, non-fleshy leaflets. This is a monotypic group including only *O. furcillata* (which includes the typical variety and *O. furcillata* var. *caulescens*). The latter taxon is the main focus of the present study. Morphological characters of members of this section display a certain level of variation and the following discussion will highlight some of the variation as described by Salter (1944).

4. 1. 1. Character analysis of species with well-exserted stems, Group 1: (*O. convexula* and *O. attaquana*).

a. Vegetative characters of subterranean parts

The subterranean parts of members of this group mainly consist of only a bulb. Rhizomes have not been described in either of the two included species, and are thus considered inconspicuous. Bulbs of *O. convexula* are narrowly ovoid with attenuate or subrostrate apices and covered with imbricating, rather thin, rough, reddish-brown tunics (Figure 4.1 C). In *O. attaquana*, the bulbs are ovoid and attenuate at the apex, covered with blackish-brown, longitudinally ribbed tunics. In the latter species a contractile root is also present, which is lacking in *O. convexula*.

b. Vegetative characters of the above-ground parts

Characters (and character states) of above-ground parts that are compared include characters of the stems, leaves, petioles and leaflets. The stems of *O. convexula* are thick (Figure 4.1 A) and usually exerted (rarely not), while the stems of *O. attaquana* are unbranched (Figure 4.1 D) or bifurcate, with several large, brown, ovate or ovate-lanceolate cuspidate, amplexicaul scales. Leaves of *O. convexula* are often numerous, and closely congested or spreading. *O. attaquana* has 8–24 leaves per plant that are imbricate and congested at the upper part of the stem. The petioles of *O. convexula* are longer (up to 50 mm) than those of *O. attaquana* (up to 30 mm). Petioles of *O. convexula* are dilated into prominent submembranaceous-stipuliform wings below the basal articulation, while the petioles of *O. attaquana* are squamiform below the basal articulation. Both species have three fleshy leaflets per leaf, and in *O. convexula* leaflets are entire, and the medial leaflets are shortly petiolulate, subrotund and widely attenuate at the base. The lateral leaflets are obliquely rotund or sub-semicircular, and rather smaller than the median leaflets. Leaflets of *O. attaquana* are conspicuously lobed and rounded at the apex. The medial leaflets are shortly petiolulate and the lateral leaflets are sessile, obreniform and attenuate at the apex.

c. Reproductive characters

Peduncles

In *O. convexula* the peduncles are usually longer than the petioles, while the peduncles of *O. attaquana* are about twice as long as the leaves. Both species have two linear, alternate bracts on their peduncles. The bracts are oblanceolate, membranous and occur toward the calyx in *O. convexula*, whereas in *O. attaquana* the bracts occur just above the middle of the peduncle.

Floral parts

Sepals are ecallose, ovate or oblong, obtuse and sub-membranaceous in *O. convexula* and broadly lanceolate, subobtuse and often purplish in *O. attaquana*. In *O. convexula*, corollas are pale salmon-rose, with a short, widely funnel-shaped yellow tube. Petals are broadly and obliquely cuneate or subtriangular or obliquely truncate. They are twice or three times as long as the attenuate claw (Figure 4.1 A–C). Ovaries have about 18 ovules per locule. In *O. attaquana* corollas are rose coloured, with a narrowly funnel-shaped yellow tube. Petals are obliquely cuneate, slightly attenuate at the base and rounded at the apex (Figure 4.1 D). Ovaries have about 8 ovules per locule.

d. Indumentum

All parts of *O. convexula* are glabrous, except for a few glandular hairs on the filaments and on the upper half of the ovaries. Styles are also minutely glandular. In contrast, many parts of *O. attaquana* are covered with long hyaline, pluricellular hairs. *O. attaquana* leaflets are sparsely ciliate with pluricellular and capitate hairs along the margins. Similar hairs also occur abaxially along the main vein. Pluricellular hairs are also found in the yellow corolla tube of *O. attaquana*.

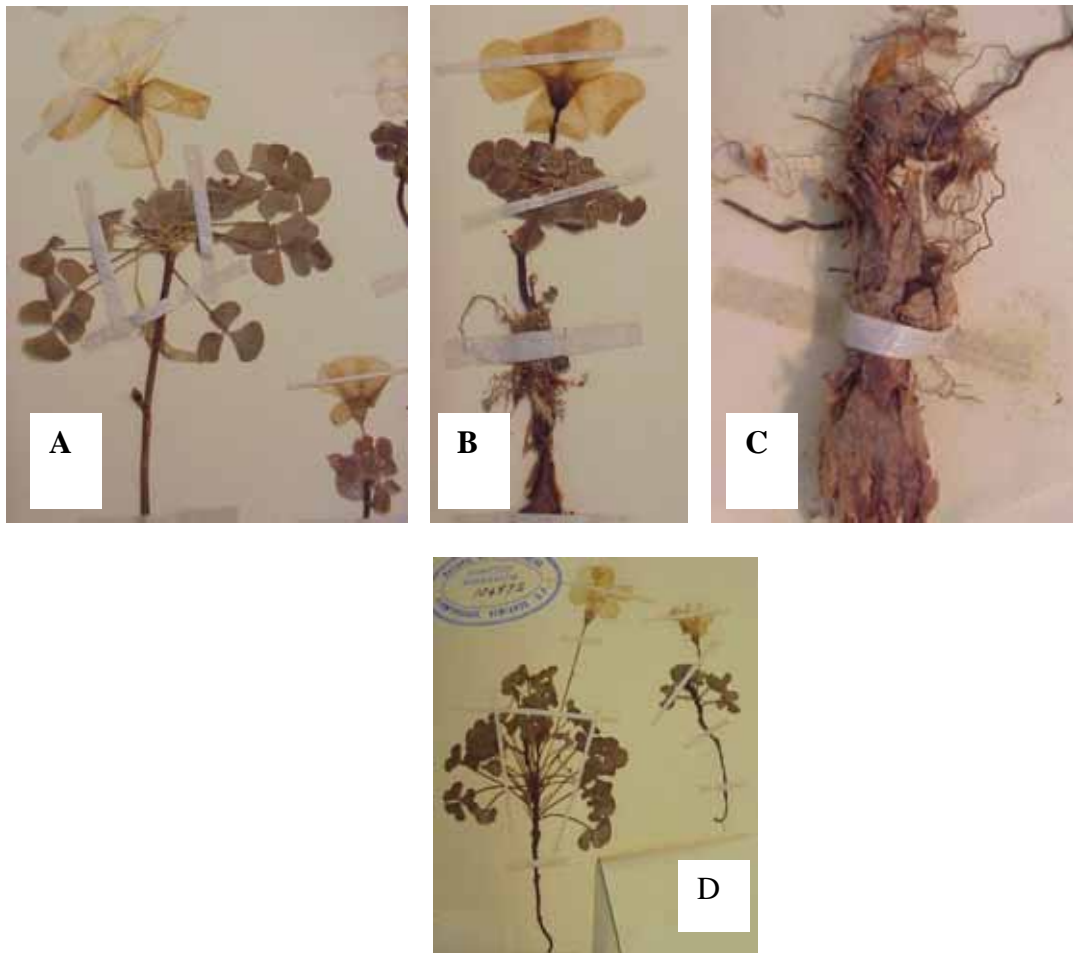


Figure 4. 1. A–C: Macro-morphology of *O. convexula*, Salter 1049 (BOL). (A) Plant with long petioles. (B) Plant with congested leaves. (C) Bulb covered with reddish brown tunics. D: Macro-morphology of *O. attaquana*, Salter 2341 (BOL), showing the unbranched stem of this species.

4. 1. 2 Character analyses of the stemless species, Group 2: (*O. pulchella*, *O. foveolata*, *O. punctata*, *O. senecta* and *O. densa*).

Although this group in section *Foveolatae* includes a total of 22 species, only the species *O. pulchella* Jacq., *O. foveolata* Turcz., *O. punctata* L. f., *O. senecta* Salter and *O. densa* N.E.Br. were selected for comparison with Group 3 (*O. furcillata*), which form the focus of the present study. The choice of *O. pulchella* and *O. foveolata* was motivated by the fact that they both occur in Namaqualand in the Northern Cape of South Africa, the same area to which *O. furcillata* is confined. The selection of *O. densa* and *O. senecta* was motivated by the fact that Salter (1944) regarded them to be more closely related to *O. furcillata* than the rest of the members of section *Foveolatae*. Additionally, the selection of these taxa allowed an assessment of Salter's (1944) demarcation between related, morphologically similar species (*O. foveolata* and *O. pulchella*), between different varieties of *O. pulchella* (var. *tomentosa* Sond., var. *glaucula* Salter, var. *leucotricha* (Turcz.) Salter and var. *beneprotecta* R. Knuth) and between different forms (form A, B and C) of the species *O. punctata*.

Comparison between *O. pulchella* and *O. foveolata*

a. Vegetative characters of subterranean parts

The underground parts of both of these species comprise both bulbs and rhizomes. *O. foveolata* has ovoid bulbs with acute apices. The bulbs are covered with dark brown, gummy tunics. The rhizomes are slender with a few, small, semi-amplexicaul scales at the apex. In contrast, bulbs of *O. pulchella* are obclavate or narrow-ovoid, with attenuate or rostrate apices and rough, gummy, dark brown tunics (Figure 4.2 C). The inner tunics are vertically ridged. The rhizomes are rather robust, with large broadly ovate scales near the apex that are often partly enclosed within the old tunics through the action of the contractile root.

b. Vegetative characters of above-ground parts

O. foveolata has 6–10 leaves per plant, borne on short (10–20 mm long) petioles. Each leaf has three subsessile, rather fleshy leaflets. The median leaflets have rotund apices,

and more or less cuneate to attenuate bases. The lateral leaflets are oblique, somewhat smaller and narrower than the medial leaflet, and often slightly retuse on the inner margin (Figure 4.2 A). *O. pulchella* has 6–30 leaves per plant, borne on 5–30 mm long petioles. All three leaflets are subsessile and fleshy. The median leaflets are subsecuriform, semicircular in the upper half and retusely attenuate toward the base. The lateral leaflets are rather smaller and narrower than the medial leaflet, and is retuse along the inner margin (Figure 4.2 B).

c. Reproductive characters

Peduncle

The peduncle of *O. foveolata* carries two callus-tipped, alternate bracts, situated on the upper half of the peduncles, while the peduncle of *O. pulchella* has two alternating, linear bracts near the base, both with a few calli on their upper regions.

Floral characters

Both species have ovate or oblong sepals with apical calli. In *O. pulchella* the sepals are also obtuse, submembranous and pale straw-coloured, whereas in *O. foveolata* they are straw-coloured, sometimes with purple striations along the margins. The corollas of *O. foveolata* have yellow, cylindric to funnel-shaped tubes and the petals are cuneate, obovate or subtruncate and slightly longer than the narrow claw. The filaments are edentate and there are about 7 ovules per locule. The longest styles are well-exserted from the corolla tube. The corollas of *O. pulchella* have pale yellow, funnel-shaped tubes and white, pale yellow or pale salmon-rose petals. The petals are broadly cuneate, obovate or obliquely subtruncate at the apices, and they are rather longer than the claw. The filaments are edentate and the ovaries have many ovules per locule.

d. Indumentum

In *O. foveolata* the petioles and peduncles are coarsely pubescent, the leaflets adaxially glabrous or pilose and abaxially more or less pilose, the sepals pubescent and ciliate, ovaries densely pubescent and the filaments very minutely glandular. The petioles of

O. pulchella are densely hirsute, the leaflets adaxially hirsute along the veins and abaxially pilose, and the peduncles and sepals are pilose, although the sepals can also be ciliate. Both the corolla and filaments are glabrous, although the filaments may also be minutely glandular. The ovaries are hirsute on the upper half and the styles glandular towards their apices.



Figure 4. 2: Macro-morphology of *O. fovoelata* and *O. pulchella*:

A: *O. fovoelata* leaves showing the morphology of the lateral and the medial leaflets, Salter 913 (BOL). B: *O. pulchella* leaves, Salter 3707 (BOL). C: bulb of *O. pulchella*, Salter 3707 (BOL).

Character analysis of the four varieties of *O. pulchella*

O. pulchella includes the varieties *O. pulchella* var. *tomentosa*, *O. pulchella* var. *glauca*, *O. pulchella* var. *leucotrichia* and *O. pulchella* var. *beneprotecta* that differ mainly in terms of leaflet and corolla characters. In *O. pulchella* var. *tomentosa* leaflets are rotund, greenish, usually abaxially glabrous, with numerous minute calli along the margins. The median leaflets are usually as broad as or broader than long (Figure 4.3 E). The corolla is pale or salmon rose and the limbs of the petals are proportionately long and broad. In *O. pulchella* var. *glauca* the medial leaflets are more or less rotund, broadly cuneate or sub-rhomboid (Figure 4.3 C). Plants are more densely covered with hairs and the leaves are glaucous-grey. The leaflets are adaxially evenly pilose-glabrescent, sometimes with a few inconspicuous calli at the apices. The corollas are pale yellow or white with a yellow tube. The limbs of the petals are broad and the apices truncate. In *O. pulchella* var. *leucotrichia* the leaflets are oblong or ligulate, obtuse and adaxially sparsely hirsute. The lateral leaflets are slightly oblique (Figure 4.3 F). The corollas are pale yellow to salmon. The petioles and peduncles of this variety are densely hirsute and the upper half of the ovary is pilose, interspersed with glandular hairs and with a few hyaline hairs near the apex. Members of *O. pulchella* var. *beneprotecta* are smaller in terms of all plant parts and the indumentum is less dense. The leaves are rosulate, spreading, often very numerous (up to 200) forming dense flat tufts (Figure 4.3 A). The leaflets are glaucous-grey, almost glabrous. The median leaflets are cuneate, rotund at the apex or cuneate or rhomboid in shape. The corollas are pale yellow and the corolla tubes are broad. The petioles are usually pilose and the peduncles are very short.

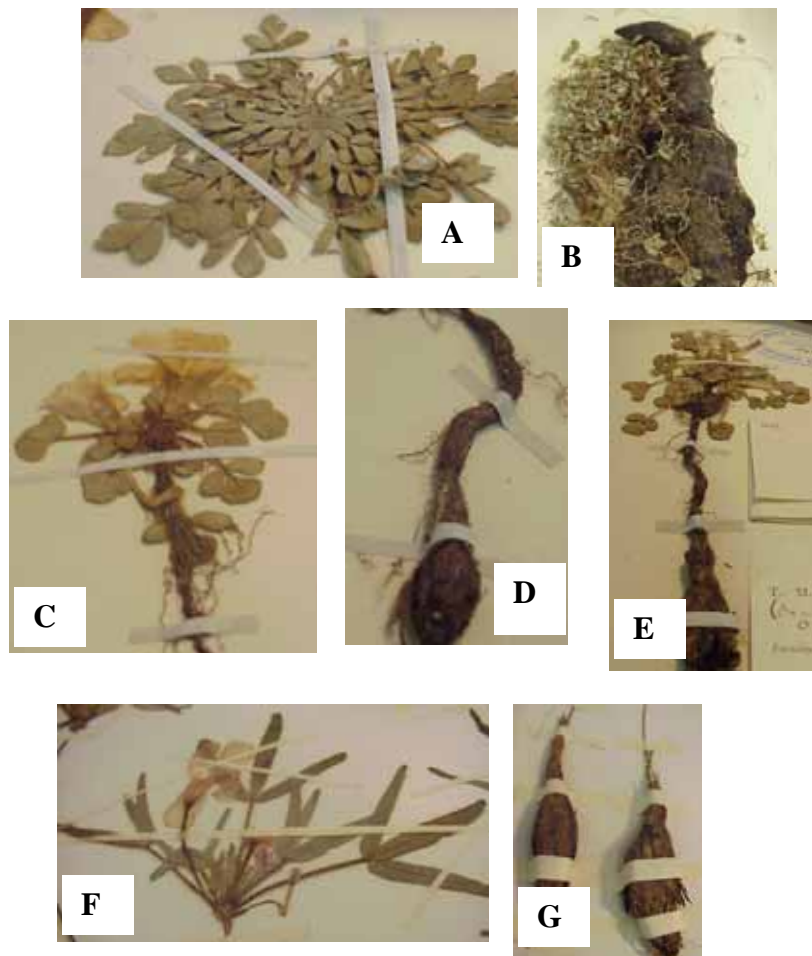


Figure 4. 3. Macro-morphology of *O. pulchella*:

A—B. var. *beneprotecta* (A), plant showing a dense flat tufted growth form, *Salter1407* (BOL). (B), the bulb of var. *beneprotecta*, *Salter 4590* (BOL).

C—D. var. *glauca* (C), plant with broadly cuneate or sub-rhomboid medial leaflets, *Salter 847* (BOL). (D), bulb of var. *glauca*, *Salter 803* (BOL).

E. var. *tomentosa*, *Salter1256* (BOL) whole plant.

F—G. var. *leucotrichia* (F), whole plant showing the slightly oblique lateral leaflets and (G), picture of the narrow, ovoid bulbs, *Salter 6651* (BOL).

Character analysis of *O. punctata*

a. Vegetative characters of subterranean parts

Bulbs and rhizomes represent the underground parts of all the forms of this species. Bulbs are broadly ovoid, attenuate at the base and often shortly rostrate at the apex. The bulbs are covered with hard, dark brown, pitted tunics that are sharply and irregularly angled. Rhizomes are slender and usually short.

b. Vegetative characters of above ground parts

The number of leaves per plant varies from 3–10 (rarely numerous) (Figure 4.4 A, C & E). The petioles are between 10–20 mm long, and the older petioles are usually broadened with stipule-like wings below the basal articulation. The leaflets are subsessile or shortly petiolulate, the medial leaflets are widely cuneate or rotund and flattened and slightly incised or retuse.

c. Reproductive characters

Peduncle

The peduncles are twice as long as the leaves (Figure 4.4 A, C & E), with two minute, alternate bracts situated on the upper part.

Floral characters

Sepals are narrowly oval, ovate or obovate with obtuse apices. The corollas are white or pale violet, with a rather wide yellow or greenish-yellow, funnel-shaped tube. Petals are basally cuneate and rounded at the apex. The filaments are gibbose and edentate and the ovaries include 4–6 ovules per locule.

d. Indumentum

Plants of *O. punctata* are more or less densely covered with pluricellular glandular hairs, except on the leaflets. The sepals and corollas are glandular and pilose and ciliate, while the filaments and styles are minutely glandular-pilose.

Character analysis of the three forms of *O. punctata*

Salter (1944) recognized three forms (A, B and C) in *O. punctata*. Form A is the typical form, which includes small plants (Figure 4.4 A) with sharply angled bulbs (Figure 4.4 B). Form B includes intermediate sized plants (Figure 4.4 C) with scarcely angled bulbs (Figure 4.4 D), while form C includes plants that are larger in terms of all plant parts (Figure 4.4 E), often with numerous leaflets and roughly veined bulbs (Figure 4.4 F).

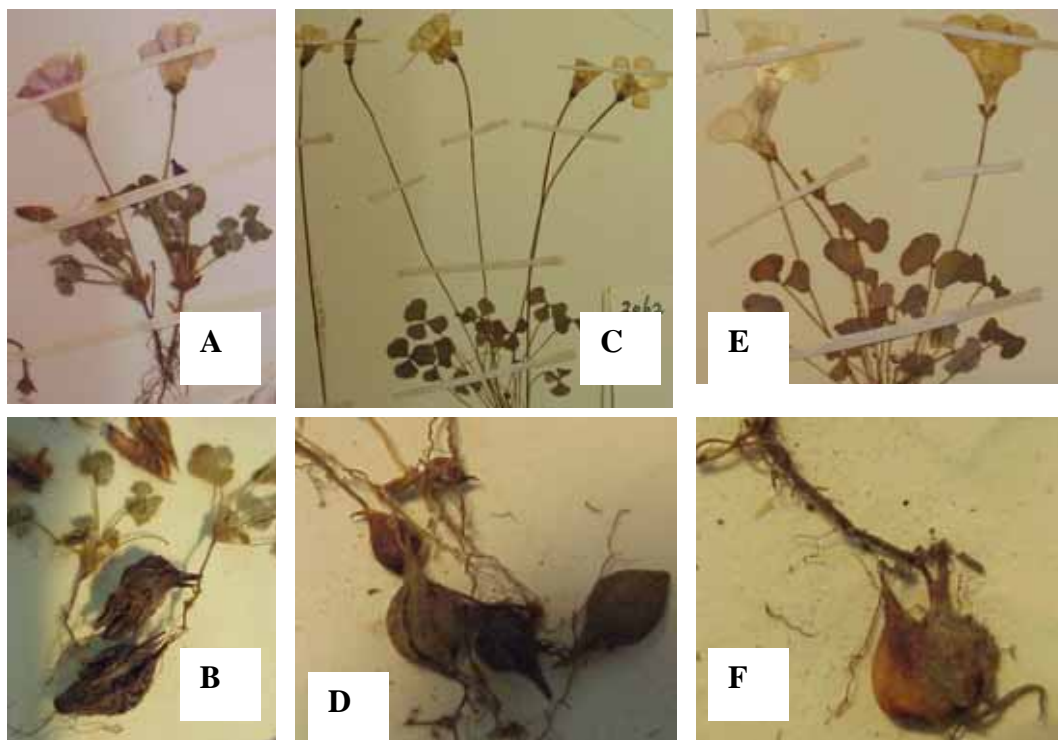


Figure 4. 4. Macro-morphological characters of *O. punctata*. A & B: Form A, *Salter 8090* (BOL). (A) small plant, (B) angled bulb. C & D: Form B, (C) *Salter 2060* (NBG), intermediate sized plant, (D) *Salter 3277* (NBG), scarcely angled bulb. E & F: Form C, *Salter 3177* (NBG). (E) large plant and (F) roughly veined bulb.

Species *O. senecta* and *O. densa*

In the species analysis of section *Foveolatae*, Salter (1944) placed *O. senecta* and *O. densa* next to *O. furcillata*, probably indicating that he regarded them as being more closely related to *O. furcillata* than the rest of the members of section *Foveolatae*.

a. Vegetative characters of subterranean parts

The subterranean parts of *O. senecta* and *O. densa* consist of bulbs and rhizomes. The bulbs of these two species are very different from each other in terms of shape and tunic type. The bulbs of *O. senecta* are elongated and surrounded by a congested mass of papery, shiny, brownish tunics (Figure 4.5 D). The outer tunics are lanceolate and sharply pointed at the apices, while the inner tunics are paler and much thinner than the outer tunics. Its rhizome is short and slender. Specimens of *O. densa* have elongated bulbs (Figure 4.5.B). The outer tunics are blackish brown, lanceolate or linear-lanceolate, sharply acute, with three conspicuous dark veins splitting from the base. The inner tunics are linear and pale brown. Rhizomes are slender and 80–100 mm long, rarely branched, and with a few, small, membranous scales.

b. Vegetative characters of above-ground parts

The features of the above-ground vegetative parts include characters of the stems, leaves, petioles and leaflets. The number of leaves per plant in *O. senecta* varies from 9–15. Petioles of this species are dilated and squamiform below the basal articulation. There are three petiolulate leaflets that are thin, basally cuneate, incised at the apex and usually conduplicate (Figure 4.5 C). In *O. densa* the leaves are numerous and densely congested. This species has scale-like, membranous petioles with three veins below the basal articulation. The leaflets are subsessile, cuneate or attenuate at the base and bilobed to about the middle. The individual lobes are linear or oblong (Figure 4.5 A).

c. Reproductive characters

Peduncle

Both species have two alternate bracts on their peduncles. In *O. senecta* the bracts are linear, villous and occur slightly below the calyx, whereas bracts of *O. densa* are filiform and occur toward the apex of the peduncle.

Floral parts

The sepals of *O. senecta* are ecallose, while those of *O. densa* are calli-dotted or lined. Both species have white corollas with short and broad, funnel-shaped, yellow tubes. The flower morphology of *O. senecta* and *O. densa* only differ in terms of the shape of their petals. *O. senecta* specimens have broadly cuneate or obovate petals that are obliquely subtruncate at the apex. The petals are rarely abaxially purple dotted on the outer margin and are three times as long as the tapering claws. *O. densa* has cuneate, subtruncate petals, which are abaxially purple-dotted along the outer margin. The filaments of both species are slightly gibbose with more or less the same dimensions. In *O. senecta* the ovaries are oblong with about 24 ovules per locule. In *O. densa* there are about 12 ovules per locule and the ovaries are pilose on the upper half. The lower half of the styles of *O. senecta* is sparsely pilose and the upper half minutely glandular, whereas in *O. densa* the styles are glandular or pubescent (Figure 4.5).

d. Indumentum

The different plant parts of both species are covered with hairs. The petioles of *O. densa* are densely villous with patent hairs, while *O. senecta* petioles are villous. The leaflets of *O. senecta* are both ad- and abaxially villose with ciliate margins, while the leaflets of *O. densa* are only abaxially villose. In *O. senecta* peduncles are densely retrorse-villose in the apical region, sepals are ciliate and the petals are densely pilose. In *O. densa*, the peduncles are villose and the sepals villose or pubescent and ciliate. The petals are pubescent and purpled-dotted along the abaxial side of the outer margin.

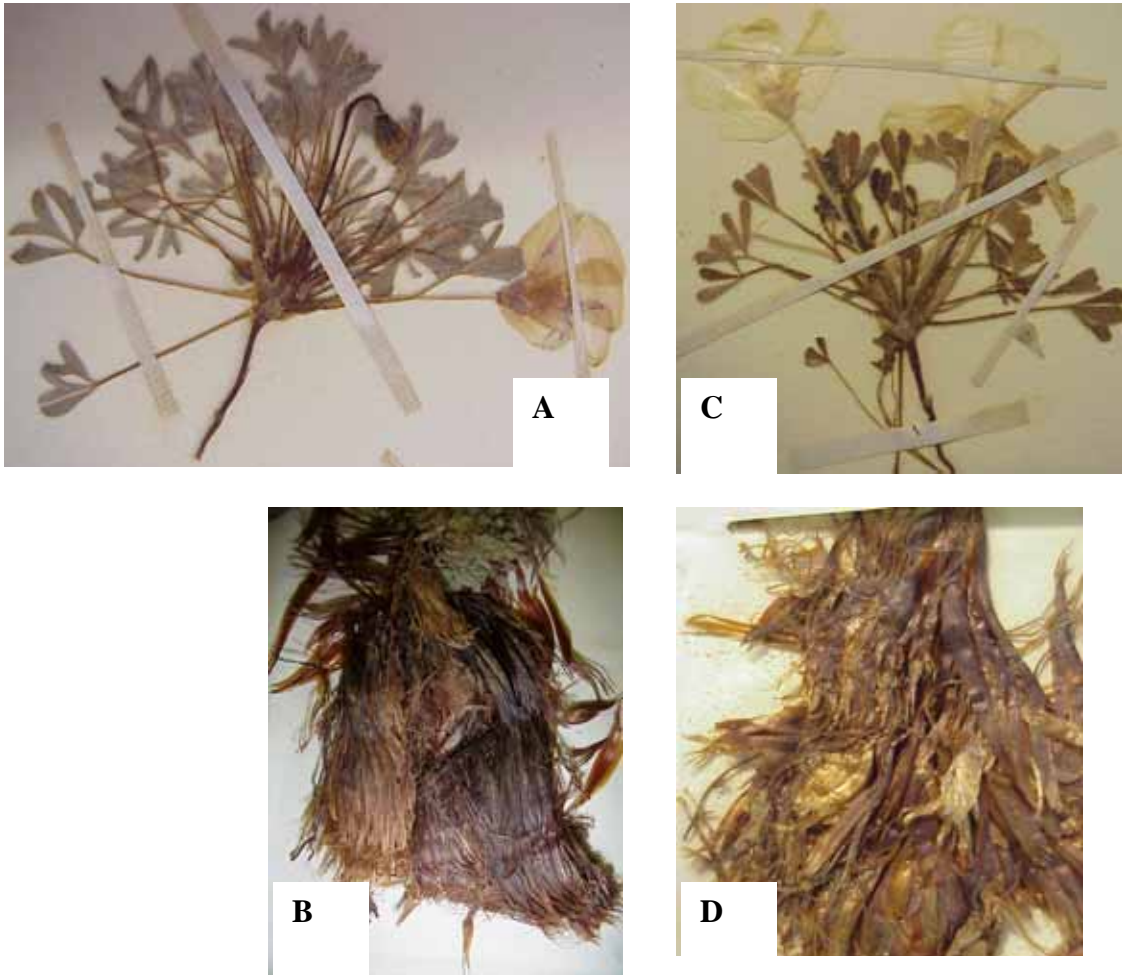


Figure 4. 5 Macro-morphology of *O. densa* and *O. senecta*. A & B: *O. densa*, Salter 4456 (BOL), (A) showing the congested leaves with linear and oblong leaflets; (B) a bulb with blackish brown tunic; C & D: *O. senecta*, Salter 5490 (BOL), (C) showing the conduplicate leaflets and (D) a bulb with a mass of papery, shiny brownish tunics.

4. 2 Discussion

4. 2. 1 Comparison between species, varieties and forma within *Foveolatae*

It is clear that each of the three groups in section *Foveolatae* includes species that differ from each other with regard to various characters. This section thus displays considerable morphological variation. Firstly, the indumentum is a source of considerable variation, both in terms of the type and density of hairs on the different organs. *O. convexula* is entirely glabrous, while the leaflets and corolla of *O. attaquana* are covered with long, hyaline, pluricellular hairs that give the plant a dewy appearance. *O. foveolata* and *O. pulchella* have hairs on their petioles, leaflets, sepals, filaments, ovaries and styles, but with different hair types on different parts. The petioles of *O. foveolata* are pubescent and the leaflets adaxially glabrous or pilose and abaxially more or less pilose, whereas the petioles of *O. pulchella* are densely hirsute, the leaflets abaxially pilose and adaxially the hairs are restricted to the veins.

The differences between these species also extend to their bulb morphology. Bulbs are ovoid in *O. attaquana* and *O. foveolata* and ovoid to narrowly ovoid in *O. convexula* and *O. pulchella*. In *O. senecta* the bulbs are congested and surrounded by a mass of loose tunics, and in *O. densa* bulbs are distinctly elongated. The stems of *O. attaquana* have cuspidate amplexicaul scales, while these structures are absent from the stems of *O. convexula*. The number, size and arrangement of leaves also display marked differences. *O. convexula* and *O. densa* have numerous leaves that are closely congested and spreading in the case of *O. convexula*. In contrast, *O. attaquana* has about 8 to 24 leaves that are congested or loosely imbricate on the upper part of the stem. Like *O. foveolata*, *O. senecta* has 9 to 15 leaves, and *O. pulchella* has 6 to 30 suberect or prostrate leaves. Leaflets in these species are all fleshy. Leaf shape also displays variation between the different species. The leaflets may be subrotund (*O. convexula*), rotund (*O. pulchella* var. *tomentosa*), oblong or ligulate (*O. pulchella* var. *leucotricha*). Sometimes the medial leaflets are shortly petiolulate and the lateral leaflets sessile. The leaflets can be incised (*O. senecta*) or bilobed (*O. densa*) to about the middle. The petioles of the selected species of section *Foveolatae* show some interesting variations. Petioles of *O. convexula* are dilated below the basal articulation into prominent

sub-membranaceous, stipuliform wings. These differ from the squamiform petioles of *O. attaquana*. In *O. senecta* petioles are also dilated and squamiform below the basal articulation, while in *O. densa* the petioles are scale-like and membranous, with three veins below the basal articulation.

The differences observed between varieties and forms are only minor. The morphological distinctions are restricted to differences in the shape and dimensions of leaflets, the presence or absence of calli, the colour of the corolla and the presence or absence of hairs on specific plant parts. These variations were discussed in the analysis of the four varieties of the *O. pulchella* in order to assess how Salter (1944) motivated the demarcating of these varieties. The demarcations were mainly based on only two or three conspicuous, variable characters. However, in *O. punctata*, the three forms differ only on the basis of the shape of the bulbs. In Form A bulbs are sharply angled, while in Form B bulbs are scarcely angled and Form C has roughly veined bulbs. These morphological distinctions are minor compared to the differences between the four varieties of *O. pulchella*.

Despite the differences outlined above, all of the species studied from section *Foveolatae* resemble each other to some extent. In all species peduncles are more or less longer than the leaves, and they all have two alternate, linear bracts. The bracts can vary from being oblanceolate and membranous in *O. convexula* to filiform toward the apex in *O. densa*. Morphological characters of the flowers exhibit very limited variation. In all the species studied the flowers have funnel-shaped yellow tubes, and the petal colour varies from pale salmon to rose (*O. convexula* and *O. pulchella*), rose (*O. attaquana*) to white (*O. senecta* and *O. densa*). In terms of petal shape, no major differences were observed between these species. Petals are sometimes basally obliquely cuneate, and truncate, subtruncate or rounded at the apex. The filaments are minutely glandular or glandular, sometimes with the longest filaments exerted from the corolla tube. The number of ovules per locule differs from species to species. Styles are always sparsely and minutely glandular or pilose.

4. 2. 2 Comparison between *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens*

Macro-morphology

Salter (1944) described *O. furcillata* var. *caulescens* as a variety of *O. furcillata*. According to him, these two varieties are morphologically very similar, and he highlighted only the following differences between them: (1) the presence or absence of an above-ground stem, (2) petiole length and (3) the position of the peduncles. He described *O. furcillata* var. *furcillata* as being stemless and *O. furcillata* var. *caulescens* as having a stem well-exserted above the ground. This demarcation is justified when only the specimens studied by Salter (1944) are considered. However, when these and other specimens are collectively studied, it becomes evident that a stem can be present and even well exserted above the ground in both taxa (Figure 3.1 and Figure 3.2). When species with or without well-exserted above-ground stems are mapped onto the *trnL-F* and ITS based molecular phylogenetic reconstruction of the southern African members of *Oxalis*, the plasticity of this character becomes evident (Oberlander, *pers. com.*). Stem length seems to be a very variable character that has evolved independently many times, and that bears limited systematic value. A comprehensive study of all available herbarium material of *O. furcillata* has also revealed that the presence of an above-ground stem can lead to misinterpretation of the position of the peduncle. Salter (1944) described the peduncles of *O. furcillata* var. *caulescens* as often being cauline, because they arise directly from the stem. Since *O. furcillata* var. *furcillata* sometimes also has visible stems, this may sometimes be true for the typical variety as well. These two characters, that were initially used to differentiate between the two varieties, are thus inconsistent, and not suitable to be used in the demarcation of the varieties. However, during the present study, other morphological characters were revealed that appear to be more accurate and consistent in the demarcation of these two varieties as separate taxa.

The most obvious character, the robustness of the plants, was also to some extent used by Salter (1944) in the delimitation of the two varieties. This character provided a baseline

distinctive difference by which the specimens examined in the present study could be separated into two groups. The robustness of specimens of *O. furcillata* var. *furcillata* is obvious in all individual plants studied. However, this taxon shows considerable morphological variation. As mentioned in the results (Chapter 3), these variations are mainly restricted to characters of the stems and the leaves. In some specimens of *O. furcillata* var. *furcillata*, a well-developed medium-length stem is present, while in others the stems are much longer and in the third group the stems are very short almost lacking. All members of the typical variety have many leaves (Figure 3.1 E), while specimens of *O. furcillata* var. *caulescens* always have a small number (Figure 3.2) of leaves and shorter stems. Specimens of *O. furcillata* var. *caulescens* display much less morphological variation, and are thus morphologically rather uniform. The distinction in terms of robustness between members of these two varieties serves as a good starting point to distinguish between them. This difference is so marked that the two taxa may be separated at a higher taxonomic level than the variety level. Specimens of *O. furcillata* var. *furcillata* may form a single taxon that can be subdivided again based on intraspecific variation. Specimens with prominent stems could represent one form, while specimens with very long stems may constitute another form and the third form may be composed of specimens that lack a stem all together. Stuessy (1990) commented that such variants usually represent small genetic changes as a result of a mutation and/or recombination. He also suggested that the total genetic composition of different forms differs very little from the typical form. The morphological distinctions are usually based on a single, conspicuous difference. Taking this into account, one can argue that the variations displayed among the individual groups may be viewed as forms within *O. furcillata* var. *furcillata*. A similar case, whereby a species is defined to include a number of slightly variant forms, was discussed above in the case of *O. punctata*. This species exhibits three different morphological forms based on the shape of the bulbs. Should this level of demarcation (as used by Salter (1944) in *O. punctata*) be adopted in the present study, *O. furcillata* var. *furcillata* could also be regarded as a distinct species with three morphological forms.

There is almost no variation among the less robust specimens of *O. furcillata* var. *caulescens*. All plants appear to be of a smaller size and specimens show limited morphological variation, thus preventing any further delimitation of morphological units within this taxon. According to Stace (1989), one of the main criteria for defining a species is that “*individuals should bear a close resemblance to one another such that they are always readily recognizable as members of that group*”. Based on this view, one could consider elevating *O. furcillata* var. *caulescens* to specific rank as a species separate from *O. furcillata* var. *furcillata*, which in itself exhibits considerable intraspecific variation.

Various morphological characters can be used to support the elevation of *O. furcillata* var. *caulescens* to specific level. One such a character is plant height. The robust plants are always taller than the less robust ones. All *O. furcillata* var. *furcillata* specimens are therefore distinctly taller (180–190 mm) than the *O. furcillata* var. *caulescens* (70–90 mm) specimens. Again, *O. furcillata* var. *furcillata* displays more obvious intraspecific variation in terms of this character than *O. furcillata* var. *caulescens*. Plant height in *O. furcillata* var. *furcillata* ranges from very tall (190 mm) individuals to medium-height (170 mm) individuals. This variation is not present among the specimens of *O. furcillata* var. *caulescens*, all of which are rather short plants (90 mm). This character of plant robustness also, in part, separates the species *O. pulchella* and *O. foveolata*. *O. pulchella* is 30–60 mm high and more robust than *O. foveolata*, which only attains a height of about 30 mm (Figure 4.2 A & B). Although *O. foveolata* resembles *O. pulchella* var. *beneprotecta*, Salter (1944) identified them as separate species.

Bulb characters also contribute to the variation between these two taxa. Salter (1944) used bulb characters to some extent in the delimitation of species and to determine their affinities within the genus. *O. crispula* Sond. and *O. stenoptera* Turcz. var. *undulata* Salter, for example, have similar above-ground morphologies, but were placed in totally different sections based on bulb morphological differences. In this case bulb characters provided information that indicated a lack of affinity between these two species. This also suggests that bulb characters are highly relevant in *Oxalis*, and can be used to improve the placement of taxa of doubtful affinities. In the present study the bulb morphological

differences between *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* support their separation as separate species. *O. furcillata* var. *furcillata* have darker, compound, lanceoid bulbs that are 30–35 mm long, while *O. furcillata* var. *caulescens* have lighter brown, solitary, ovoid bulbs that are only 10–15 mm long.

Another consistently variable character between the two taxa is the rhizome length.

O. furcillata var. *furcillata* has longer (40–70 mm) rhizomes than *O. furcillata* var. *caulescens* (40–50 mm). The difference in length suggests that the larger bulbs of *O. furcillata* var. *furcillata* grow at a greater depth than the smaller bulbs of *O. furcillata* var. *caulescens*.

Salter (1944) used petiole length as diagnostic in his separation of the two varieties. Results of the present study support the use of this character to distinguish between these two taxa. However, the outer leaves that have shorter petioles in both taxa also have petioles that are winged below the basal articulation, confirming a close relationship between them. However, winged petioles also occur in several other species of *Oxalis*. Some of these species are members of section *Foveolatae* (for example *O. punctata* and *O. convexula*), while others belong to different sections altogether.

Leaflet dimensions and number of flowers per plant also proved to be important characters by which to distinguish between these two taxa, as they differ consistently. Leaflets of *O. furcillata* var. *furcillata* are longer (mean = 8 mm) and broader (mean = 3.7 mm) than leaflets of *O. furcillata* var. *caulescens*, which are shorter (5 mm) and narrower (mean = 2.3 mm). *O. furcillata* var. *furcillata* usually has 4–12 flowers per plant, while *O. furcillata* var. *caulescens* always has only 1–2 flowers per plant.

Palynology

The scanning electron microscope (SEM) analyses of pollen grains provided strong arguments in favor of the separation of the two varieties of *O. furcillata*. The two varieties were found to have consistently different pollen types. Differences in the tectum type, lumina shape and presence or absence of intra-luminary baculae clearly separate these two taxa. Dreyer (1996) regarded these characters as significant in the demarcation

of pollen types and subtypes within *Oxalis*. The typical variety of this species has pollen of the subtype C2 (Figure 3.8), as classified by Dreyer (1996), while *O. furcillata* var. *caulescens* has pollen of the subtype C10 (Figure 3.9). Dreyer (1996) concluded that the presence of two such different pollen types in the two varieties of the same species is extraordinary. In addition, the presence of pollen subtype C10 in section *Foveolatae* is incongruent with the general trend in the section, since the majority of the included species display pollen of the subtype C2.

Geographical distribution

The two varieties of *O. furcillata* have very similar geographical distributions, ranging from the northern to the southern Kamiesberg. In many localities (for example in quarter degree grid square 2917) individuals of both taxa grow side by side or in very close proximity to each other, and can thus be regarded as sympatric. Both taxa also have the same or at least partially overlapping flowering times. Despite this, no intermediate forms between *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* are known or have been identified during the present study. The biological species concept defines species as a group of interbreeding natural populations that are reproductively isolated from other such groups (Mayr as quoted by Wheeler and Meier 2000). If biological species are distinct reproductive groups, barriers to prevent hybridization should exist between them. Since the two taxa are sympatric, there are no geographical barriers operational. So, if these taxa do, in fact, represent two separate biological species, there must be other reproductive barriers operational between them. Detailed artificial crossing-experiments between the two taxa should be done to test their ability to cross. Stuessy (1990) listed a number of characters for the demarcation of varieties and forms among flowering plants. These characters include morphological attributes, the geographical distribution and the likelihood of natural hybridization. He argued that, in the case of varieties, morphological distinctions are based on one to a few conspicuous differences. The geographical patterns must be cohesive, largely allopatric with some overlap, and if overlap is present, there would be a possibility of natural hybridization. When demarcating forms, the morphological distinctness required is often limited to one conspicuous difference. The geographical patterns are sporadically sympatric and the likelihood of natural

hybridization is always high. When applying these defining guidelines to the two taxa in this study, it is clear that more than two clear morphological distinctions have been identified. The most obvious character is the difference in robustness between the two taxa. This further supports the hypothesis that *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* represent two different species. When considering the definition of a taxon as a form, the level of morphological distinctions matches perfectly with the intraspecific forms observed among individuals of *O. furcillata* var. *furcillata*. *O. furcillata* var. *furcillata* displays definite intraspecific forms, which do not occur in *O. furcillata* var. *caulescens*. In terms of geographical distribution and the possibility for the occurrence of natural hybridization, one must remember that *Oxalis* is widespread in southern Africa (Oberlander *et al.* 2002), and displays three centres of diversity. *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* co-occur in the Kamiesberg centre. Within this centre, the quarter degree grid square (2917DB) in the northern Kamiesberg contains 21 *Oxalis* species, and the quarter degree grid square 3017BB in the southern Kamiesberg contains 25 *Oxalis* species (Oberlander *et al.* 2002). *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* occur in both of these quarter degree grid squares, where their distributions thus overlap with many other *Oxalis* species. Despite the co-occurrence of so many *Oxalis* species in this limited area, to date no natural hybrids have been recorded from the region, although it is possible that hybrids occur among the extensive collections of incertae in South Africa herbaria. Salter (1944) did not mention any case of natural hybridization in *Oxalis* in the field. The breeding systems of southern African *Oxalis* species are not well-studied yet, but all species are thought to be functionally tristylous (Salter 1944). The apparent absence of hybrids suggests that there are strong reproductive isolating mechanisms operational between these overlapping species. Thus, the criteria proposed by Stuessy (1990) of large allopatric separations, overlapping distribution and expected hybridizations could not be applied here. Indeed, many good species do co-occur in this centre of diversity, and do not display allopatric separation. There is thus no biogeographic reason why *O. furcillata* var. *furcillata* and *O. furcillata* var. *caulescens* cannot be regarded as separate biological species.

Salter (1944) only used three distinguishing characters (the presence or absence of an above-ground stem, the position of the peduncles and the petiole length) to define the varieties within this species. As discussed above, two of these characters were found to be inconsistent, and only the differences in the petiole length were found to be consistent. In the present study several new characters were, however, identified to distinguish between the two taxa. These characters all suggest that the two varieties of *O. furcillata* represent two distinct species. Salter (1944) already questioned the affinity of *O. furcillata* with other members of section *Foveolatae*. He suggested that *O. furcillata* var. *caulescens* might belong in section *Angustatae* subsection *Sessilifoliae*, implying the inclusion of two varieties of the same species in two different sections. The proposed new taxonomic placement of these two taxa will be discussed in the next chapter.

4.3 Conclusions

Based on the aspects outlined in the discussion above we see two major distinctions that can aid the demarcation of the two taxa, namely a suite of morphological differences and distinct palynological differences. It is possible to readily distinguish between the strong, robust plants of *O. furcillata* var. *furcillata* and the small plants of *O. furcillata* var. *caulescens*. This is further supported by the pollen morphology of the two taxa, with the robust plants having a C2 pollen type and the smaller plants having pollen of the type C10. In addition three different forms are recognized within *O. furcillata* var. *furcillata*. The designation of forms in *O. furcillata* var. *furcillata* is justified by the fact that they all have the same pollen subtype (C2). *O. furcillata* var. *caulescens* exhibits several morphological similarities with *O. furcillata* var. *furcillata* and the possibility of regarding the former as a fourth form of the latter does exist. However, when considering the different pollen type (C10) present in *O. furcillata* var. *caulescens*, together with the data outlined above, it becomes clear that the latter should rather be separated from *O. furcillata* var. *furcillata* and regarded as a species of its own. Therefore, *O. furcillata* var. *furcillata* represents a single species with three forms and *O. furcillata* var. *caulescens* must be raised to specific rank as *O. caulescens* (Salter) Bissiengou. We will use molecular phylogenetic reconstruction of South African *Oxalis* taxa to decide on the

most natural placement of this species once this phylogeny becomes available (Oberlander, in prep.).

Chapter 5 Taxonomic placement of *O. furcillata* and *O. caulescens*

5. 1 Taxonomic demarcation of *O. furcillata*.

Oxalis furcillata Salter, Journal of South African Botany 1:111 (1935); Salter: 175 (1944). **Type:** Northern Cape Province, 2917 DD (Springbok): Mesklip. 14 July 1932, Salter 2576 (BOL).

5. 1. 1 Description

Geophyte, robust plant, 180–190 mm tall when in flower. **Bulb** 30–35 mm long, lanceoloid, usually in clusters of 2–5, tunics of old bulbs black to brownish, bulbils sometimes arise from a lateral rhizome. **Rhizome** 40–70 mm long, glabrous but hairy near apex. **Stem** usually absent, if present erect, 12–80 mm (sometimes up to 200 mm) tall, with petioles arising from stem apex, puberulent with multi-cellular hairs. **Scales** brownish, alternate on rhizome, ovate or widely ovate, apex acute, base cuneate or widely cuneate, ciliate with multi-cellular hairs, similar hairs also found abaxially along the mid-vein. **Leaves** clustered at the stem apex, whorled, lamina ternate, with three sessile leaflets; petioles 14–16 mm long, flattened, sometimes winged below the basal articulation in the outer, shorter leaves, covered with long multicellular hairs; leaflets non-fleshy, arising from apex of petiole, conduplicate, furcate with both apices narrowly obtuse, bases cuneate, margins entire, basal vein divided into two apically branched veins. **Peduncle** 30–35 (–52 mm) long, erect, glabrous. **Flowers** 4–12 per plant, solitary at the apex of a long peduncle. **Sepals** 5, all of equal size, 3.5–4 mm long, narrowly ovate, apex acuminate, base narrowly cuneate, abaxially hirsute with multi-cellular hairs, margin ciliate. **Petals** 5, white, widely obovate, broadly truncate, narrowly cuneate, glabrous. **Stamens** 10, arranged in two whorls, filaments pilose, interspersed with glandular hairs. **Style** 1–3 mm (short morph), 4–5 mm (medium morph) 7–10 mm (long morph), pilose interspersed with glandular hairs. **Ovary** superior, elliptic, 1.5 mm long, covered with simple hairs, 3–4 ovules per locule. Mature seed exendospermous.

5. 1. 2 Diagnostic characters

Oxalis furcillata is characterized by its robustness, widely lanceoloid bulbs, and non-fleshy leaflets. The leaflets are conduplicate and furcate and the apices of the leaflet lobes are obtuse. The numerous leaves have long petioles that are flattened, and sometimes winged below the basal articulation in the shorter, outer leaves. Flowers are white, 4 to 12 per plant and petals are broadly truncate. Hairs on the petioles are mostly long and multi-cellular, while the filaments sometimes have minute unicellular hairs interspersed with the glandular hairs. The pollen grains of *O. furcillata* has a micro-reticulate tectum with rounded to oblong to slightly angular muri. *O. furcillata* has seeds without endosperm.

5. 1. 3 Geographical distribution and ecology

O. furcillata occurs in Namaqualand, from Steinkopf in the north to Karkams in the south and flowers from June to July. This species occurs in the succulent Karoo Biome, where rainfall varies between 20 and 290 mm per year (Bredenkamp *et al.* 1996). The area is covered by a lime-rich, weakly developed soil over rock and the vegetation type is dominated by dwarf, succulent shrubs, of which the Vygies (Mesembryanthemaceae) and Stonecrops (Crassulaceae) are particularly prominent. Some Asteraceae species often occur on degraded lands. Grasses are rare in these areas, except in sandy soil (Bredenkamp *et al.* 1996).

5. 1. 4 Designation of forms

The specimens of *O. furcillata* display three morphological forms that are here designated as form A (the typical form), form B and form C. These three forms differ in terms of bulb and stem characters, and in terms of the number of leaves per plant. Form A groups together specimens that have broadly lanceoloid bulbs and very short (almost lacking) stems. The leaves are numerous and have long petioles. Form B is characterised by its lanceoloid bulb and medium-length stems. These two forms occur in a restricted area around Springbok (Figure 5.1). Form C is quite different from the other two forms in terms of its ovoid brownish bulbs and its well-developed long stems. It is also characterized by its very long petioles. Form C is known from a single collection, which was made near Kamieskroon. It is thus geographically isolated from the other two forms (Figure 5.1).

5. 1. 5 Key to the forms of *O. furcillata*

1. Bulbs lanceoloid to broadly lanceoloid, petioles long (ca. 20 mm).....2
1. Bulbs ovoid, petioles very long (220–250 mm)..... Form C
2. Stems short (30–50 mm), leaves numerous (more than 50).....Form A
2. Stems medium length (60–90 mm), leaves few (10–15).....Form B



Figure 5. 1. Geographical distribution of *O. furcillata*. Form A (!); Form B (#) and Form C (&).

Selected specimens studied

Form A

—**2917** (Springbok): 13 miles south of Steinkopf (–BC), *Salter 2593* (BOL); 2 miles from Concordia (–DB), *Salter 5538* (NBG); Hester Malan Nature reserve (–DB), *Van Wyk 5739* (PRE); Mesklip (–DD), *Salter 2576* (BOL).

Form B

—**2917** (Springbok): Between Spektakel Pass and Springbok (–DA), *Dreyer 702* (STEU); Farm Narab Boedery (–DA), *Oberlander 149* (STEU); 18 miles north east of Springbok (–DB), *Schleiben 9071* (BOL, PRE); 6 miles north by east of Concordia (–DB), *Leistner 2567* (PRE); Hester Malan Nature reserve (–DB), *Struck 3* (NBG); *Struck 24* (NBG).

Form C

—**3017** (Hondekliibaai): Karkams (–BB), *Bayer 2236b* (NBG).

5. 2 Taxonomic demarcation of *O. caulescens*.

Oxalis caulescens (Salter) Bissiengou nom. nov.

O. furcillata var. *caulescens* Salter, Journal of South Africa Botany, supplement I vol. 1: 175 (1944). Type: Northern Cape Province, 3017 BB (Hondeklipbaai): Kamieskroon. 11 June 1931, *Salter 854* (BOL).

5. 2. 1 Description

Geophyte, small plant, 80–90 mm tall when in flower. **Bulb** 10–15 mm long, ovoid, usually solitary, rarely two small bulbs clustered together, covered with a brownish (sometimes darker) tunic, bulbils sometimes arise from a lateral rhizome. **Rhizome** 40–50 mm long, minutely hairy near apex. **Stem** erect, ca. 10–15 mm long with petioles arranged into loose whorls, minutely hairy. **Scales** brownish, alternate on the stem, ovate to widely ovate, apex acute, base cuneate to widely cuneate, ciliate with multi-cellular hairs along the margin and similar hairs also found abaxially along the mid-vein. **Leaves** clustered, loosely whorled. **Petioles** 40–60 mm long, terete, winged below the basal articulation, covered with long multicellular hairs; lamina with three leaflets. **Leaflets** sessile, arising from the apex of petiole, conduplicate, apex furcate and both apices are obtuse, base cuneate, margins lobed ciliate with multicellular hairs. **Peduncle** 20–25 (–40) mm long, erect, glabrous. **Flowers** 1–2 flowers per plant, solitary at the apex of a short peduncle. **Sepals** 5, 2 large and 3 smaller, 3.5–4 mm long, narrowly lanceolate to ovate, acuminate, narrowly cuneate, abaxially hirsute with multi-cellular hairs, ciliate. **Petals** 5, white, obovate, truncate, cuneate, glabrous. **Stamens** 10, arranged in two whorls, filaments covered with glandular hairs. **Style** 1–2 mm (short morph), 4–5 mm (medium morph), 6–12 mm (long morph), pilose interspersed with glandular hairs, ovary superior, elliptic, 1 mm long, covered with simple hairs, 3–4 ovules per locule. Mature seed exendospermous.

5. 2. 2 Diagnostic characters

Oxalis caulescens differs from *O. furcillata* with regard to a number of morphological characters. Although both species have non-fleshy and conduplicate leaflets, *O. caulescens* is rather a small plant with short stems, short petioles and fewer leaves.

Bulbs are solitary (rarely two together) with lighter brown tunics. The leaflets are short and narrow. Petioles are short and winged below the basal articulation, unlike those of *O. furcillata*, which are longer, flattened and sometimes winged on the outer leaves. Flowers are also white like in *O. furcillata* and there are only 1–2 flowers per plant. Petioles have multi-cellular hairs and stems have glandular hairs toward their apices. The indumentum of the filament comprises minute glandular hairs that are sparsely distributed over the entire filament. In addition, *O. caulescens* is exendospermous and has reticulate pollen with intra-luminary bacules clustered around the muri. This pollen type differs distinctly from the micro-reticulate pollen that lack intra-luminary bacules found in *O. furcillata*.

5. 2. 3 Geographical distribution and ecology

O. caulescens occur in Namaqualand, ranging from Steinkopft in the north to Garies in the south. Its distribution is scattered between the 29° and 30° latitudes and between 17° and 18° longitudes (Figure 5.2). It flowers from June to July. It occurs under the same ecological conditions as *O. furcillata* as discussed above.

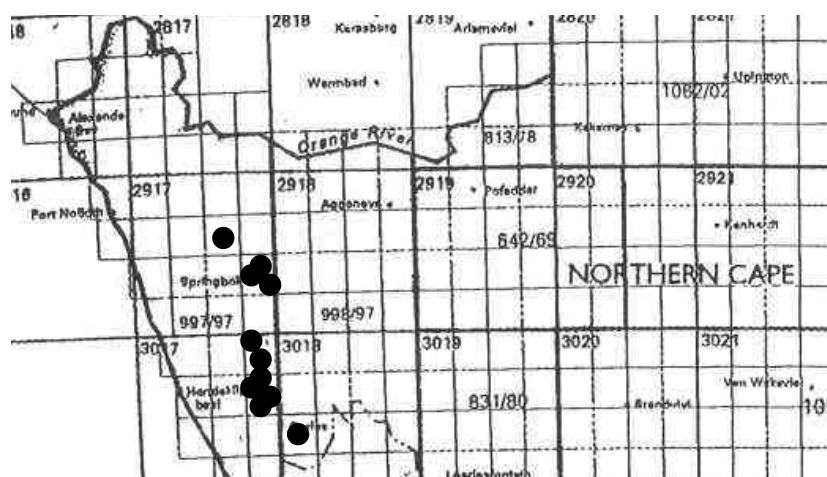


Figure 5. 2. Geographical distribution of *O. caulescens*.

Selected specimens studied

—**2917** (Springbok): 13 miles south of Steinkopf (–BC), *Salter 2593* (BOL); 2 miles north of Concordia (–DB), *Salter 890, 4580* (BOL & NBG); Hester Malan Nature Reserve (–DB), *Le Roux 3936* (PRE).

—**3017** (Hondeklipbaai): Kamieskroon (–BB), *Salter 854, 890* (BOL & NBG); 6 miles south of Kamieskroon (–BD), *Salter 4607* (NBG); 7 miles south of Kamieskroon (–BD), *Salter 1412* (BOL & NBG); 13 miles south of Kamieskroon (–BD), *Salter 5571* (BOL); 10 miles south of Kamieskroon (–BD), *Salter 4570* (BOL); 14 miles south of Kamieskroon (–BD), *Salter 2559* (BOL).

—**3018** (Kamiesberg): 16 miles north-east of Garies (–CA), *Salter 6674* (BOL).

5. 3 Proposed taxonomic placement of *O. furcillata* and *O. caulescens*

The taxonomic placement of the two species will be discussed here using two different approaches. Firstly the characters used by Salter (1944) in his keys to identify members of section *Foveolatae* are used to determine whether or not these two species belong to this section. Thereafter the diagnostic characters of the two species are evaluated in search for similarities between them and the rest of the species in the section.

Salter (1944) analysed the species and divided them into 24 groups. This grouping of species was artificial and intended purely as a means of identification. He then arranged the species into sections and subsections in an attempt to group species in relation to their natural affinities. Based on its conduplicate leaflets, *O. furcillata* was placed into group 3 in the analysis of species by Salter (1944). Within this group, *O. furcillata* was grouped along with species such as *O. densa*, *O. obtusa* Jacq., *O. smithiana* E. & Z., *O. heterophylla*, Form B D.C, *O. extensa* Salter, *O. tysoni* Phillips, *O. orthopoda* Salter, *O. bifurca* E. & Z., *O. comosa* E. Mey. ex Sond. and *O. bifida* Thunb. Eventually some of these species were placed in completely different sections or subsections in Salter's (1944) final arrangement of the species into subsections. *O. smithiana*, *O. heterophylla* form B, *O. extensa*, *O. tysoni*, *O. orthopoda*, *O. bifurca*, *O. comosa*, and *O. bifida* are grouped together in section *Oppositae* subsection *Bifurcatae*. Members of this subsection are characterized by bifurcate leaflets to above the middle or beyond and the plants are usually caulescent.

O. densa and *O. furcillata* share these leaf characters, but lack opposite bracts on their peduncles, a defining character of members of section *Oppositae*. *O. densa* and *O. furcillata* were thus placed in section *Foveolatae* instead. The majority of members of section *Foveolatae* belong to Salter's (1944) group 6, except for *O. furcillata* (group 3), *O. caulescens* (group 3), *O. setosa* E. Mey. Ex Sond. (groups 6 and group 7), *O. fourcadei* Salter (group 8), *O. attaquana* (group 16) and *O. convexula* (group 17). One can deduce from this grouping that section *Foveolatae* includes groups of species with discontinuous variability. But despite this, Salter (1944) identified key characters that unambiguously unite members of *Foveolatae*. These species are separated on the basis of either having a stem or being stemless. Their leaflets are fleshy, often small, with comparatively large epidermal cells rendering the leaflet surfaces conspicuously impresso-punctate or honeycombed in the dried state (owing to the collapsing of the large epidermal cells), their corolla tubes are more or less funnel-shaped and their seeds are endospermous. Of these characters, only the epidermal characters of the leaflets are restricted to this section, and allow easy identification of a species as a member of this section or not. The surfaces of the leaflets of both *O. furcillata* and *O. caulescens* are more or less impresso-punctate or honeycombed, and are thus slightly similar to the epidermal surfaces of members of *Foveolatae*. This character can thus justify the placement of *O. furcillata* and *O. caulescens* within this section. In addition, the funnel-shaped corolla tubes of these two species also agree with the corolla tubes of all other members of this section. Based on these two characters, *O. furcillata* and *O. caulescens* belongs to section *Foveolatae*, and should thus be retained in it. Besides these two obvious characters, *O. furcillata* and *O. caulescens* also share some other, minor characters with some of the species in the section. Firstly in terms of robustness, *O. furcillata* is more robust than *O. caulescens*. In section *Foveolatae* similar differences are also found between *O. attaquana* and *O. convexula*, with the former species being more robust than the latter (Figure 4.1 B & D). Similarly *O. furcillata* has lanceoloid bulbs similar to those of *O. densa* or *O. senecta*, while the bulbs of *O. caulescens* are ovoid like the bulbs of *O. convexula* and *O. attaquana*. Bulbs of the latter two species differ in tunic colour and type and the segregate nature of this structure, as was described in the previous chapter. Within section *Foveolatae* bulb differences of this kind are mostly seen between different species. Leaf characters display a similar level of variation between species within this section. *O. furcillata* has numerous leaflets, while *O. caulescens*

has only a few leaves per plant. Both *O. attaquana* (8–24 leaves) and *O. convexula* (numerous leaflets) have many leaves per plant and are thought to be closely related to each other (Salter 1944), but this needs to be tested. The petiole lengths of the species within this section also display interesting patterns. Petioles of most species are long, sometimes up to 20–30 mm (*O. senecta*, *O. densa* and *O. furcillata*), while others are substantially shorter (*O. caulescens* and *O. convexula*). Of the other characteristics examined, petal apices also display some taxonomic correlations between the species of *Foveolatae*. The apex of the petals may be truncate (*O. caulescens*), broadly truncate (*O. furcillata*), broadly and obliquely truncate (*O. convexula*), subtruncate (*O. senecta*), obliquely cuneate (*O. attaquana*) or rounded (*O. attaquana* and *O. punctata*).

Another character that shows considerable variation between the species included in this section is the extent to which an above-ground stem is developed. All species are stemless, except for *O. convexula* and *O. attaquana*, both of which have a well-developed above-ground stem. Results of the present study showed that *O. furcillata* may be stemless (Form A) or have a well-developed stem (Form B and C). *O. caulescens* usually has a stem. The fact that both stemless and caulescent species have been recorded within this section thus permits the inclusion of both *O. furcillata* and *O. caulescens* without conflict in terms of stem characters.

The comparison of the diagnostic characters of the two species and some of the key characters of section *Foveolatae* thus largely supports the inclusion of these two species in section *Foveolatae*. They should both remain in this section, and appear to be rather closely related to *O. densa* and *O. senecta* as already proposed by Salter (1944). Including these two species into different sections enjoys little support, as they resemble one another and both show similarities with other species of this section.

There are, however, other key characters of the section that do not occur within these two species. These pertain mostly to certain leaflet and seed characters. Such characters contradict the taxonomic placement of the two species within section *Foveolatae*. The leaflets of the two species are very similar in terms of shape. Both have conduplicate leaflets, similar to the leaves of *O. densa* and *O. senecta* and their

leaflets are not fleshy. This is quite unique, as most species included in this section have fleshy leaflets. This does question the inclusion of these two species, and indeed that of *O. densa* and *O. senecta* in section *Foveolatae*. In addition, all the species in *Foveolatae* have endospermous seeds. Endospermy is thought to be quite a reliable character within *Oxalis*, which probably represents the plesiomorphic state in the genus (Oberlander *pers comm.*). In contrast, both *O. furcillata* and *O. caulescens* produce exendospermous seeds, and are thus the only species in the section without endosperm in their mature seeds. The uniqueness of this character within section *Foveolatae* suggests a lack of affinity between these two species and the rest of the section. Based on this character, these two species may be better placed in another section that includes species with exendospermous seeds. In addition, the pollen grains of all the species in section *Foveolatae* are micro-reticulate to reticulate, with intra-luminary bacules, when present, always randomly scattered throughout the lumina. Interestingly, the pollen of *O. furcillata* fits in with that of the rest of the section (type C2), but the pollen grains of *O. caulescens* differs markedly (type C10). As the overall similarity in morphology between *O. furcillata* and *O. caulescens* suggests that they are best included within the same section, this difference in pollen morphology is conflicting and problematic. Either both species must remain within section *Foveolatae* or they should both be moved to a section with variable pollen morphology.

In conclusion there are thus two possible placements for these two species. They can either both remain in the section *Foveolatae* despite the seed and pollen conflicts discussed above. Another alternative is that both species may be moved to the highly variable section *Latifoliolatae*. The first option is supported by many morphological characters that these two species share with members of section *Foveolatae*. The most convincing of these morphological similarities pertain to the unique honeycombed surface of the leaflets, a character which is restricted to members of this section. Within *Foveolatae*, they are best placed near *O. senecta* and *O. densa* based on several morphological similarities, including leaflet shape and types of epidermal hairs. The one (*O. furcillata*) or two (*O. caulescens*) characters that differ from other species in this section may simply represent non-taxonomically significant variation. This is supported by the discussion above, which did emphasize fairly substantial

morphological variation already present between the species currently included in this section.

The suggestion that these species may be better placed within section *Latifoliolatae* is supported by three factors. Firstly, subsection *Latifoliolatae* consists of non-succulent plants, while succulence is a fairly diagnostic character of most species in section *Foveolatae*. Secondly, members of the entire subsection have seeds that lack endosperm. Finally this section is dominated by species with pollen type C10, although many different pollen types are also present within this variable section (for example subtypes C2, C8, C11, D1 and D2 sensu Dreyer (1996)). *O. furcillata* with pollen subtype C2 and *O. caulescens* with pollen type C10 can, on these grounds, easily be placed in section *Latifoliolatae*, since both of their pollen subtypes already occur in this section. Based on the distribution of the pollen subtype C2 and C10 in this section, *O. caulescens* may be placed near *O. aurea* Schltr. and *O. stenoptera* Turcz. Both of these species have pluricellular hairs and ovoid bulbs similar to that of *O. caulescens*. *O. furcillata* may be better placed near *O. suavis* R. Knuth because of its pollen morphology, although *O. furcillata* does not share many macro-morphological character with this species. Based on DNA-based evidence, these three species are more closely related to *O. furcillata* and *O. caulescens* than to other members of section *Foveolatae* (Oberlander in prep).

There are thus two different options for the taxonomic placement of the species *O. caulescens* and *O. furcillata*. Retaining them within the section *Foveolatae* appears to be the better alternative, despite the few character conflicts. The reason for this is that section *Latifoliolatae* is a very poorly defined entity that appears to group many unrelated taxa without strong morphological support (Salter 1944). This was confirmed by the palynological results of Dreyer (1996) and the preliminary DNA sequence-based phylogeny of Oberlander *et al.* (2004). Supra-areolate pollen (pollen type D) has been recorded in sections *Latifoliolatae*, *Angustatae* subsection *Sessilifoliolatae* and *Angustatae* subsection *Lineares*. Oberlander *et al.* (2004) convincingly showed that this represents an artificial placement of species, as all taxa with supra-areolate pollen consistently grouped together into a very well-supported clade in the *trnL-F* based molecular phylogeny of *Oxalis*. The co-occurrence of reticulate and supra-areolate pollen within section *Latifoliolatae* thus seriously

questions the taxonomic integrity of this section. It thus makes little sense to include two additional species in this taxonomically questionable section. The more conservative and systematically more sound option would be to retain these two species in section *Foveolatae*, and to wait for the results of the species-level DNA-based phylogeny of the southern African members of *Oxalis*. Work towards obtaining this phylogeny is progressing well (Oberlander, *pers. comm.*), and should soon enable us to resolve the final placement of *O. furcillata* and *O. caulescens*. Both of these species have been included in this phylogeny, and the species demarcation presented within the present study should enable the correct interpretation of the pending phylogenetic results.

References

Angiosperm Phylogeny Group (APG). 1998. **An ordinal classification for the families of flowering plants**. Annals of the Missouri Botanical Garden 85: 531-553.

Angiosperm Phylogeny Group (APG II). 2003. **An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants**. Botanical journal of Linnean society 141: 399-436.

Barrett, S. C. H., Cole, W. W., ArroyoJ., Mitchell, B., Cruzan and Lloyd, D.G. 1997. **Sexual polymorphisms in *Narcissus triandrus* (Amaryllidaceae): is this species tristylous?** Heredity 78: 135-145.

Boesewinkel, F. D. 1985. **Development of ovule and seed-coat in *Averrhoa* (Oxalidaceae) with notes on some arid genera**. Acta Botanica Neerlandica 34(4): 413-424.

Boesewinkel, F. D. 1988. **The seed structure and taxonomic relationships of *Hypsocharis Remy***. Acta Botanica Neerlandica 37: 111-120.

Bredenkamp, G., Granger, J. E. and van Rooyen, N. 1996. Succulent Karoo Biome. In: Low, A. B. & Robelo, A. G. (eds), **Vegetation of South Africa, Lesotho and Swaziland**. Department of Environmental Affairs and Tourism, Pretoria.

Chant, S. R. 1978. **Oxalidaceae**. In: Heywood (ed.), Plants of the world. Oxford University Press, Oxford.

Chant, S. R. 1993. **Oxalidaceae**. In: Heywood (ed.), Plants of the world. B. T. Batsford Ltd., London.

Chase, M., Soltis, D. E., Olmstead, R. G., Morgan, D., Les, D. H., Mishler, B. D., Duvall, M. R., Price, R. A., Hills, H. G., Qiu, Y., Kron, K. A., Rettig, J. H., Conti, E., Palmer, J. H., Manhart, J. R., Sytsma, K. J., Michaels, H. J., Kress, W. J., Karol, K. G., Clark, W. D., Hedrén, M., Gaut, B. S., Jasen, R. K., Kim, K., Wimpee, C. F., Smith, J. F., Furnier, G. R., Strauss, S. H., Xiang, Q., Plunkett, G. M., Soltis, P. S., Swensen, S. M., Williams, S. E., gadek, P. A., Quinn, C. J., Eguiarte, L. E., Golenberg, E., Learn Jr., G. H., Graham, S. W., Barrett, S. C. H., Dayanandan, S., & Albert, V. A. 1993. **Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL***. Annals of the Missouri Botanical Garden 80: 528-580.

Cowling, R. M. and Hilton Taylor, C. 1997. **Phytogeography, flora and endemism**. In R. M. Cowling, D. M. Richardson and S. M. Pierce, Vegetation of Southern Africa. Cambridge University Press. Cambridge.

Cronquist, A. 1881. **An integrated System of Classification of the Flowering Plants**. Columbia University Press, New York, USA.

Dahlgren, R. M. T. 1983. **General aspects of Angiosperm evolution and acrosystematics**. Nordic Journal of Botany 3: 119-149.

Dreyer, L. L. 1996. **A panylogical review of *Oxalis* (Oxalidaceae) in southern Africa**. Ph.D. thesis, University of Pretoria, Pretoria, South Africa.

Goldblatt, P. and Manning, J. 2000. **Cape plants. A conspectus of the Cape Flora of South Africa**. National botanical Institute of South Africa, Pretoria & Missouri Botanical Garden Press, St. Louis.

Hutchinson, J. 1959. **The families of flowering plants**. Dicotyledons, ed. 2. Clarendon Press. Oxford.

Knuth, R. 1930. **Oxalidaceae**. In Engler, Das Pflanzenreich 95, IV: 130. Wilhelm Engelman, Leipzig.

Leistner, O. A. and Morris, J. W. 1976. **Southern African place Names**. Annals of the Cape Provincial Museums 12: 1-565.

Lourteig, A. 1979. **Oxalidaceae extra-austroamericanae II. *Oxalis* L. Section *Corniculatae* DC**. Phytologia 42(2): 57-198.

Nandi, O. I., Chase, M. W. and Endress, P. K. 1998. **A Combined Cladistics Analysis of Angiosperms Using *rbcL* and Non-Molecular Data sets**. Annals of the Missouri Botanical Garden 85: 137-212.

Oberlander, K. C., Dreyer, L. L., Bellstedt, D. U., and Reeves, G. 2004. **Systematics relationships in southern African *Oxalis* L. (Oxalidaceae): congruence between palynological and plastid *trnL*-F evidence**. Taxon 53 (4) 977-985.

Oberlander, K. C., Dreyer, L. L. and Esler, K. J. 2002. **Biogeography of *Oxalis* (Oxalidaceae) in South Africa: a preliminary study**. Bothalia 32: 97-100.

Ornduff, R. 1974. **Heterostyly in South African flowering plants: a conspectus**. Journal of South African Botany 40:169-187.

Price, R. A. and Palmer, J. D. 1993. **Phylogenetic Relationships of the Geraniaceae and Geraniales from *rbcL* sequence comparisons**. Annals of the Missouri Botanical Garden 80: 661-671.

Rama Devi, D. and Narayana, L. L. 1990. **Systematic position of *Averrhoa* (Oxalidaceae)**. Feddes Repertoire 101 (3-4): 165-170.

Rama, Devi, D. 1991. **Floral anatomy of *Hypseocharis* (Oxalidaceae) with a discussion on its systematic position.** Plant Systematics and Evolution. 177: 161-164.

Robertson, K. R. 1975. **The Oxalidaceae in the south-eastern United States.** Journal of Arnold Arboretum 56: 223-239.

Salter, T. M and Compton . 1935. *Plantae novae Africanae*. The Journal of South Africa Botany I (3): 111-113.

Salter, T. M. 1944. **The genus *Oxalis* in South Africa.** Journal of South African Botany. Supplement I Vol. I: 1-355.

Savolainen, S., M. W. Chase, S. B. Hoot, C. M. Morton, D. E. Soltis, C. Bayer, M. F. Fay, A. Y. De Bruijn, S. Sullivan, and Y. L. Qiu. 2000. **Phylogenetics of Flowering Plants Based on Combined Analysis of Plastid *atpB* and *rbcL* Gene Sequences.** Systematic Biology 49 (2): 306-362.

Stace, C. A. 1989. **Plant taxonomy and biosystematics.** Edward Arnold, London.

Steussy, T. F. 1990. **Plant taxonomy: the systematic evaluation of comparative data.** N.Y. Columbia University.

Takhtajan, A. 1980. **Outline of the classification of flowering plants (Magnoliophyta).** Botanical Review. 46: 225-359.

Thorne, R. R. 1983. **Proposed new realignments in the angiosperms.** Nordic Journal of Botany 3: 85-117.

Veldkamp, J. F. 1971. **Oxalidaceae.** In: Flora Malesiana Ser. 1, 71: 151-159.

Wheeler, Q. D & Meier, R. 2000. **Species concepts and phylogenetic theory: a debate.**
Columbia University Press. New York.