

**Systematic Significance of Bulb Morphology of the Southern
African Members of *Oxalis* L. (*Oxalidaceae*)**

By

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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.

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ABSTRACT

The systematics of the southern African members of the genus *Oxalis* L. (Oxalidaceae) is in a state of flux. The bulbs of these species contain potential taxonomically important characters and therefore require detailed study (Salter, 1944). A pilot study assessed the homology of bulbs among southern African *Oxalis* species (Gebregziabher, 2001), and found that they are all homologous structures. This pilot study also emphasized the range of potentially informative characters from different bulb parts.

The aim of the present study was to assess the taxonomic significance of bulb morphology in selected southern African *Oxalis* species. As far as possible, efforts were made to represent both the taxonomic (Salter, 1944) and palynological diversity (Dreyer, 1996) present in the genus.

Detailed bulb morphological studies of 30 species of southern African *Oxalis* species revealed 41 potentially informative characters. Different bulb-types were identified based on these characters. Bulb-type affinities of taxa included in this study, as well as bulb descriptions from the pilot study (Gebregziabher, 2001), were discussed. Comparison with the current taxonomic classification (Salter, 1944), palynological classification (Dreyer, 1996) and a preliminary phylogeny based on the non-coding plastid *trnL-trnF* DNA region (Oberlander, 2003), were also made. Bulb morphology conflicted with the current taxonomic classification (Salter, 1944), but showed greater congruence with both the palynological groupings and the *trnL-trnF* based phylogeny.

Based on this study, bulb morphology is found to be taxonomically significant. Further studies on the bulb morphology and anatomy of southern African *Oxalis* species are merited.

Key words: bulb morphology, *Oxalis*, informative characters, basal plates, fleshy leaves, tunics

OPSOMMING

Die sistematiek van die suider Afrikaanse lede van *Oxalis* L. (Oxalidaceae) is labiel. Die bolle van hierdie spesies sluit potensieel taksonomies belangrike kenmerke in, en behoort daarom in detail bestudeer te word (Salter, 1944). 'n Loodsstudie het die homologie van die bolle van die suider Afrikaanse *Oxalis* spesies ge-evalueer (Gebregziabher, 2001), en gevind dat hulle homoloë strukture is. Resultate van hierdie loodsstudie het ook die reeks van potensieel informatiewe kenmerke van verskillende boldele beklemtoon.

Die doel van hierdie studie was om die taksonomiese belang van bolmorfologie in geselekteerde suider Afrikaanse *Oxalis* spesies te ondersoek. Pogings is aangewend om, sover moontlik, beide die taksonomiese (Salter, 1944) en die palinologiese (Dreyer, 1996) diversiteit van die genus in die studie in te sluit.

Gedetailleerde bol-morfologiese studies van 30 suider Afrikaanse *Oxalis* spesies het 41 potensieel informatiewe kenmerke uitgewys. Gebaseer op hierdie kenmerke, is verskillende bol-tipes geïdentifiseer. Verwantskappe tussen die bol-tipes van die spesies ingesluit in hierdie studie, sowel as beskrywings van bolle volgens die loodsstudie (Gebregziabher, 2001), word bespreek. Vergelykings met die huidige taksonomiese klassifikasie (Salter, 1944), palinologiese klassifikasie (Dreyer, 1996) en 'n voorlopige filogenie gebaseer op die nie-koderende plastied *trnL-F* DNA-streek (Oberlander, 2003) is ook getref. Bolmorfologie weerspreek die huidige taksonomiese klassifikasie (Salter, 1944), maar toon groter ooreenstemming met beide die palinologiese groeperings en die *trnL-F* gebaseerde filogenie.

Hierdie studie het bevind dat bolmorfologie van taksonomiese waarde is. Verdere studies op die bolmorfologie en -anatomie van die suider Afrikaanse *Oxalis* spesies word aanbeveel.

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Oxalis leptogramma

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CHAPTER ONE: INTRODUCTION

Morphological attributes of plants have been indispensable properties in species identification, descriptions and for tracing the relationships between taxa. Morphology of a particular plant gives an observer a visual impression, enabling the observer to allocate the plant to a specific family, genus and/or species. In systematics, morphology is not the sole tool used for classification, but it is the most prominent and essential tool for a preliminary step. The most important aspect of systematics is finding the relationships between taxa, and this has been done by analytical methods ranging from basic morphological deduction to more sophisticated molecular phylogeny level analyses. Whichever method is used, the analysis has to provide informative and unambiguous results to understand natural affinities between taxa. However, in order to obtain the best results, the choice of appropriate plant attributes is crucial.

This study focuses on identifying and determining bulb morphological attributes to understand the systematic relationships among southern African *Oxalis* L. species. In his monograph, Salter (1944) indicated the importance of bulb morphology in the systematic classification of southern African *Oxalis*. This genus, although distributed throughout the world, is one of the most prolific genera in the winter-rainfall region of southern Africa in terms of number of species. Despite its horticultural potential and importance in weed science, the genus *Oxalis* is one of the lesser studied taxa in southern Africa.

Oxalis belongs to the family Oxalidaceae. Oxalidaceae is a cosmopolitan family and members of this taxon are predominantly distributed in tropical and subtropical regions of the world, with few species present in the temperate regions (Chant, 1978; Takhtajan, 1997; Judd *et al.*, 1999). This family is commonly known as 'the wood sorrel family', because of the sour taste of their leaves and stems (Chant, 1978; Cronquist, 1981).

The family Oxalidaceae is characterised by alternate leaves that lack stipules and that are palmately to pinnately compound. Members have bisexual flowers that are regular, with 5 free sepals and 5 free petals. The petals might be connate at the base along with two whorls of ten stamens that are also connate at the base. All members also have five distinct styles that are always heterostylous. Fruits are either capsules or berries (Chant, 1978; Judd *et al.*, 1999).

1. 1. The taxonomy of Oxalidaceae

As far as the traditional classification is concerned, the taxonomic placement of the family Oxalidaceae is controversial. Cronquist (1981), Takhtajan (1997) and Thorne (2000) assumed, based on morphology and growth habit, that this family is closely related to the family Geraniaceae. Moreover, the genera *Lepidobotrys* Engl. and *Hypseocharis* J. Rémy are considered to represent intermediate genera that link these two families. These intermediates are sometimes included in the families Geraniaceae or Oxalidaceae, or sometimes in their own separate families, the Lepidobotryaceae and the Hypseocharitaceae, respectively. Cronquist (1981) and Thorne (2000) placed the family Oxalidaceae in the order Geraniales. Takhtajan (1997) elevated the family to the ordinal level as the Oxalidales and the genus *Lepidobotrys* to family level as Lepidobotryaceae, which is included in the Oxalidales. Cronquist (1981) included the genera *Lepidobotrys* and *Hypseocharis* in the Oxalidaceae, while Thorne (2000) and Takhtajan (1997) placed *Hypseocharis* in the Geraniaceae. Thorne (2000) removed *Lepidobotrys* from the order Geraniales and placed it in the Rurales as family Lepidobotryaceae along with the genus *Ruptiliocarpon* Hammel & N.Zamora. These different views raise questions about the relationship of the two families, Oxalidaceae and Geraniaceae.

The first comprehensive *rbcL* based molecular systematic reconstruction of the angiosperms was done by Chase *et al.* (1993). They proposed completely new affinities for the family Oxalidaceae. Price and Palmer (1993) also conducted an *rbcL* based molecular phylogenetic study of the family Geraniaceae and closely related families, including the Oxalidaceae. Their finding indicated that the Oxalidaceae is only distantly related to the Geraniaceae, but thought that it could still be included in order Geraniales.

Recently, the Angiosperm Phylogeny Group (APG, 1998) reconstructed a revised angiosperm classification mainly based on plastid *rbcL* and *atpB* and nuclear 18S *rDNA* molecular evidence. More recently the APG II (2003) published an updated angiosperm phylogeny in which the Oxalidales clade formed an unresolved bush along with the Malpigiales and Celastrales in the Eurosids I clade. Both the APG (1998) and APG II (2003) classifications thus suggest a placement for Oxalidaceae well removed from the Geraniaceae to which it was previously thought to be affiliated.

A nearly complete familial phylogenetic analysis for the Eudicots was done by Savolainen *et al.* (2000) based on *rbcL* sequence data. According to their analysis, as well as the analysis

done by the APG II (2003), the Oxalidales clade is monophyletic (with 88% BS and branch length of 12 steps). This clade includes the Brunelliaceae, Elaeocarpaceae, Cunoniaceae, Cephalotaceae, Oxalidaceae and Connaraceae. Within this clade the Oxalidaceae and Connaraceae form a well-supported monophyletic group (BS 86%) sister to the rest of the families in the main clade. Savolainen *et al.* (2000) only included the oxalidaceous genera *Oxalis* and *Averrhoa* in their analysis. The genus *Hypseocharis* resolved in the family Geraniaceae, while *Lepidobotrys* resolved in the Lepidobotryaceae clade. The suggested close affinity between the Oxalidaceae and *Connarus* (Connaraceae) has never before been suspected or suggested by any classical taxonomic revision. According to earlier morphologically based classifications, the family Connaraceae was placed in the order Rosales (Cronquist, 1981). This new suggested affinity is corroborated by floral morphology (Matthews & Endress, 2002; Chant, 1978), the shared presence of exstipulate compound leaves, seeds with an aril (Chant 1978), the presence of P-type sieve-elements (Behnke, 1982) and other characters listed by Nandi *et al.* (1998).

There is also controversy about the genera that belong to the family Oxalidaceae. Chant (1978) included only three genera *Oxalis*, *Biophytum* DC. and *Eichleria* Progel. in the family, while Takhtajan (1997) removed *Eichleria* and added three other genera, *Averrhoa* L., *Sarcotheca* Blume and *Dapania* Korth. Most current researchers hold the view that only *Averrhoa*, *Biophytum*, *Dapania*, *Oxalis* and *Sarcotheca* are true oxalidaceous genera.

1. 2. The genus *Oxalis*

Oxalis is a large and cosmopolitan genus comprising *ca.* 800 species worldwide (Cronquist, 1981; Chant, 1978; Judd *et al.*, 1999). This genus has two diversity centres: Central and South America and southern Africa. Few member species are endemic to Europe (De Azku, 2000) and a few others are found in the Great Rift Valley (Kelbessa, 2000). Species of this genus, such as *O. pes-caprae* and *O. corniculata* are cosmopolitan weeds (Denton, 1973; Dreyer, 1996; Oberlander *et al.* 2002).

The American members of the genus are known to display major morphological variation and adaptation to different environmental conditions (Mark, 1955). They also comprise the highest number of taxa, including more than 500 species, exhibiting different growth habits including herbs, shrubs and geophytes. Unlike the American members, the southern African

members of *Oxalis* exhibit only a geophytic growth habit due to the presence of subterranean bulbs. This type of growth habit helps a geophytic species to survive during the dry summer season of the winter-rainfall region in the south western Cape of South Africa. Due to this lifestyle, *Oxalis* taxa are able to survive recurrent fires characteristic of the region, like other elements of the Fynbos Biome.

The southern African members include *ca.* 210 geophytic species, a total of 270 taxa (Dreyer, 1996), of which ± 150 species are concentrated in the Winter-rainfall region which covers *ca.* 90000 km² (Cowling & Hilton-Taylor, 1999). In this region, Oberlander *et al.* (2002) identified three major diversity centres for *Oxalis*, namely the Cape Peninsula, Clanwilliam/Nieuwoudtville area and the Kamiesberg.

The genus has potential economic importance in horticulture, as some of the species are already being grown and marketed for rock gardening (Du Plessis & Duncan, 1989; Jim Holms, pers.com.). The leaves, tubers and stems of some species are used for human consumption. The potential economic importance of *Oxalis* warrants a thorough systematic study of at least the southern African members (Chant, 1978; Du Plessis & Duncan, 1989).

The most comprehensive taxonomic study that exists for the southern African members of the genus is the work by Salter (1944). According to him, southern African *Oxalis* species are classified into 11 sections and 13 subsections, of which *Corniculatae* and *Ionoxalis* are naturalised sections and the rest are native to southern Africa. Since the publication of his revision, two further significant contributions to the taxonomy of southern African *Oxalis* were made by Dreyer (1996) and Oberlander (2003). Dreyer (1996) completed a palynological review of all known southern African members of the genus and identified four major pollen types and 19 subtypes. Dreyer's (1996) results confirmed the delimitations of some sections proposed by Salter (1944), while it was incongruent with other sections. Oberlander (2003) did a preliminary phylogenetic analysis using plastid non-coding *trnL-trnF* sequence data of 74 southern African *Oxalis* taxa. His work mainly focused on testing the monophyly of section *Angustatae* subsection *Lineares* and thus his sampling was biased to facilitate this. His results revealed that section *Angustatae* subsection *Lineares* is polyphyletic, rendering its delimitation artificial. His work also highlighted that the large section *Angustatae* appears to be unnatural. A comparison of his results with the palynological results of Dreyer (1996) showed significant congruence between these two

datasets (Oberlander *et al.*, 2003), which implies a need for a new classification of the southern African members of the genus.

1. 3. The bulbs of southern African *Oxalis* taxa

The underground structures of southern African *Oxalis* species consist of three parts: a rhizome, a bulb and roots. According to Salter (1944) and Gebregziabher (2001), the bulb comprises tunics, fleshy leaves, a young bulb (axillary bud) and a basal plate. The organization of these parts is demonstrated in Figure 1.1. The underground rhizome is usually vertically elongated, originating from the basal plate and extending to just below the ground level. It displays clear scales/bracts at each node, and supports the aerial part of the plant. Anatomical studies indicated that this rhizome is a true underground stem (Gebregziabher, 2001). Anatomy also indicated that the fleshy leaves are true leaves modified for storage. The tunics are usually hard and modified for protection. According to the explanation provided by Rees (1992), these types of leaves are scales that are modified from entire laminae and petioles fused together. The lower end of the bulb is the basal plate, which is the point of origin for almost all parts of the bulb. Usually this part is narrow, with alternately attached modified leaves. When the basal plate is wide, the modified leaves are usually attached spirally. Young bulbs are always present when the plant is in flower. This young bulb represents the next season's matured bulb. At this stage, tunics of the young bulbs are not dry or matured. Rarely, a single contractile root can be found during the flowering stage as well, but it is more commonly found in young plants. This root is specialised to pull the bulb mechanically deeper into the soil. A detailed report on the mechanism of this action is given by Thoday and Davey (1932). During the flowering stage, however, either a tap-root or adventitious roots are commonly found at the base of the bulb instead of a contractile root. Bulbs are usually clustered together.

According to the most widely accepted definition, a bulb is a bud with leaves that are modified into scales or fleshy leaf bases acting as storage organs. These leaves are arranged on an abbreviated, usually vertical stem. Or a bulb can be regarded as an abbreviated branching system with at least one future generation daughter bulb present (Rees, 1992). Although the bulbs of *Oxalis* differ from the commonly known bulbs in having a shortly compressed region in the basal plate area and then raised stem instead of only a compressed

or abbreviated stem, it is considered a special type of bulb as it fulfils the rest of the requirements to be a true bulb (Gebregziabher, 2001; Du Plessis & Duncan, 1989).

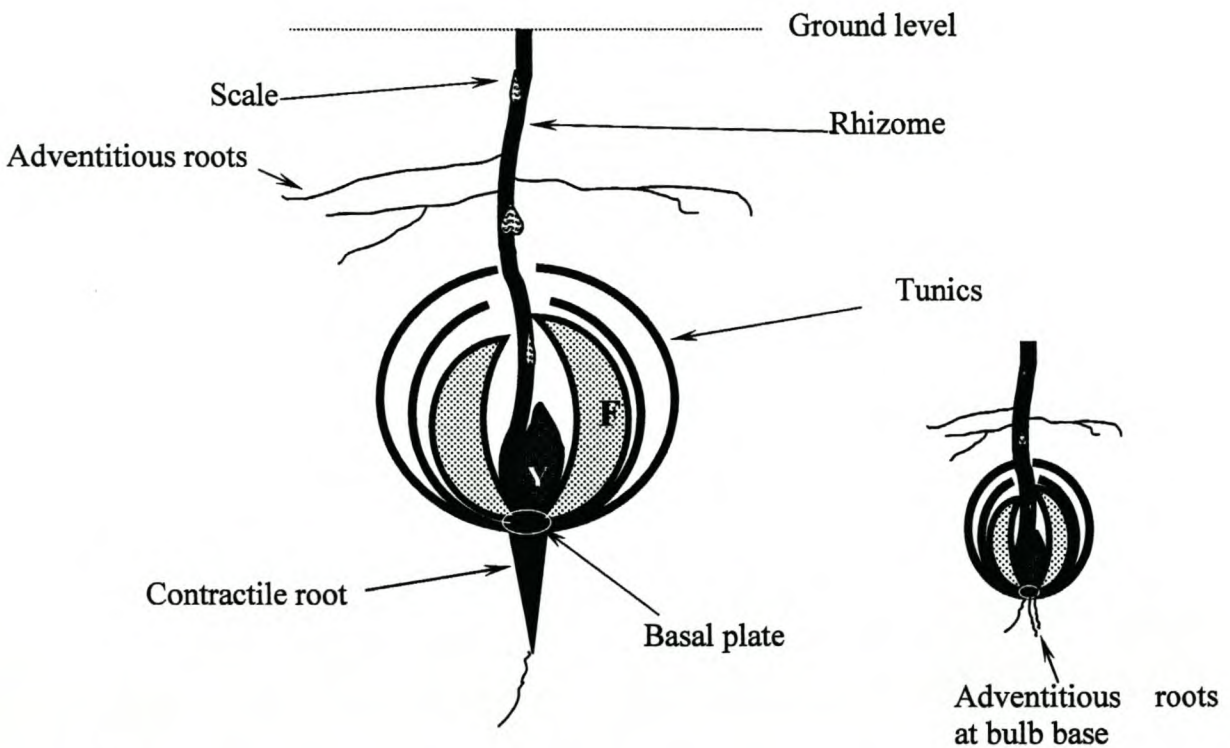


Figure 1.1. A diagram of a longitudinal section through the underground parts of southern African members of *Oxalis*. F = fleshy leaf or nutritive scale; Y = next growing season's young bulb.

Although all parts of plants are regarded as taxonomically valuable, underground plant structures are often neglected in taxonomic studies. Salter (1944) used some bulb characters in his taxonomic treatment of the genus, but suggested that these structures should be studied more intensively.

1. 4. Aims of study

The main aim of the present study is to prove the significance of bulb morphological characters in the systematics of the southern African *Oxalis*. The hypothesis of this study is that bulb morphological characters are systematically informative. To achieve this aim the following objectives were set:

- to generate a comprehensive bulb character database
 - to provide a list of potentially informative bulb morphological characters
- to identify different bulb types among the southern African *Oxalis* species
- to compare bulb morphological variation with the current taxonomic classification (Salter, 1944), the palynological classification (Dreyer, 1996) and with the preliminary phylogeny based on the non-coding plastid *trnL-trnF* DNA region (Oberlander, 2003).

CHAPTER TWO: MATERIALS AND METHODS

2. 1. Plant material

Fresh specimens of different *Oxalis* species were collected during field trips to different areas in the Western Cape region (list of species and locality details are given in Table 2.1). For every specimen collected, voucher specimens were prepared and kept in the University of Stellenbosch Herbarium (STEU). At the same time, living specimens were preserved in formalin-alcohol-acetic-acid (FAA) solution for morphological studies.

Specimens were identified using the keys in Salter (1944). In addition, herbarium specimens from Compton (NBG) and Bolus (BOL) herbaria were used for confirmation of identification.

2. 2. Specimen collection

The primary aim during specimen collection was to include as many of the sections and subsections that Salter (1944) proposed as possible. To achieve this, the diversity centers of *Oxalis* as identified by Oberlander *et al.* (2002), locality details as given by Salter (1944) and the information on herbarium specimens were used to locate the distribution of natural populations. The number of species included per section or subsection was determined by two factors. Firstly, whether Salter (1944) recognized the given section or subsection as a natural or artificial taxon and secondly the extent to which major pollen types varied among the members of the given section or subsection according to Dreyer (1996).

Considering these two factors and the availability of fresh material, natural sections and subsections were represented by single species and heterogeneous or artificial sections and subsections were represented by as many species as possible in order to include as much variation as possible. Table 2.2 shows the variation in pollen types within the taxonomic groups along with an indication of how natural or artificial Salter (1944) deemed these respective groups.

Table 2.1. Species studied, along with their specimen details, including: collector, collector's number, locality and project number.

Species name	Collection numbers	Locality	Project number
<i>O. adspersa</i>	Dreyer 769	Between Citrusdal and Clanwilliam	MO 265
<i>O. aridicola</i>	Dreyer 778	Between Pakhuis and Botterkloof, 1,9km from Wupperthal turnoff.	MO 274
<i>O. campylorrhiza</i>	Dreyer 696	Springbok, Spektakel Pass	MO 127
<i>O. caprina</i>	Dreyer and Oberlander 1	J. S. Marais Park, Stellenbosch	MO 7
<i>O. cf. callosa</i>	Dreyer 789	Van Rhyn's Dorp, Just north of Sout river Bridge on N7	MO 285
<i>O. cf. helicoides</i> var. <i>helicoides</i>	Dreyer 688	6km from Steinkopf on Port Nolloth road, in natural veld at roadside	MO 119
<i>O. commutata</i>	Dreyer 632	Ceres, near summit of Theronsberg Pass	MO 43
<i>O. dregei</i>	Cultivated by J. Holmes	-	MO 398
<i>O. ebracteata</i>	Dreyer 644	Piekenier's Kloof, Kardoesie	MO 75
<i>O. eckloniana</i>	Oberlander 30	Ceres, summit of Theronsberg Pass	MO 303
<i>O. engleriana</i>	Oberlander 71	Near Villiersdorp	MO 372
<i>O. grammophylla</i>	Dreyer 779	Between Pakhuis and Botterkloof, 1,9km from Wupperthal turnoff.	MO 275
<i>O. hirta</i> var. <i>tubiflora</i>	Dreyer 767	Piekenier's Kloof, Kardoesie	MO 263
<i>O. lichenoides</i>	Dreyer 785	Between van Rhyn's Dorp and van Rhyn's Pass	MO 281
<i>O. linearis</i>	Dreyer 679	Niewoudtville, On road to Niewoudtville after Botterkloof turnoff	MO 110
<i>O. monophylla</i>	Azieb 1	J. S. Marais Park, Stellenbosch	MO 4
<i>O. obtusa</i>	Dreyer 723	Montagu, Farm "Protea", in fynbos/renosterveld/karoo transition	MO 159
<i>O. oculifera</i>	Dreyer 799	Giftberg, 1km from Ouberg, at Ouberg turnoff	MO 295
<i>O. oligophylla</i>	Dreyer 797	Giftberg Pass	MO 293
<i>O. oreophila</i>	Dreyer 774	Summit of Pakhuis Pass	MO 270
<i>O. pes-caprae</i>	Oberlander 67	J. S. Marais Park, Stellenbosch	MO 367
<i>O. pulchella</i>	Dreyer 685	+/- 20km North of Springbok on N7	MO 116
<i>O. purpurea</i>	Dreyer 787	Between van Rhyn's Pass and van Rhyn's Dorp	O 283
<i>O. purpurea</i>	Dreyer 795	Giftberg	O 291
<i>O. salteri</i>	Dreyer 784	Between van Rhyn's Dorp and van Rhyn's Pass	MO 280
<i>O. stenopetala</i>	Dreyer 675	Base of Botterkloof Pass	MO 106
<i>O. tenella</i>	Dreyer 639	Pools, Summit of roadside cutting	MO 70
<i>O. urbaniana</i>	Oberlander 32	On road to Saron, 500m off R44	MO 305
<i>O. versicolor</i>	Oberlander 34	Road between Malmesbury and Darling	MO 307
<i>O. viscosa</i>	Dreyer 764	Southern end of Piekenier's Kloof Pass	MO 260
<i>O. xantha</i>	Dreyer 671	Between Pakhuis & Botterkloof	MO 102

Table 2.2 Specimens studied arranged according to Salter's (1944) classification, showing the pollen diversity (Dreyer, 1996) within the sections and subsections and the pollen type of the specimen that were included in the present study. A = Artificial; N = Natural.

Section	Sub-section	Taxonomic state (Salter, 1944)	Pollen type diversity (Dreyer, 1996)	Name of species studied	Pollen type (Dreyer, 1996)
Cernuae	<i>Eu-cernuae</i>		C2, C3	<i>O. pes-caprae</i> L.	C2
	<i>Lividae</i>		C3	--	-
	<i>Costatae</i>		C8	--	-
	<i>Stellatae</i>		C1, C3, C7, C8, C9	<i>O. caprina</i> L.	C7
	<i>Purpuratae</i>		C1, C7	--	-
	<i>Goetzea</i>		C2	--	-
Oppositae	<i>Subintegrae</i>	A?	C1, C2, C3, C4, C8, C9	<i>O. obtusa</i> Jacq.	R3
	<i>Bifurcatae</i>	N	C2, C4, C8	--	-
<i>Stctophyllae</i>	--		C2, C3, C4	<i>O. purpurea</i> L. <i>O. purpurea</i> L.	C3 C3
<i>Foveolatae</i>	--		C2, C3, C4, C8, C10	<i>O. pulchella</i> Jacq. <i>O. lichenoides</i> Salter.	C3 C2
<i>Sagittatae</i>	--	N	A, B, C7	<i>O. eckloniana</i> Presl.	A
<i>Campanulatae</i>	--	N	C10, C11	<i>O. dregei</i> Sond.	C10
<i>Latifoliolatae</i>	--	A	C2, C8, C10, C11, D1, D2	<i>O. campylorrhiza</i> Salter.	C8
				<i>O. commutata</i> Sond.	C10
				<i>O. oculifera</i> E.G.H. Oliver	C10
				<i>O. tenella</i> Jacq.	D1
				<i>O. aridicola</i> Salter.	D1
				<i>O. cf. callosa</i> R.Knuth.	D1
<i>Crassulae</i>	--		C2, C7, C10	<i>O. salteri</i> L. Bolus.	C10
<i>Angustatae</i>	<i>Pardales</i>	N	C2, C3, C9	<i>O. grammophylla</i> Salter.	C2
	<i>Sessilifoliatae</i>		C2, C7, C8, C9, C15, D, D1, D4	<i>O. hirta</i> L. var. <i>tubiflora</i> Jacq.	D4
				<i>O. urbaniana</i> Schltr.	C8
				<i>O. viscosa</i> E. Mey. ex Sond.	C2
	<i>Xanthotriche</i>	N?	C10	<i>O. adspersa</i> E.& Z.	C10
	<i>Lineares</i>	A	C2, C5, C7; C8, C11, C12, C14, D1, D3	<i>O. linearis</i> Jacq.	D3
				<i>O. cf. helicoides</i> Salter. var. <i>helicoides</i> Salter.	D1
				<i>O. oreophila</i> Salter.	D1
				<i>O. xantha</i> Salter.	D
				<i>O. stenopetala</i> Salter.	C7
				<i>O. oligophylla</i> Salter.	C8
<i>O. versicolor</i> L.				C8	
<i>Glandulosae</i>	A	C2, C7, C8, C9, C13	<i>O. ebracteata</i> Savign	C8	
<i>Multifoliolatae</i>	A	C6, C8, C9, C11	<i>O. engleriana</i> Schltr.	C6	
Unallocated			C8, C10, C11	<i>O. monophylla</i> L.	C10

2. 3. Morphological assessment

2. 3. 1. Underground parts studied

The main objective of this study was to morphologically assess the underground structures of selected *Oxalis* species in search of taxonomically informative characters. Therefore all the underground parts, including the rhizome, bulb, contractile root and type of root at the base of the bulb were studied. Based on Salter's (1944) suggestion, the main focus was on the bulb morphology with morphological aspects of the rhizome as second priority. In terms of root structures, only the type of root and the presence or absence of contractile root was considered.

One generally expects to find contractile roots in young plants before they start flowering. The occurrence of contractile roots at this early stage might be taxonomically informative. However, when digging out the specimens, it is likely that some contractile roots may be left behind in the ground, hence using presence or absence of this structure as a character is not plausible.

Based on Salter's (1944) observation of the rhizome, trichomes are preferred to scales and adventitious roots as taxonomic informative characters. In this study all consistent variation was considered as potentially important taxonomic characters. Whenever consistency failed, as in a few of the sampled species, it was recorded and considered as within-species variation, and thus less informative. Roots attached to the rhizome were not considered at all in the present study.

All parts of the bulb are considered to display potentially important taxonomic characters. Whenever a gummy or sticky bulb was encountered, benzene was used to dissolve the gummy substance and thus enable separation of the parts for further investigation.

In order to directly compare bulb characters between species, all bulbs were collected at the flowering stage. The only exception was *O. dregei*, for which bulbs of flowering specimens could not be obtained during the course of this study.

2. 3. 2. Materials used

The morphological assessment of the underground structure was based on material preserved in FAA. Usually five to six number of bulbs per specimen was studied with Nikon C-PS or Leitz WILD M3Z stereomicroscopes. Pictures were taken using a Nikon COOLPX 990 digital camera attached to a Leica MZ6 stereomicroscope.

2. 4. Terminology and definitions

Descriptive terminologies according to Stearn (1973) and Radford *et al.* (1974) were used for the bulb descriptions. Terminologies describing leaf and three-dimensional shapes were mostly used. Descriptive pictures given by Murley (1951) as referred by Stearn (1973) were used for surface ornamentation. Whenever unique patterns were observed for which no published descriptive terminology could be found, new descriptive terminology was proposed here. These are illustrated below:

Surface ornamentations (Figure 2.1 A-D)

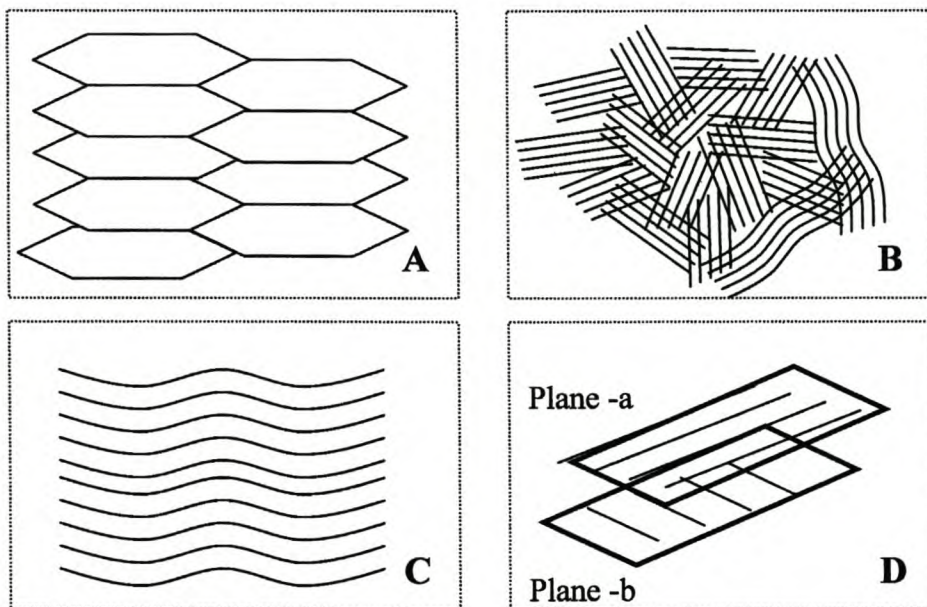


Figure 2.1 Unique surface ornamentation patterns that were defined in the present study. A = Rows of flattened cells; B = Complex mosaic of striate bunches; C = Wavy-striate; D = 'overlaid' (this is used when one type of surface ornamentation [plane -a] is observed on top of any other [plane -b])

2. 4. 1. Definitions and assumptions

- The term rhizome, as used here, only refers to the rhizome portion that extends outside of the actual bulb.
- Rhizome scales are called metabolically active if they are fleshy and dry when they are dry like tunics.
- Surface descriptions
 - Surface ornamentations are microscopic patterns seen on the abaxial and adaxial surfaces of the different tunic types and textures.
 - Surface definitions refer to the first visual impressions any given surface makes, without the aid of any optical equipment.
- Protective layers: usually composed of tunics and dried fleshy leaves, which were bulb sets of previous growing seasons. Of these, only the tunic layering was studied, while dried out fleshy leaves were ignored.
- Basal plate: a compressed or abbreviated stem from which an elongated rhizome, fleshy leaves and tunics originate. This area is well-defined and thickened in some bulbs, but can be very inconspicuous or hidden by amplexicaule fleshy leaf bases in others.
- Root types: roots are found at the base of the bulb, and can either be taproots or adventitious roots. They are viewed as taproots when a single root originates from the base of a bulb, and as adventitious roots when more than one root originate from this position.

CHAPTER THREE: RESULTS

A total of 41 potentially informative bulb morphological characters were identified (Table 3.1). These characters were then used to compile full descriptions of the bulbs of all the included species. These full descriptions are provided in the next section. In addition character states of 29 of these characters were identified and coded (Table 3.2.), for possible future inclusion in a morphology based cladistic analysis of southern African *Oxalis*. Due to the insufficient character to species ratio, such analyses were not attempted in the present study.

Table 3. 1. List of detailed bulb characters that were analysed.

List of detailed bulb characters	
<ul style="list-style-type: none"> • Rhizome <ul style="list-style-type: none"> ○ Presence of trichomes ○ Presence of sheath ○ Length ○ Diameter difference across its length ○ Clustered with other rhizomes by old bulb tunics or not • Bulbels <ul style="list-style-type: none"> ○ Presence <ul style="list-style-type: none"> ▪ Presence of stolon/dropper ▪ Presence of conical calyprate structure cupping bulbel apex originating from dropper. • Scales <ul style="list-style-type: none"> ○ Texture ○ Presence of trichomes ○ Metabolic state ○ Type of attachment ○ Arrangement • Bulb <ul style="list-style-type: none"> ○ Solitary or clustered ○ Length and mid width ○ Shape ○ Presence of apical beak ○ Base ○ Colour ○ Surface texture 	<ul style="list-style-type: none"> • Tunics <ul style="list-style-type: none"> ○ Texture types and number of textures present <ul style="list-style-type: none"> ▪ Open or closed ▪ Aestivation ▪ Margin ○ Surface description <ul style="list-style-type: none"> ▪ Colour ▪ Presence of trichomes ▪ Presence of spots (group of inflated cells) ▪ Stickiness ○ Shape <ul style="list-style-type: none"> ▪ width <ul style="list-style-type: none"> • Extent of covering the bulb ▪ Apex ▪ Base ○ Surface ornamentations <ul style="list-style-type: none"> ▪ Adaxial ▪ Abaxial • Fleshy leaves <ul style="list-style-type: none"> ○ Number ○ Colour ○ Shape ○ Apex ○ Base • Basal plate <ul style="list-style-type: none"> ○ Wideness and length • Presence of contractile root • Root type <ul style="list-style-type: none"> ○ Adventitious root/Taproot

Table 3. 2. List of non-variable, systematically informative bulb morphological characters, along with coded character states for each character.

1. Presence of trichomes on rhizome: glabrous [0] / hairy (trichomes present) [1] / both (in some present) [2]
2. Rhizome sheath coating: absent [0] / present [1]
3. Rhizome length: 0.0mm – 40.0mm [0] / 41.00 mm – 100.00 mm [1] / 101.00mm – 160.00 mm [2] / 161.00 mm–∞ [3]
4. Bulbels on rhizome: absent [0] / present [1]
5. Presence of trichomes on tunic: glabrous [0] / trichomes present [1]
6. Presence of trichomes on scale: glabrous [0] / trichomes present [1]
7. Contractile root: absent [0] / present [1]
8. Types of roots at the base of bulb: absent [0] / tap-root [1] / adventitious root [2]
9. Woody / corky tunic texture: absent [0] / present [1]
10. Leathery tunic texture: absent [0] / present [1]
11. Membranous tunic texture: absent [0] / present [1]
12. Striate surface ornamentation: absent [0] / absent [1]
13. Surface ornamentation with flattened cells in vertical rows: absent [0] / present [1]
14. Reticulate type of surface ornamentation (areolate, alveolate, scalariform): absent [0] / present [1]
15. Surface ornamentation with complex mosaic of striate bunches: absent [0] present [1]
16. Tunic surface: non-spotted [0] / spotted [1] / not always (rarely spotted) [2]
17. Tunic base: none [0] / wrinkled [1] / finger like projections [2] / longitudinal undulated [3]
18. Tunic aestivation: concentric / rings [0] / imbricate [1] / equitant [2] / convolute [3]
19. Angular tunic / raised ridges: absent [0] / present [1]
20. Deeply pitted and irregular tunic: absent [0] / present [1]
21. Smooth tunic: absent [0] / present [1]
22. Potential of bulb tunics to secrete sticky substance: absent [0] / present [1]
23. Size difference between tunics: all similar [0] / width [1] / length [2] / both length and width [3]
24. Colour of fleshy leaves: white [0] / brown apex & base [1] / brown [2]
25. Shape of fleshy leaves: columnar [0] / lingulate [1] / winged lingulate [2]
26. Number of fleshy leaves: one [0] / few (2 – 3) [1] / many (3 - ∞) [2]
27. Fleshy leaf base: sessile [0] / petiole like narrow articulation [1] / sheathing [2]
28. Basal plate: wide [0] / narrow or elongated [1]
29. Apical beak: absent [0] / present [1]

3. 1. Bulb Descriptions

Oxalis adspersa (Figure 3.1A)

Project number: O 265

Rhizome: glabrous, with tunic-like sheath, 74.0–220.0 mm (176.0 mm average) long, diameter decreasing gradually towards the bulb, clustered by old bulb tunics.

Bulbels: produced at tip of vertical dropper/stolon, cupped successively by conical calyptrate scales originating from nodes of the dropper.

Scales: membranous, glabrous, dry, amplexicaule, alternately arranged.

Bulb: solitary, 15.0–18.0 mm (17.0 mm average) long, 4.0–6.0 mm (5.3 mm average) wide in middle, oval, dull brown, surface smooth, apex beaked, base round to flattened.

Tunics: membranous, brown; both outer and adaxial surfaces dull, non-spotted, glabrous, non-sticky; open, aestivation imbricate, all similar in size, cover more than 80% of bulb body, margins not conspicuous; apex acute/acuminate; base wrinkled, amplexicaule; adaxial surface ornamentation scalariform intermixed with areolate, along veins scalariform with narrow elongated cells; abaxial surface ornamentation scalariform with flattened cells in some areas.

Fleshy leaves: 3–5, white, narrowly winged, shape lingulate, apex obtuse, with a point, base sessile.

Basal plate: narrow

Contractile root: not seen

Root type: adventitious

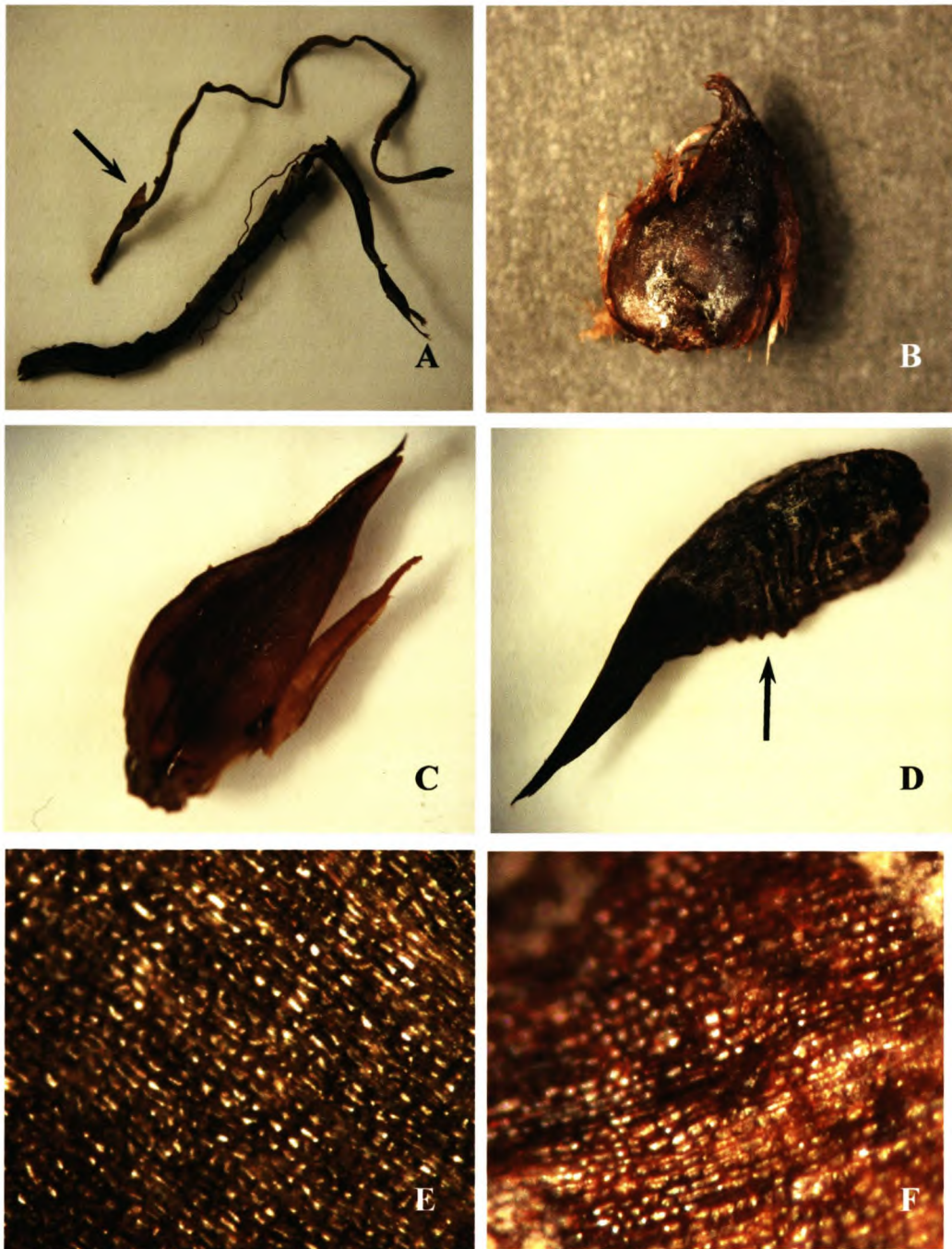


Figure 3.1 A *Oxalis adspersa*: [A] Rhizome of this species is sheathed by a tunic-like structure (structure below), scale on the rhizome indicated by arrow (structure at top); [B] Bulb with membranous tunics; [C] Adaxial side of membranous tunic; [D] Abaxial side of membranous tunic with arrow showing wrinkling, [E] Adaxial surface of tunic showing mixed scalariform and areolate ornamentation; [F] Abaxial surface of tunic showing scalariform ornamentation scalariform with flattened cells

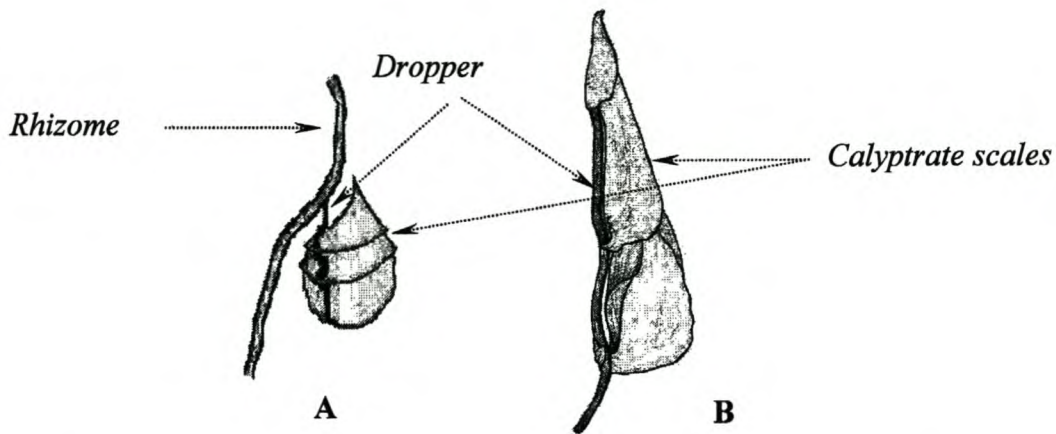


Figure 3.1 B Dropper and bulbel of *O. adspersa*. [A] Droppers keep bulbels attached to rhizome while it grows deeper into the soil. [B] Conical calyprate scales grow from the nodes of droppers and cup the upper most half of bulbels for protection.

Oxalis aridicola (Figure 3.2)

Project number: MO 274

Rhizome: glabrous, sheath absent, 12.5–59.0 mm (35.0 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, amplexicaule, alternately arranged.

Bulb: solitary, 10.0–25.0 mm (17.0 mm average) long, 5.0–12.5 mm (8.3 mm average) wide in middle, ovate to widely ovate, dark-brown; surface smooth, non-sticky; apex acute, non-beaked; base with finger-like projections.

Tunics: leathery¹, dark brick-brown; surface slightly shiny, spotted by creamy groups of inflated cells, glabrous, non-sticky; adaxial surface smooth, non-spotted, glabrous, non-sticky; closed circular units, aestivation concentric, all similar in size, covering 100% of the bulb body; margins absent; apex acute; base with small finger-like projections; adaxial surface ornamentation horizontally striate; abaxial surface ornamentation flattened-areolate.

Fleshy leaves: two, white with brown apex, shape lingulate², apex acute; base amplexicaule, with folding.



Figure 3.2 *Oxalis aridicola*: [A] Bulb with leathery tunics; [B] Bulb base with distinct finger-like projections; [C] Cross section through bulb showing the two fleshy leaves surrounded by concentrically arranged tunics; [D] Adaxial surface of tunic showing horizontally striate ornamentation; [E] Abaxial surface of tunic showing flattened-areolate ornamentation; [F] Fleshy leaf with arrow indicating distinct basal folding; [G] Elongated basal plate attached to fleshy leaf; arrow depicts young bulb

Basal plate: narrow (elongated)

Contractile root: not seen

Root type: adventitious

Note:

1. *There are delicate membranous tunic-like structures enclosed within the tunic layers. These are considered here as epidermal tissue of the leathery tunics.*
2. *The bigger leaf usually has wide and membranous margins (wings).*

Oxalis cf. callosa (Figure 3.3)

Project number: MO 285

Rhizome: glabrous, sheath absent, 20.0–65.0 mm (46.3 mm average) long, of even diameter, not clustered by previous years' bulb tunics, bulbels absent.

Scales:¹ membranous, glabrous, dry, amplexicaule, apex obtuse, alternately arranged, usually with longitudinal split at center².

Bulb: solitary, 17.0–30.0 mm (24.2 mm average) long, 9.0–27.0 mm (18.2 mm average) wide in middle, spheroid, honey-brown, surface slightly shiny, apex non-beaked; base rounded, cuneate; usually with exposed fleshy leaves³.

Tunics: membranous, golden-brown, surface shiny, non-spotted, glabrous, non-sticky, open, aestivation imbricate, all similar in size, covering 25% of bulb; lateral margins not conspicuous; apex acute; base sessile, split; adaxial surface ornamentation scalariform with elongated narrow cells; abaxial surface ornamentation scalariform with fine vertical striations overlaid, striate along veins.

Fleshy leaves: 6–9, brown, winged, shape lingulate, apex obtuse-apiculate, base sessile.

Basal plate: wide

Contractile root: not seen

Root type: adventitious

Note:

1. *There are usually only scars of scales at the nodes, since the scales fall off easily.*
2. *Buds are usually big, forcing the scales to split in the middle.*
3. *Young bulbs are covered with tightly packed tunics.*

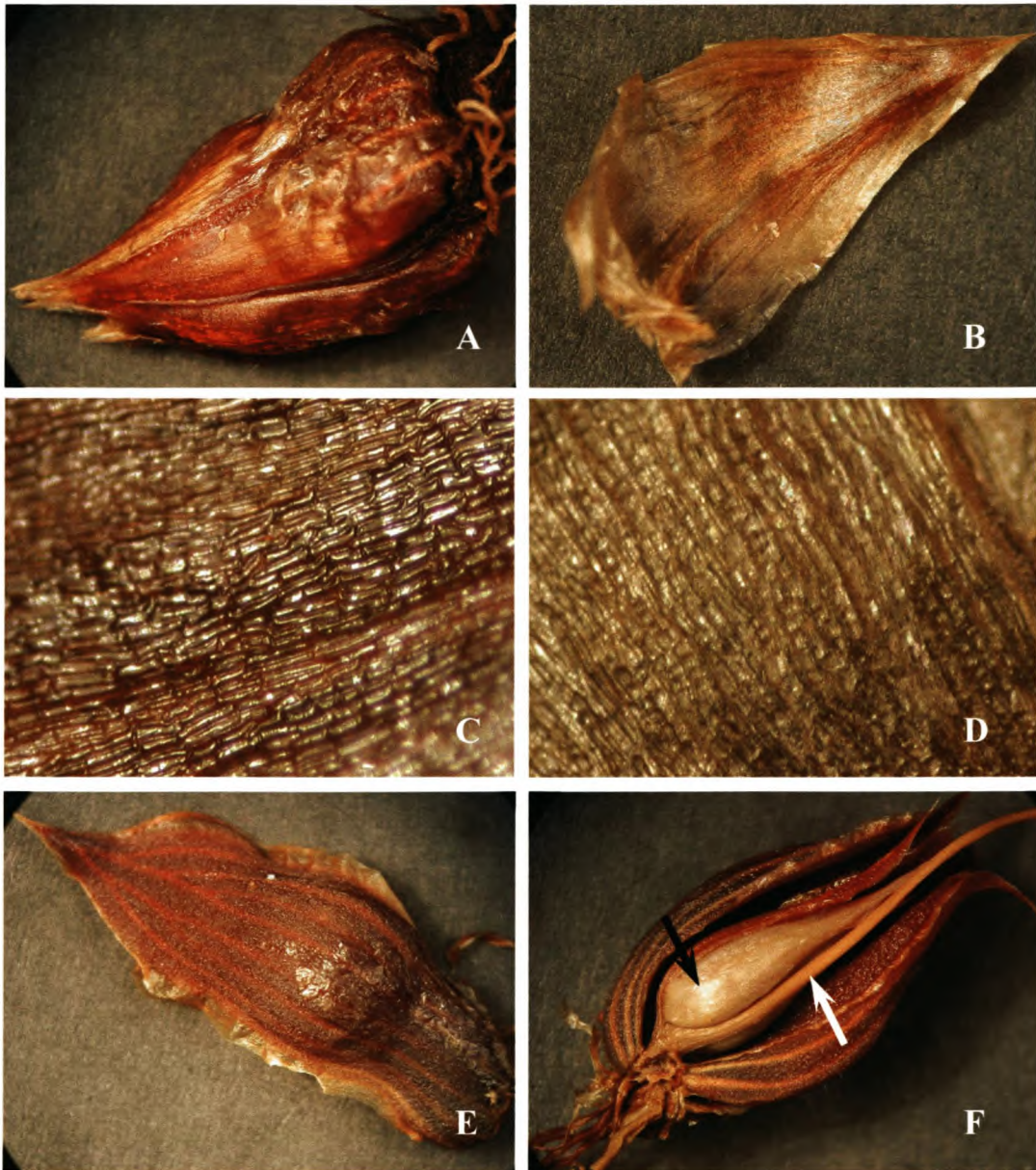


Figure 3.3 *Oxalis* cf. *callosa*: [A] Bulbs with membranous tunics; [B] A single membranous tunic; [C] Adaxial surface of tunic showing scalariform ornamentation with elongated narrow cells; [D] Abaxial surface of tunic showing scalariform ornamentation; [E] Winged fleshy leaf with membranous margins; [F] Longitudinal section through bulb showing wide basal plate, fleshy leaves and the young bulb (indicated by black arrow) attached to the rhizome (indicated by white arrow)

Oxalis campylorrhiza (Figure 3.4 A & B)

[Single specimen]

Project Number: M0 127.

Rhizome: with capitate trichomes, sheath absent, 38.0 mm long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, with capitate trichomes, dry, semi-amplexicaule, alternately arranged.

Bulb: solitary, 14.0 mm long, 8.0 mm wide in middle, elliptical in outline, honey-brown; surface smooth, apex shortly beaked; base with short tapering, flat; with thimble shaped outer tunic.

Tunics: comprise two textures: membranous and leathery. **Leathery tunics:** honey-brown, surface dull, non-spotted, glabrous, non-sticky, some closed, others open; closed leathery tunics: outermost layer, thimble shaped tunic, aestivation concentric, covers only 60% of bulb length; apex shortly beaked; base dentate; lateral margins not clearly differentiated; adaxial surface ornamentation striate; abaxial surface ornamentation areolate; open leathery tunics: covering half of bulb width, apex shortly beaked, base with short folding projecting outward; adaxial surface ornamentation areolate with elongated cells; abaxial surface ornamentation areolate. **Membranous tunics:** golden-brown, abaxial surface dull, adaxial surface slightly shiny, non-spotted, glabrous, non-sticky, closed, aestivation concentric, margins absent, apex shortly beaked, base with folding projecting outward; adaxial surface ornamentation horizontally striate crossed by vertical striations placed at wider intervals; abaxial surface ornamentation a complex mosaic of striate bunches overlaid on an areolate surface.

Fleshy leaves: two, white, non-winged, shape lingulate, apex acute, base amplexicaule.

Basal plate: narrow

Contractile root: not seen

Root type: taproot

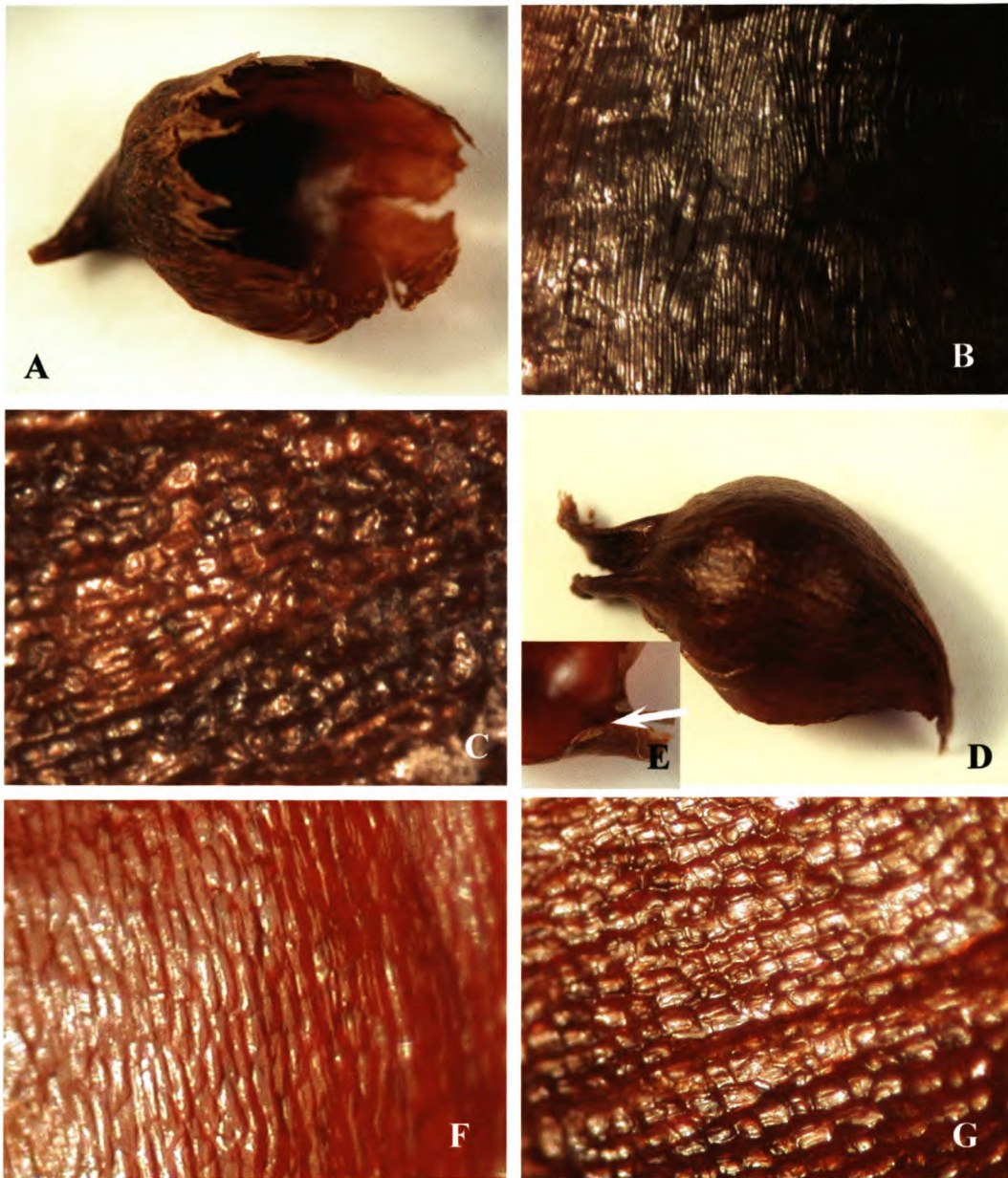


Figure 3.4 A *Oxalis campylorrhiza*: [A] Thimble-shaped, closed, leathery outermost tunic; [B] Adaxial surface of thimble-shaped tunic showing striate ornamentation; [C] Abaxial surface of thimble-shaped tunic showing areolate ornamentation; [D] Open leathery tunic; [E] Adaxial view of base of open leathery tunics with arrow indication distinct basal folding; [F] Abaxial surface of open leathery tunic showing areolate ornamentation with elongated cells; [G] Abaxial surface of open leathery tunic showing areolate ornamentation

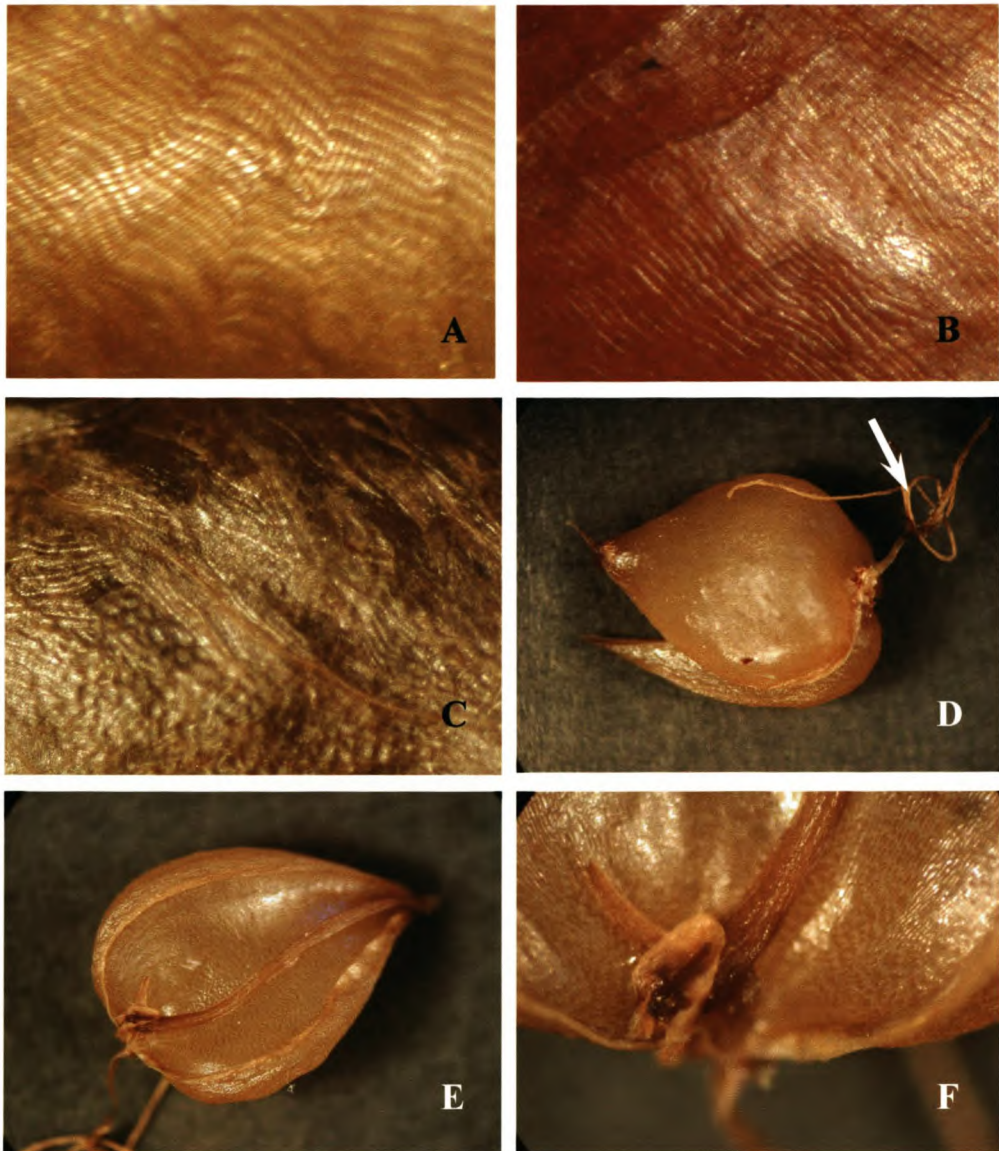


Figure 3.4 B *Oxalis campylorrhiza* (continued): [A] & [B] Adaxial surface of closed membranous tunics showing horizontally striate ornamentation crossed by vertical striations; [C] Abaxial surface of closed membranous tunics showing a complex mosaic of striate bunches; [D] Two fleshy leaves with roots arising from their bases (arrow); [E] Adaxial view of a single fleshy leaf showing a rhizome attached to the basal plate; [F] Closer view of the point of attachment of the fleshy leaves to the basal plate

Oxalis caprina (Figure 3.5)

Project number: MO 7

Rhizome: glabrous or sometimes with capitate trichomes, sheath absent, 3.0–240.0 mm (167.2 mm average) long, of even diameter, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, some still metabolically active, amplexicaule, alternately arranged.

Bulb: solitary, 13.0–8.0 mm (11.3 mm average) long, 5.0–7.0 mm (5.8 mm average) wide in middle, oval, pale-brown to brown; surface with non-raised longitudinal ridges at intervals, between ridges: non-shiny, irregular/glebulate, reticulate; apex beaked; base cupped by a basal amplexicaule tunic.

Tunics: brittle-leathery, honey-brown to pale-brown; abaxial surface with shortly raised longitudinal ridges at intervals, surface between ridges glebulate; adaxial surface smooth, shiny; open, aestivation equitant, glabrous, non-spotted; outermost tunic: short, cupping only the bulb base; inner tunic layers covering the whole bulb body with a small opening in the lower half; margins membranous, apex acute, base sessile, amplexicaule, embracing; adaxial surface ornamentation rows of flattened cells; abaxial surface ornamentation areolate, with longitudinal non-raised ridges at intervals.

Fleshy leaves: two, white, non-winged, shape lingulate, apex acute, base amplexicaule.

Basal plate: wide

Contractile root: not seen

Root type: taproot

Oxalis commutata (Figure 3.6)

Project number: M0 43

Rhizome: either glabrous or with capitate trichomes, sheath absent, 8.0–18.0 mm (12.0 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, some with capitate trichomes, dry, semi-amplexicaule, alternately arranged.

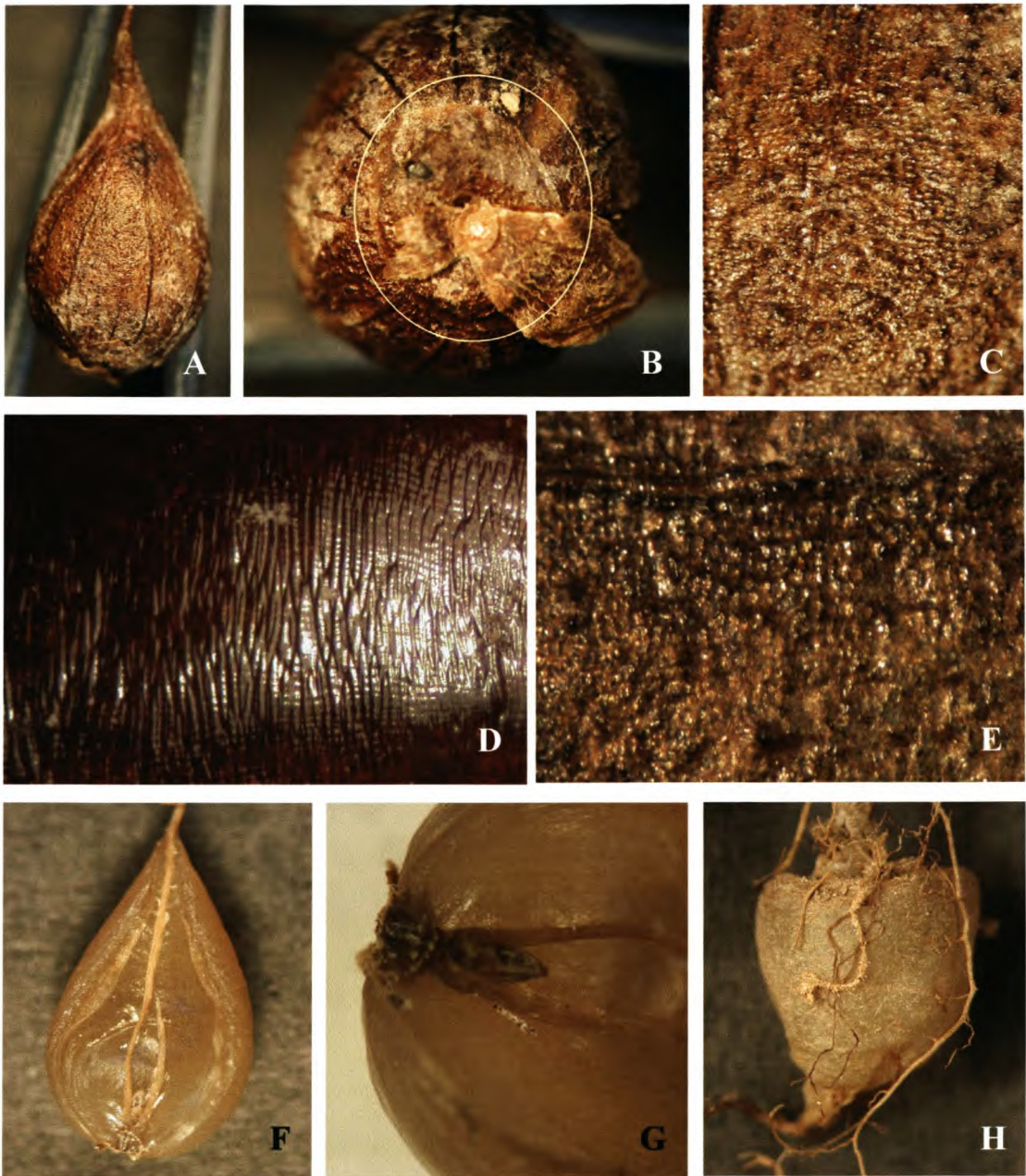


Figure 3.5 *Oxalis caprina*: [A] Bulb with leathery, brittle tunics showing longitudinal ridges; [B] Bulb base showing basal tunic inside the yellow circle; [C] Rough abaxial tunic surface; [D] Adaxial tunic surface with rows of flattened cells superimposed on a striate lower layer; [E] Closer view of the rough abaxial tunic surface showing areolate-reticulate ornamentation; [F] Adaxial view of a single fleshy leaf showing a rhizome attached to the basal plate; [G] Closer view of the point of attachment of the fleshy leaves to the basal plate; [H] Contractile root of a young plant

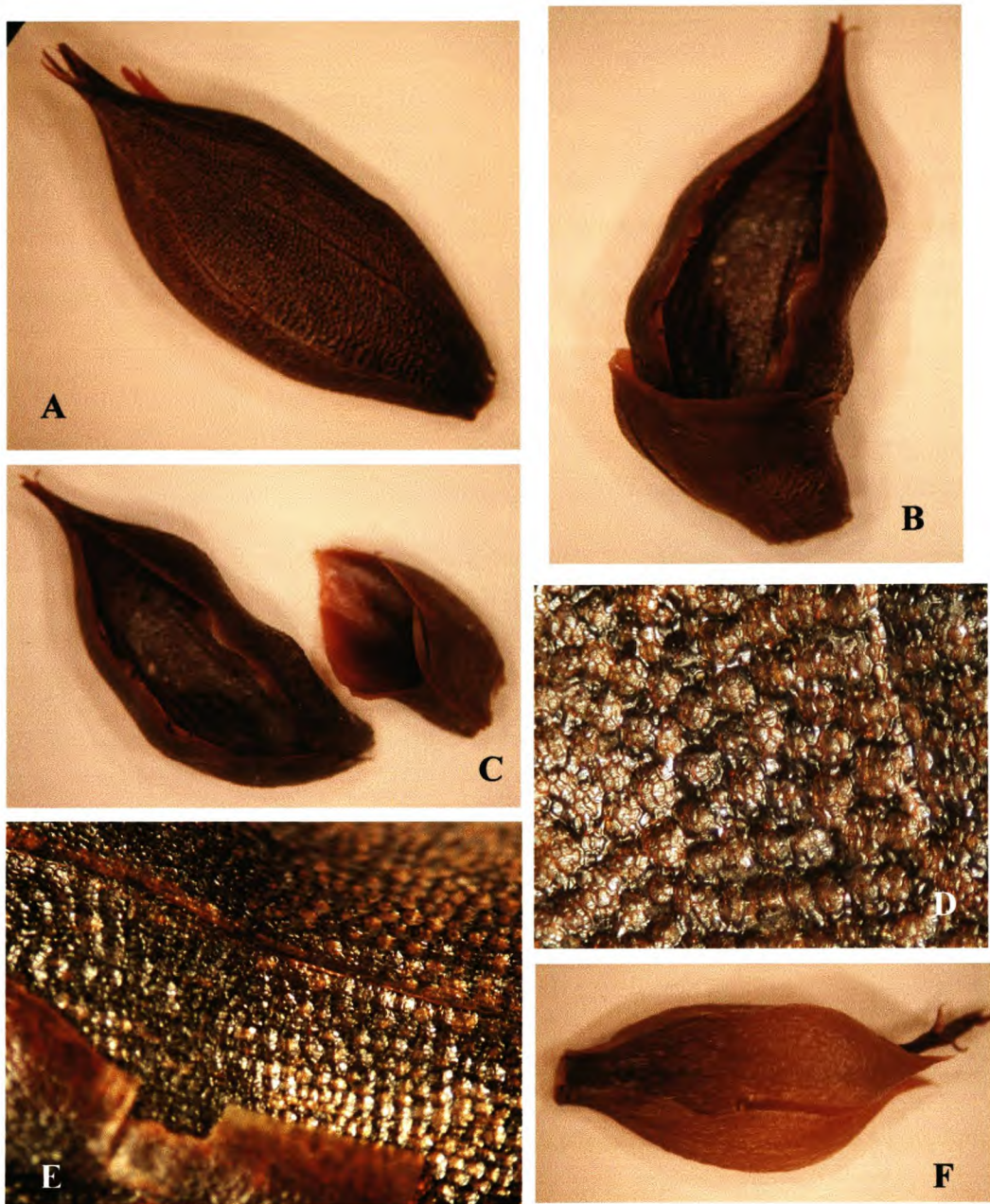


Figure 3.6 *Oxalis commutata*: [A] Bulb with leathery tunics showing low longitudinal ridges; [B] Tunics of two different sizes, the outermost restricted to bulb base; [C] Adaxial view of outermost two tunics, showing the distinct size difference between these two structures; [D] Adaxial tunic surface showing areolate surface ornamentation overlaid on wide reticulate elevations; [E] Overlap between two tunics showing the membranous tunic margins [F] Two imbricate fleshy leaves with their bases tapering cuneately towards the basal plate

Bulb: solitary, 17.0–23.0 mm (21.0 mm average) long, 7.0–8.5 mm (7.8 mm average) wide in middle, oblong, dark-brown; surface with few shortly elevated longitudinal ridges at intervals, with reticulate elevations between ridges; apex shortly beaked; base flat, cupped by a basal tunic.

Tunics: leathery, dark-brown, surface non-spotted, glabrous, non-sticky; open, aestivation equitant, outer most tunic only basal, covering 90% of bulb body; margins brittle, membranous; apex acute, embracing the bulb; base sessile, not split; adaxial surface ornamentation areolate; abaxial surface ornamentation areolate overlaid on wide reticulate elevations, with short longitudinal ridges placed at intervals.

Fleshy leaves: three, white, narrowly winged, shape flattened lingulate, apex acute, base sessile.

Basal plate: wide

Contractile root: not seen

Root type: adventitious

Oxalis dregei (Figure 3.7)

Project number: MO 398

Rhizome: glabrous, sheath absent, 20.0 mm long, diameter decreasing gradually towards the middle, angular, not clustered by previous years' bulb tunics, bulbels present.

Bulbels: borne laterally, with horizontally orientated stolons attached to base, calyprate scales absent.

Scales: membranous, glabrous, dry, amplexicaule, alternately arranged.

Bulb: solitary, 7.0 mm long, 5.0 mm wide, spheroid, light-brown, surface smooth, apex shortly beaked, base widely cuneate.

Tunics: leathery, light-brown, surface dull, non-spotted, glabrous, non-sticky, open, aestivation equitant, all similar in size, cover 95% of bulb body, margins leathery, apex beaked; base split, widely cuneate; adaxial surface ornamentation a complex mosaic of striate bunches; abaxial surface ornamentation areolate.

Fleshy leaves: two¹, white, non-winged, shape lingulate, apex acute, base amplexicaule.

Basal plate: narrow

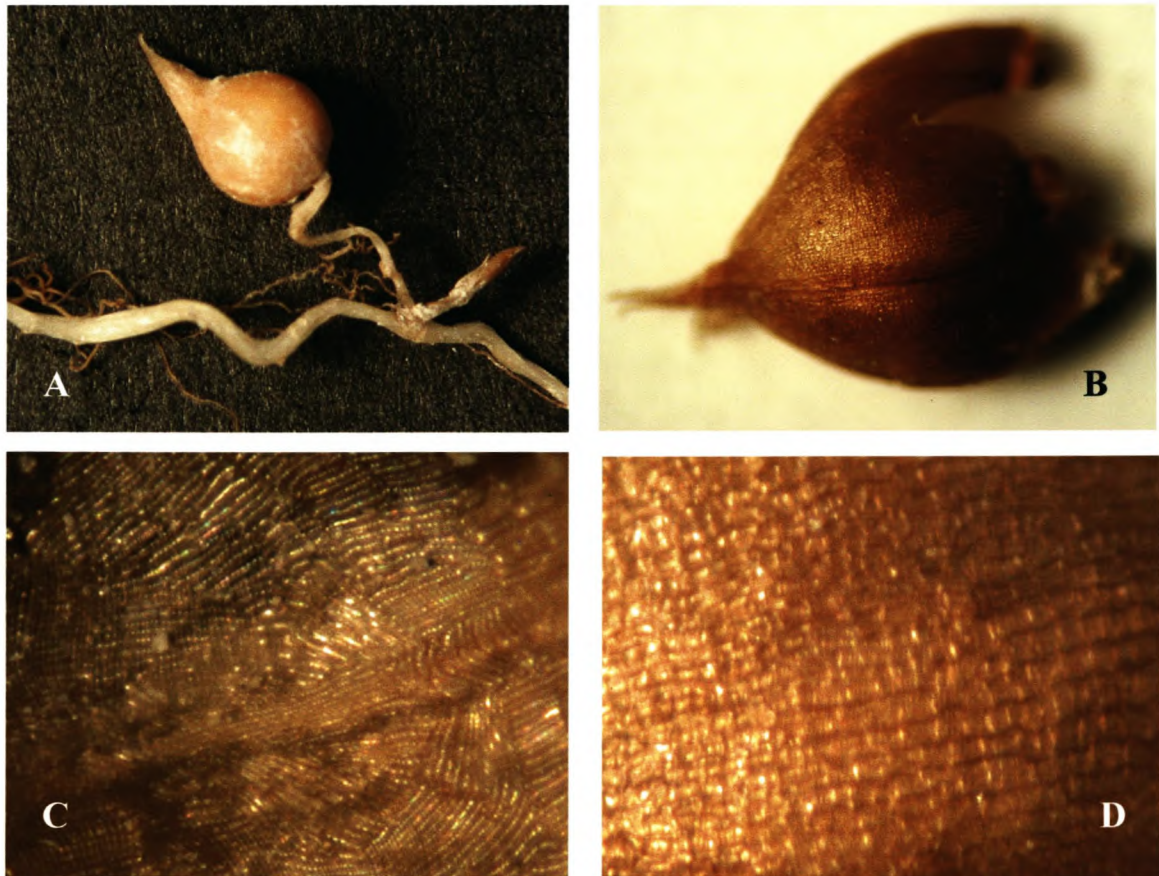


Figure 3.7 *Oxalis dregei*: [A] Bulbel on a lateral stolon attached to the rhizome; [B] Leathery tunic split at the base; [C] Adaxial tunic surface ornamentation showing a complex mosaic of striate bunches; [D] Abaxial tunic surface showing areolate surface ornamentation

Contractile root: not seen

Root type: not seen

Note:

1. *There are two fleshy leaves: one is very large and constitutes almost the entire bulb body, while the second one is small and thin.*

Oxalis ebracteata (Figure 3.8)

Project number: MO 75

Rhizome: glabrous, sheath absent, 12.0–13.0 mm (12.5 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent, rhizomes sometimes horizontally orientated.

Scales: membranous, glabrous, dry, amplexicaule to semi-amplexicaule, alternately arranged.

Bulb: solitary, 16.0–18.0 mm (17.0 mm average) long, 5.5–7.0 mm (6.3 mm average) wide in middle, fusiform to oval, dark-brown, surface smooth; apex shortly beaked, acute; base shortly cuneate to obtuse-apiculate.

Tunics: two texture types recognized, namely membranous and leathery. **Membranous tunics:** constitute outer two layers, golden-brown to honey brown, surface smooth, non-spotted, glabrous, sticky, open, aestivation equitant, usually shorter than leathery tunics, usually with overlapping margins along lower half of the bulb, margins not conspicuous, apex beaked/rostrate; base sessile; adaxial surface ornamentation ruminant; abaxial surface ornamentation scalariform. **Leathery tunics:** constitute the inner layers, honey-brown, surface smooth, non-spotted, glabrous, sticky, open, aestivation equitant, cover entire inner part of the bulb, usually with overlapping margins along lower half of the bulb, margin membranous, apex beaked/rostrate; adaxial surface ornamentation ruminant; abaxial surface ornamentation areolate.

Fleshy leaves: three, white, shape lingulate, narrowly winged in lower half, apex beaked, base amplexicaule.

Basal plate: narrow

Contractile root: not seen

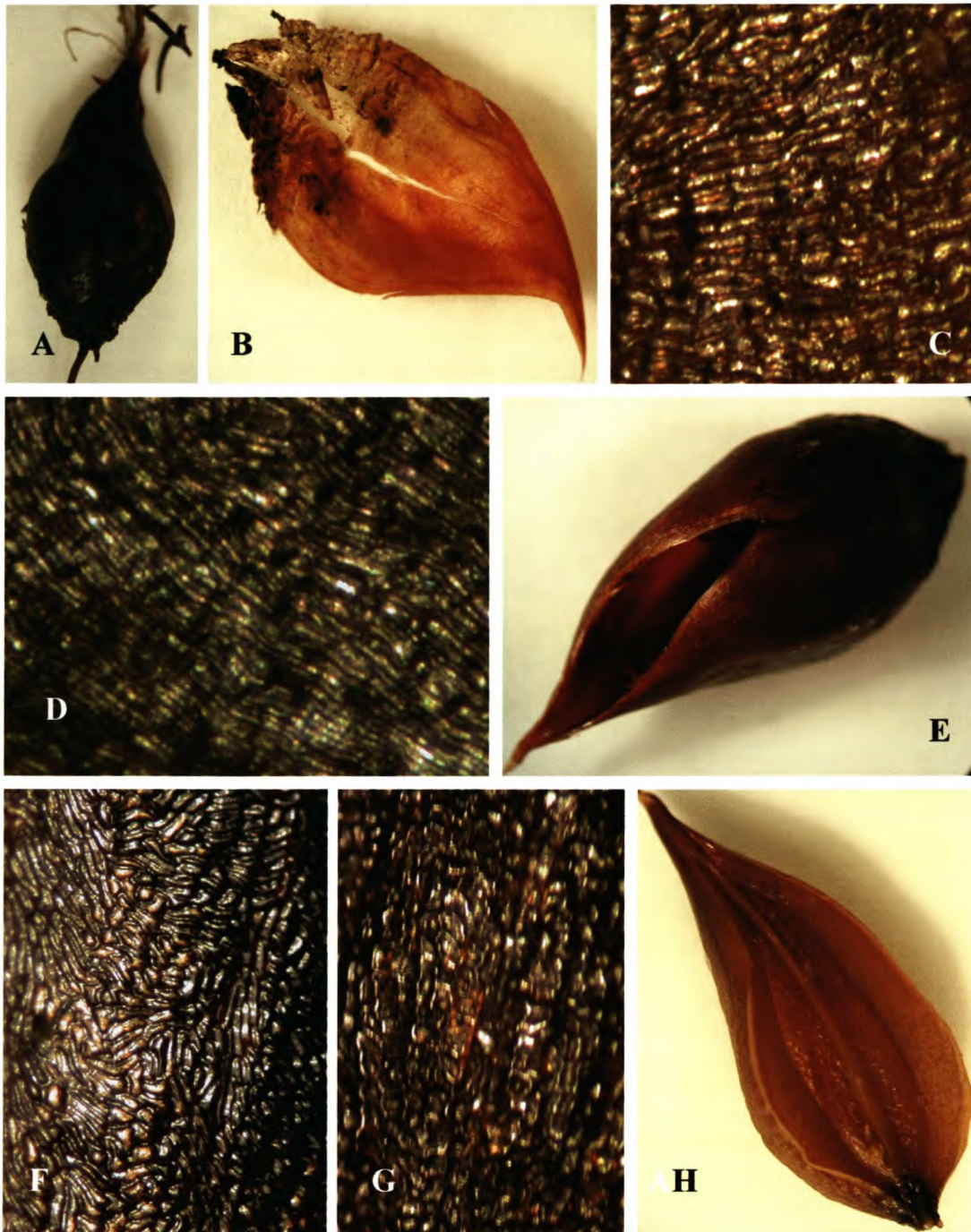


Figure 3.8 *Oxalis ebracteata*: [A] Bulb with sticky membranous and leathery tunics stuck together; [B] Abaxial view of membranous tunic with wrinkled base; [C] Adaxial surface of membranous tunic showing ruminant ornamentation; [D] Abaxial surface of membranous tunic showing scalariform ornamentation; [E] Leathery tunic showing overlapping margins that cover the lower half of the bulb; [F] Adaxial surface of leathery tunic showing ruminant ornamentation; [G] Abaxial surface of leathery tunic showing areolate ornamentation; [H] Adaxial view of two fleshy leaves showing a rhizome attached to the basal plate

Root type: taproot

Oxalis eckloniana (Figure 3.9)

Project number: M0 303

Rhizome: glabrous, sheath absent, 10.0–56.0 mm (26.9 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, only some metabolically active, semi-amplexicaule, alternately arranged.

Bulb: solitary, 13.0–20.0 mm (16.1 mm average) long, 8.0–12.0 mm (9.1 mm average) wide in middle, shape variable ranging from oblong to ovate, golden-brown, surface smooth but not shiny; apex non-beaked, acute; base usually cuneate.

Tunics: rigid leathery¹, golden-brown, abaxial surface dull, adaxial surface shiny, non-spotted, glabrous, non-sticky, open, aestivation imbricate, some short, covers 50% of bulb body, margins leathery, apex acute or acuminate, base with finger-like projection; adaxial surface ornamentation areolate; abaxial surface ornamentation alveolate overlaid on fine striate lines.

Fleshy leaves: two, white, non-winged, shape lingulate, apex acute, base amplexicaule with finger-like projections².

Basal Plate: narrow³

Contractile root: not seen

Root type: adventitious²

Note:

1. *Membranous tunics are present amongst older bulb remains.*
2. *The finger-like projections arising from the fleshy leaves lead to adventitious roots that pass through the finger-like projections of the tunics. As a result no visible roots originate from the basal plate, but from the basal projections of the fleshy leaves.*
3. *A woody, dark-brown layer is present at the base of the bulb of this species.*

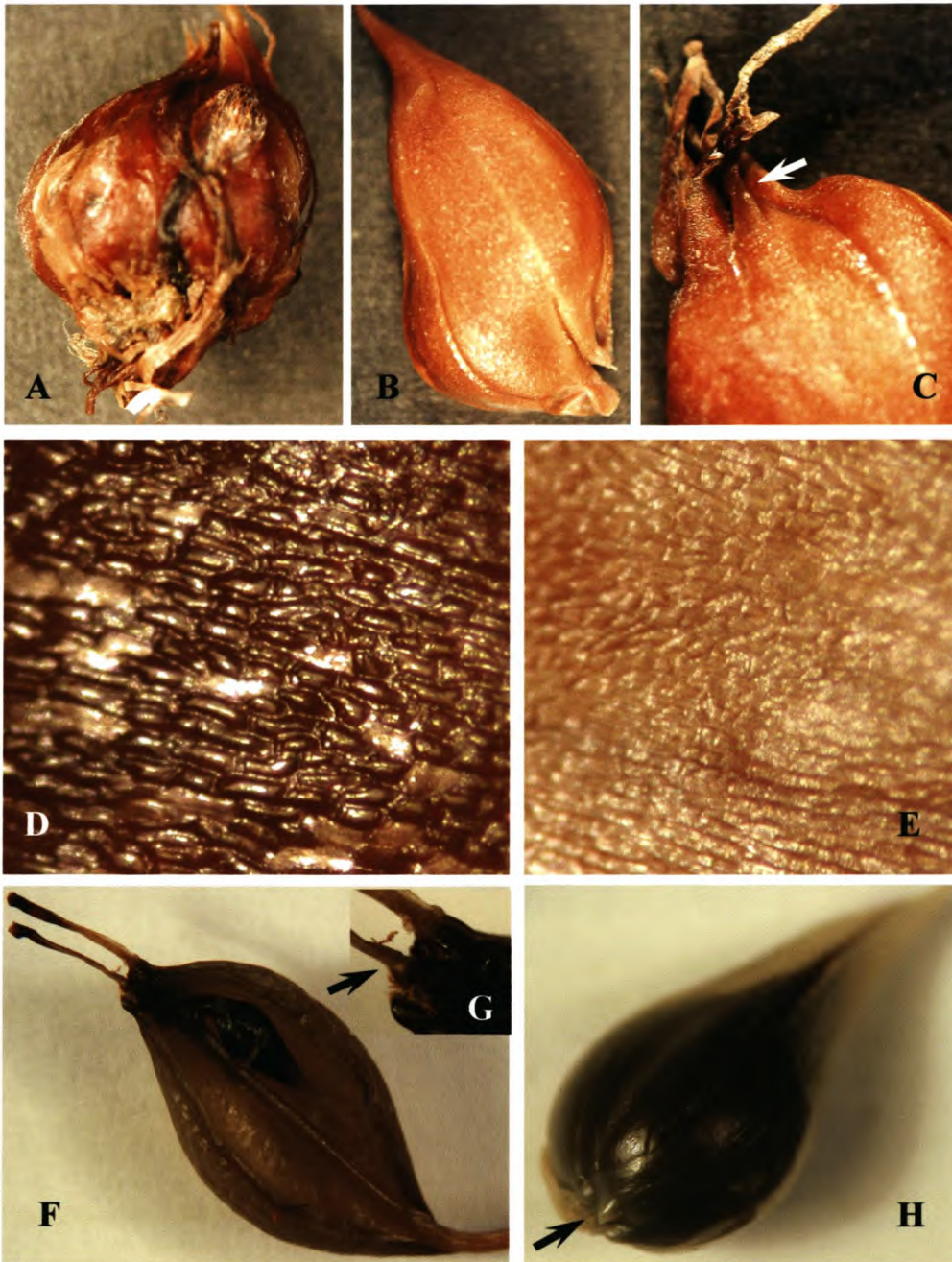


Figure 3.9 *Oxalis eckloniana*: [A] Bulb with leathery tunics; [B] Abaxial view of leathery tunic with distinct venation; [C] A closer view of the base of a leathery tunic, arrow indicate the finger-like projections; [D] Adaxial surface of leathery tunic showing areolate ornamentation; [E] Abaxial surface of leathery tunic showing alveolate ornamentation; [F] Adaxial view of two fleshy leaves showing a rhizome attached to the basal plate; [G] A closer view of the fleshy leaf base, with the arrow indicating a finger-like projection that lead to an adventitious root; [H] Young bulb with developing finger-like projection at the base (arrow).

Oxalis engleriana (Figure 3.10)

Project number: MO 372

Rhizome¹: glabrous, sheath absent, 41.0–85.0 mm (59.6 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous; covered with black-headed, capitate trichomes; dry, amplexicaule, alternately arranged.

Bulb: solitary², 35.0–55.0 mm (43.5 mm average) long, 5.0–17.0 mm (19.0 mm average) wide in middle, usually conical, light-brown; surface dull, usually wrinkled; apex non-beaked¹, shortly attenuated, base usually depressed.

Tunics: two texture types recognized, namely membranous and leathery. **Membranous tunics:** restricted to the outer layers, golden-brown, surface with abundant tuberculate secreting cells adaxially, non-spotted, sticky, open, aestivation imbricate, cover 40–60% of bulb width, apex beaked, usually wrinkled; margins not conspicuous; adaxial surface ornamentation scalariform; abaxial surface ornamentation striate. **Leathery tunics:** confined to the inner layers, reddish-brown, with dark-brown tuberculate secreting cells abundant on adaxial surface, non-spotted, sticky, open, aestivation imbricate, cover 40–60% of bulb width, margin membranous, apex beaked, base with longitudinal undulations or folds; adaxial and abaxial surface ornamentations striate.

Fleshy leaves: two, white, shape lingulate, margins membranous in the lower half, apex acuminate, base amplexicaule.

Basal plate: wide

Contractile root: not seen

Root type: taproot

Note:

1. *Rhizome may look as if it arises from the middle of the beaked bulb apex, but it extends through previous years' narrow bulb tunic remains.*
2. *Previous years' bulbs dovetail with the current years' bulb apex.*

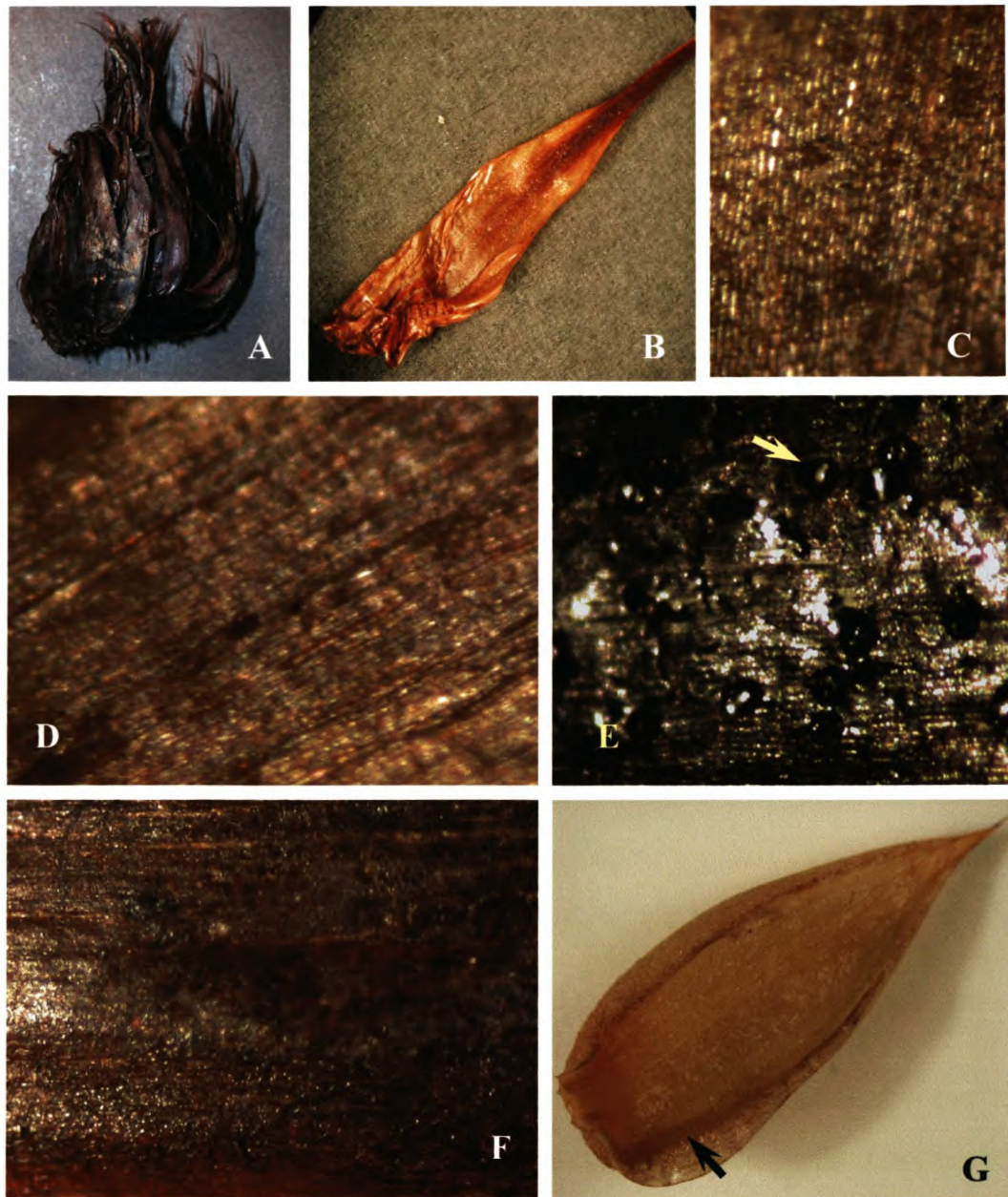


Figure 3.10 *Oxalis engleriana*: [A] Bulb with flaking, membranous tunics; [B] Abaxial view of a membranous tunic with a wrinkled base; [C] Adaxial surface of membranous tunic showing scalariform ornamentation; [D] Abaxial surface of membranous tunic showing striate ornamentation; [E] Adaxial surface of leathery tunic showing striate ornamentation, arrow indicates tuberculate secreting cells; [F] Abaxial surface of leathery tunic showing striate ornamentation; [G] Adaxial view of a fleshy leaf with membranous lower margins indicated by an arrow

Oxalis grammophylla (Figure 3.11)

Project number: MO 275

Rhizome: with short capitate trichomes, sheath absent, 74.0–80.0 mm (77.0 mm average) long, diameter decreasing gradually towards the bulb, bulbels absent.

Scales: membranous, usually glabrous, few with capitate trichomes, dry, semi-amplexicaule, alternately arranged.

Bulb: solitary, 49.0–56.0 mm (52.5 mm average) long, 13.0–15.0 mm (14.0 mm average) wide in middle, oblong, dark-brown; surface dull, covered by reversed strigose trichomes¹; apex bushy or acute, not beaked; base usually flat, with numerous loose tunics².

Tunics: leathery, honey-brown, abaxial surface with reversed strigose trichomes, adaxial surface smooth, non-spotted, with longitudinal non-raised ridges, non-sticky, open, aestivation imbricate, inner layers covering 40% of bulb width, outer layers covering less than 25% of bulb width³, margins membranous, apex beaked, base amplexicaule; adaxial surface ornamentation scalariform to areolate; abaxial surface ornamentation areolate.

Fleshy leaves: two, white, narrowly winged, shape lingulate, apex acuminate, base amplexicaule.

Basal plate: narrow

Contractile roots: not seen

Root type: taproot

Note:

1. *Reversed hairs are stiff, causing the bulb surface to be rough and feel like a cat's tongue.*
2. *The tunics are loosely packed and during field collections the outer layers were easily shed.*
3. *The outer tunic splits longitudinally from the mid position towards both ends. The inner tunic layers, however, remain intact.*

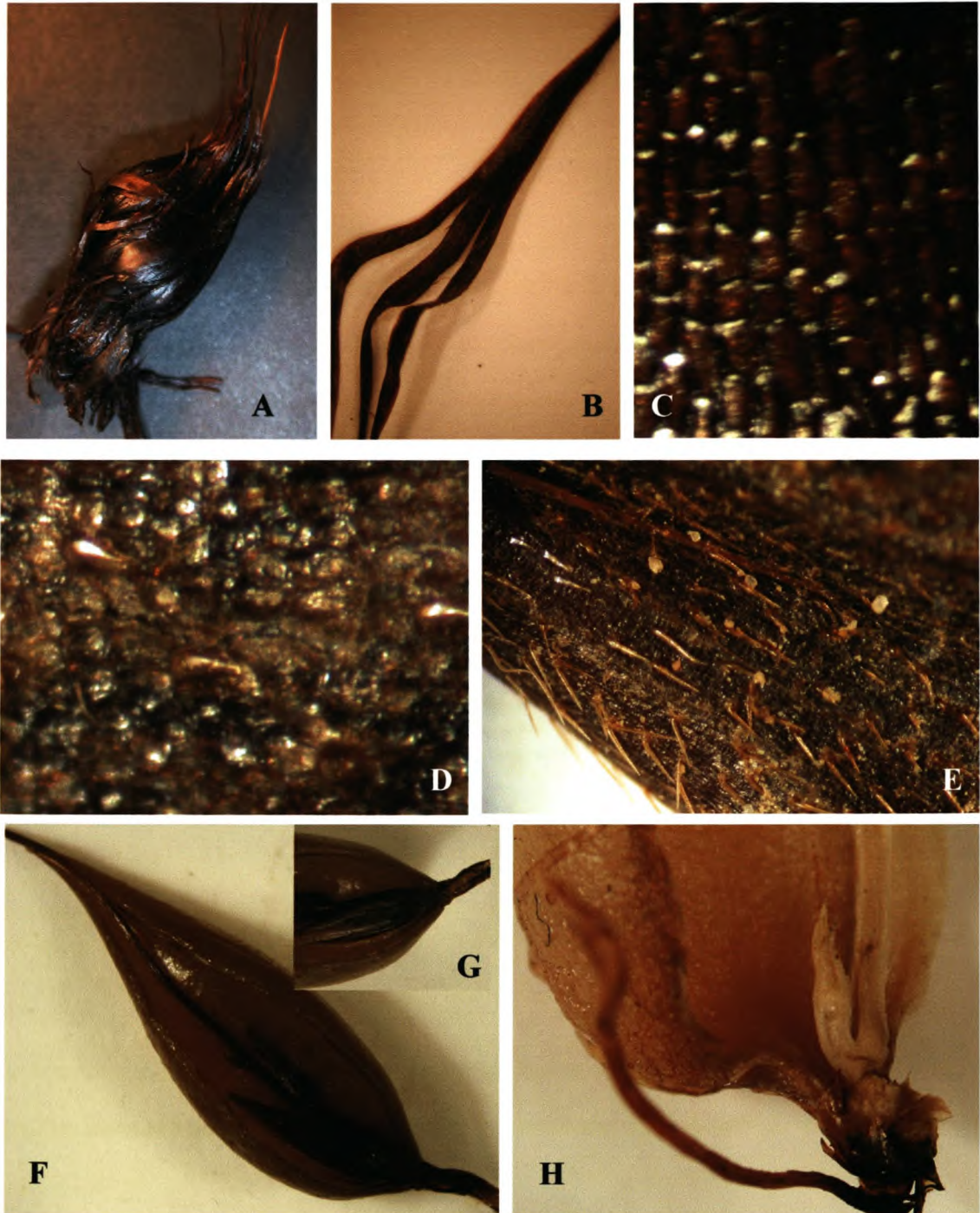


Figure 3.11 *Oxalis grammophylla*: [A] Bulbs with leathery tunics; [B] Adaxial view of leathery tunic split in the characteristic way; [C] Adaxial surface of leathery tunic showing areolate-scalariform ornamentation; [D] Abaxial surface of leathery tunic showing areolate ornamentation; [E] Enlarged portion of abaxial tunic showing the reversed strigose trichomes; [F] & [G] Adaxial view of fleshy leaves showing a rhizome attached to the basal plate and young bulbs; [H] Closer view of fleshy leaf attachment to the basal plate

Oxalis cf. helicoides var. helicoides (Figure 3.12)

Project number: MO 119

Rhizome: glabrous, sheath absent, 105.0–110.0 mm (107.5 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent, rigid, bark present.

Scales: membranous, transparent, delicate, glabrous, dry, amplexicaule, alternately arranged¹.

Bulb: solitary, 56.0–57.0 mm (56.5 mm average) long, 23.0–27.0 mm (25.0 mm average) wide in middle, ovate, honey-brown, surface smooth; apex acute, shortly beaked; base round, tunics tightly packed.

Tunics: membranous, brown to honey-brown, spotted at base and apex, glabrous, non-sticky, open, aestivation imbricate, covering about 50% of bulb width, all similar in size; margins membranous, apex acute, base wrinkled; adaxial surface ornamentation scalariform, with elongated narrow cells at base; abaxial surface ornamentation scalariform, striate or flat along the veins.

Fleshy leaves: 26, brown, winged, shape lingulate, sessile, apex beaked, base with swellings², canals with a creamy brown content present³.

Base plate: wide

Contractile root: not seen

Root type: not seen

Note:

1. *The scales are transparent and delicate. At some nodes only rudimentary scales are present.*
2. *The swellings are similar to prop roots arising from the lower nodes of the stem of maize plants.*
3. *Canals inside the fleshy leaves are filled with a creamy substance, which makes the canals visible without sectioning the leaves. The substance could fill the canals along their entire length or it could be irregularly distributed within the canals. Detailed anatomical sections would be needed to confirm this.*

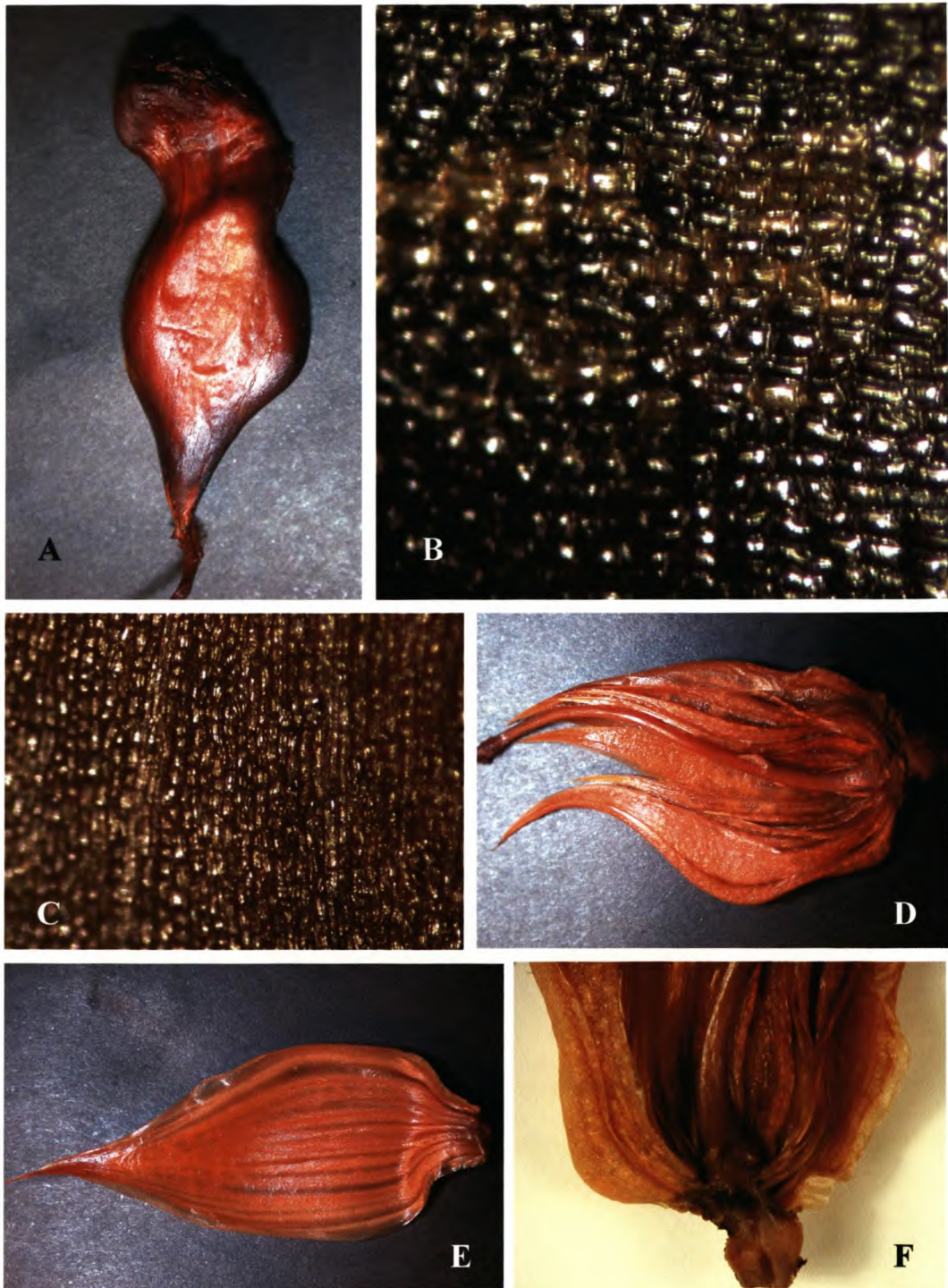


Figure 3.12 *Oxalis* cf. *helicoides*: [A] Bulb with membranous tunic; [B] Adaxial surface of membranous tunic showing scalariform ornamentation; [C] Abaxial surface of membranous tunic showing scalariform ornamentation; [D] Adaxial view of fleshy leaves, showing their attachment to the basal plate; [E] A single fleshy leaf with canals filled with a creamy-brown content clearly visible; [F] A closer view of the point of attachment of fleshy leaves to the wide basal plate

Oxalis hirta* var. *tubiflora (Figure 3.13)

Project number: MO 263

Rhizome: glabrous, sheath absent, 30.0–66.0 mm (44.0 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, amplexicaule, alternately arranged.

Bulb: solitary, 21.0–25 mm (22.9 mm average) long, 12.0–23.0 mm (17.5 mm average) wide in middle, spheroid, honey-brown, surface smooth, apex non-beaked, base round, tunics tightly packed¹.

Tunics: membranous, golden-brown, surface dull, spotted at apex and base with group of gray inflated cells, glabrous, open, aestivation imbricate, non-sticky, cover more than 50% of bulb width, all similar in size; margins delicate, transparent, membranous; apex acute, base sessile; adaxial surface ornamentation scalariform, with narrowly elongated cells along the veins; abaxial surface ornamentation scalariform, striate along veins and apex.

Fleshy leaves: nine, brown, winged, shape lingulate, apex acute, base sessile, tightly packed, with creamy brown substance inside².

Basal plate: wide

Contractile root: not seen

Roots type: adventitious

Note:

1. *Although the tunics are tightly packed, some fleshy leaves are sometimes exposed.*
2. *Canals inside the fleshy leaves are filled with a creamy substance, which makes the canals visible without sectioning the leaves. The substance could fill the canals along their entire length or it could be irregularly distributed within the canals. Detailed anatomical sections would be needed to confirm this.*



Figure 3.13 *Oxalis hirta* var. *tubiflora*: [A] Bulb of all tunics have been removed, note prominent creamy fillings of the canals in the fleshy leaves (arrow); [B] Abaxial view of a single membranous tunic; [C] Enlarged view of a portion of the abaxial tunic surface to show groups of inflated cells; [D] Adaxial surface of membranous tuncis showing scalariform ornamentation; [E] Abaxial surface of membranous tuncis showing coarse scalariform ornamentation; [F] & [G] Winged fleshy leaves displaying membranous margins (arrow); [H] Fleshy leaves attached to a wide basal plate

Oxalis lichenoides (Figure 3.14)

Project number: M0 281

Rhizome: with capitate trichomes, sheath absent, 0.1–16.0 mm (5.1 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, with short internodes, bulbels present.

Bulbels: borne terminally at the end of a stolon; stolon, short, thick, horizontal, originate from rhizome at oblique angle.

Scales: membranous, glabrous, dry, amplexicaule or semi-amplexicaule, alternately arranged, split longitudinally along the middle as the buds enlarge.

Bulbs: solitary, 11.0–21.0 mm (13.1 mm average) long, 2.5–6.0 mm (4.8 mm average) wide in middle, oval, brown, surface dull, non-spotted, glabrous, non-sticky, apex shortly beaked, base cuneate; with sharp, prominently raised angles running from the base to the upper quarter of the bulb, additional slightly raised ridges extend from the apex to the lower quarter of the bulb between the prominent wings; older bulb tunics dovetail at the apex of the current year's bulb.

Tunics: leathery, light coffee-brown, surface dull, non-spotted, glabrous, non-sticky, open, aestivation equitant, cover more than 80% of bulb body, angular (refer to bulb description), with shortly raised ridges in-between angles¹, margin membranous, apex beaked; base angular, split, open²; adaxial surface ornamentation areolate; abaxial surface ornamentation reticulate at sides of wings and apex, without a clear pattern around the slightly raised ridge, striate between angles and the slightly raised ridge.

Fleshy leaves: single, white, non-winged, shape lingulate, apex acuminate, base amplexicaule.

Basal plate: narrow

Contractile root: not seen

Root type: taproot

Note:

1. *The outward folding of the tunics form distinct angles. However, the ridges are just elevated elements that run from the apex to the lower quarter of the tunic/bulb.*
2. *Bases of the older tunics are widely split open.*

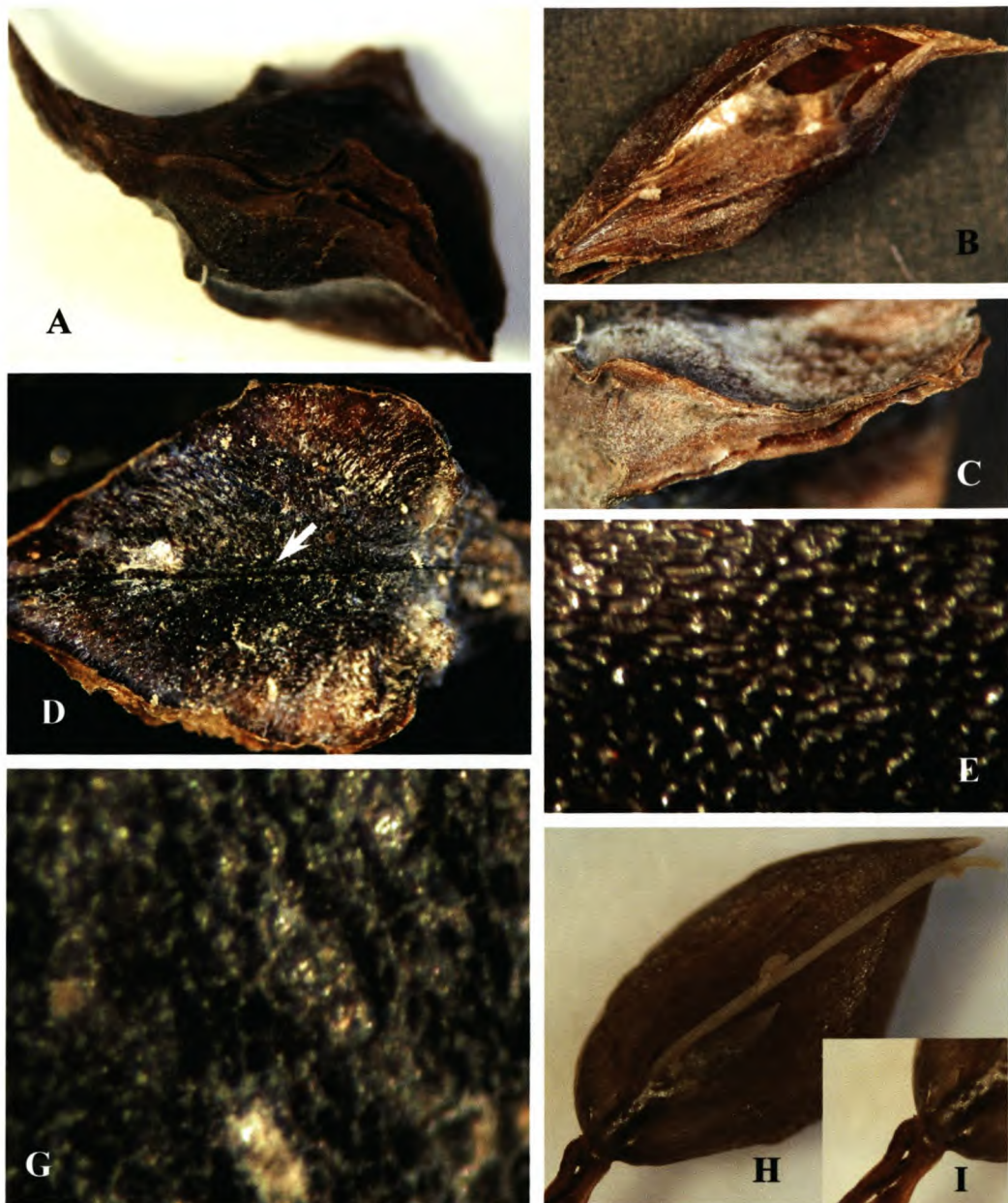


Figure 3.14 *Oxalis lichenoides*: [A] Bulb with angular leathery tunics, showing the longitudinal splits along the ridges; [B] Inner angular tunic layer showing the overlapping margins that cover the lower half of the bulb; [C] A closer view of the angular ridge of the tunic formed by sharp folding; [D] A close-up view of abaxial surface between the angular ridges showing a non-raised longitudinal ridge (indicated by arrow) along the middle; [E] Adaxial surface of leathery tunic showing areolate ornamentation; [G] Abaxial surface of leathery tunic showing areolate ornamentation; [H] Adaxial view of the single fleshy leaf showing a rhizome attached to the basal plate and young bulbs; [I] Attachment of the single fleshy leaf and adventitious roots to an elongated, narrow basal plate .

Oxalis linearis (Figure 3.15)

Project number: MO 110

Rhizome: glabrous, sheath absent, 42.0–57.0 mm (49.8 mm average) long, of even diameter, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, amplexicaule, split longitudinally along middle as buds enlarge, alternately arranged.

Bulb: solitary, 18.0–20.0 mm (19.0 mm average) long, 10.0–18.0 mm (12.5 mm average) wide in middle, ovoid or spheroid, honey-brown, surface smooth¹; apex acute, non-beaked; base round, vertically orientated in the substrate.

Tunics: membranous, golden-brown, non-spotted, glabrous, non-sticky, open, aestivation imbricate, covering 40% of bulb body, all similar in size, margins membranous; apex acute, base with longitudinal undulations²; adaxial surface ornamentation scalariform; abaxial surface ornamentation scalariform, striate along veins.

Fleshy leaves: 11–55, brown, winged, shape lingulate, apex acuminate, base sessile, with creamy brown fillings inside³.

Basal plate: wide

Contractile root: not seen

Root type: adventitious

Note:

1. *The fleshy leaves are usually exposed.*
2. *The undulations at the base of the tunics lead to the point from which adventitious roots arise.*
3. *Canals inside the fleshy leaves are filled with a creamy substance, which makes the canals visible without sectioning the leaves. The substance could fill the canals along their entire length or it could be irregularly distributed within the canals. Detailed anatomical sections would be needed to confirm this.*

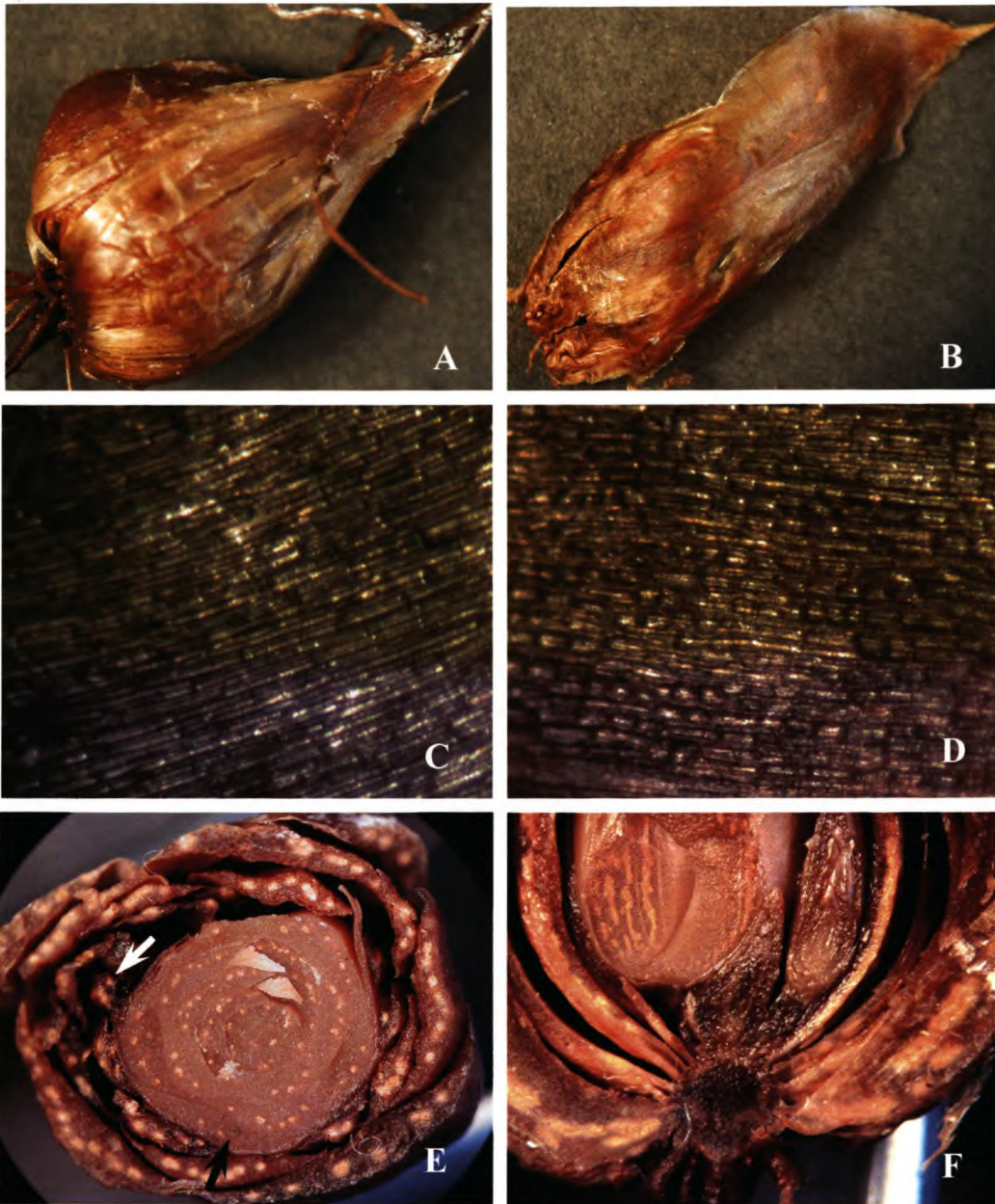


Figure 3.15 *Oxalis linearis*: [A] Bulb with membranous tunics; [B] Abaxial view of a single membranous tunic; [C] Adaxial surface of a membranous tunic showing scalariform ornamentation with elongated rectangular cells; [D] Abaxial surface of a membranous tunic showing scalariform ornamentation; [E] Cross-section through a naked bulb showing the winged, lingulate fleshy leaves surrounding a young bulb (black arrow) and the rhizome squashed in-between (white arrow); [F] Attachment of fleshy leaves to a wide basal plate

Oxalis monophylla (Figure 3.16)

Project number: MO 4

Rhizome: with capitate trichomes¹, sheath absent, 7.0–15.0 mm (11.3 mm average) long, diameter decreasing gradually towards the bulb, clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, usually with capitate trichomes, lower scales metabolically active, semi-amplexicaule, other scales dry and amplexicaule, alternately arranged.

Bulb: clustered by split reticulate tunic remains, 10.0–18.0 mm (13.7 mm average) long, 8.0–14.0 mm (10.7 mm average) wide in middle, widely ovate in outline, pale-brown (blond), surface spongy; apex acute, non-beaked; base usually depressed, meshed with split reticulate tunic remains.

Tunics: membranous, golden-brown, surface sometimes spotted by small dark circular spots, glabrous, non-sticky, split in an inverted V-pattern, open, aestivation imbricate, covers 25–75% of the bulb width², margins not conspicuous, apex acute; base sessile, split, wrinkled; adaxial surface ornamentation smoothly striate in an inverted V-pattern³; abaxial surface ornamentation striate in an inverted V-pattern³.

Fleshy leaves: more than 20, white, shape columnar, margin not flattened, apex acuminate, base shortly attenuate.

Base plate: wide

Contractile root: not seen

Root type: adventitious

Note:

1. *Trichomes on the rhizome are densely distributed just below ground level.*
2. *Outer split pieces of tunics cover most of the bulbs' body. The intact innermost tunics cover only 25% of the width of the bulb.*
3. *The striate lines are the sites where splitting occurs.*

Oxalis obtusa (Figure 3.17)

Project number: MO 159.

Rhizome: glabrous, sheath absent, 0.1–22.0 mm (13.3 mm average) long, diameter decreasing gradually towards the bulb, non-clustered, bulbels present.



Figure 3.16 *Oxalis monophylla*: [A] A rhizome with pilose capitate trichomes, amplexicaule scale attachment at the nodes and adventitious roots; [B] Bulb with flaking, membranous tunics; [C] & [D] Single membranous tunics showing the characteristic inverted V-split pattern with wrinkled and split bases; [E] Adaxial tunic surface showing striate ornamentation; [F] Abaxial tunic surface showing striate ornamentation; [G] “Naked” bulbs showing cylindrical fleshy leaves attached to a wide basal plate; [H] Adaxial view of a single fleshy leaf, showing the well-developed petiole; [I] Cross-section through a naked bulb showing the cylindrical fleshy leaves surrounding a central rhizome (indicated by arrow); [J] Bulb base showing the attachment of fleshy leaves to the wide basal plate

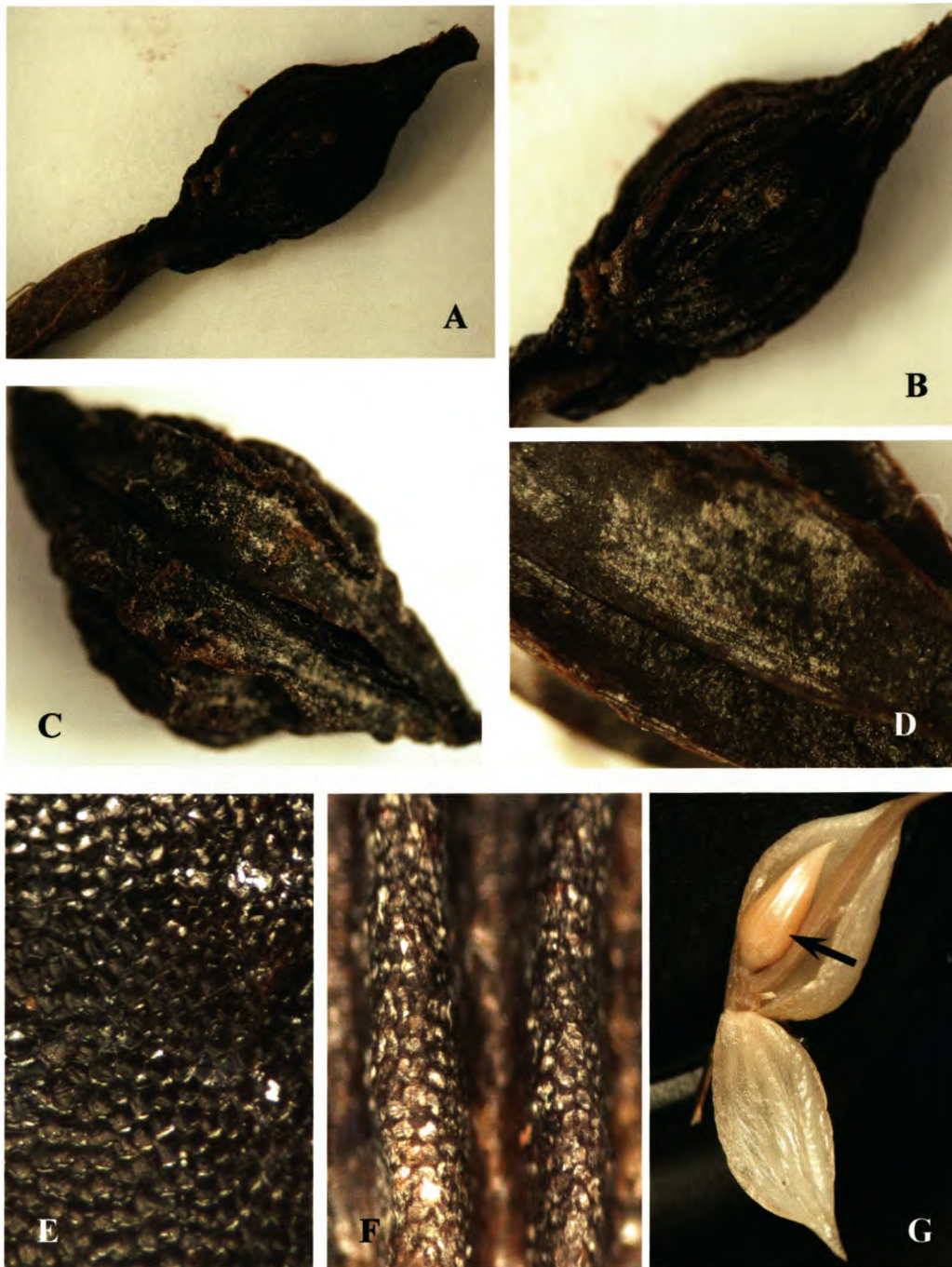


Figure 3.17 *Oxalis obtusa*: [A] Bulb with deeply pitted leathery tunics and clear contractile root arising from its base; [B] A mature bulb; [C] Irregularly angled and pitted leathery tunic; [D] Flat-overlapping tunic margins [E] Adaxial view of leathery tunic surface showing areolate ornamentation; [F] Abaxial view of leathery tunic surface showing areolate ornamentation superimposed onto irregular, raised ridges; [G] Fleshy leaves attached to a narrow basal plate, with enclosed young bulb clearly visible (arrow)

Bulbels: sessile, calyptrate scale absent.

Scales: membranous, glabrous, metabolically active, amplexicaule, alternately arranged.

Bulb: solitary, 11.0–14.0 mm (13.0 mm average) long, 5.0–7.5 mm (6.2 mm average) wide in middle, fusiform, dark-brown, surface deeply pitted and with short, longitudinally raised ridges¹, apex not beaked, base cuneate, with tightly packed tunics.

Tunics: brittle leathery, usually two or three, dark-brown, non-spotted, glabrous, non-sticky, open, aestivation equitant, with longitudinally raised ridges that vary in length², cover 100% of bulb body³, differ in width; margins leathery, flat, clasping; apex and base acute; adaxial surface ornamentation areolate; abaxial surface areolate, unevenly rough.

Fleshy leaves: two, embraced by a very thin membrane⁴, white, non-winged, shape lingulate, apex acute, base sheathing.

Base plate: narrow

Contractile root: present

Root type: taproot

Note:

1. *The abaxial surface of the bulb looks like the stone layer around a peach seed.*
2. *Outermost tunics have prominent ridges, while the ridges of the inner tunics are less prominent.*
3. *Innermost tunic covers 25% of the bulb body and it is always positioned in the gap where the margins of the next outer tunic are open.*
4. *This membrane could be part of the tunic layers. It has a finely reticulate ornamentation on both adaxial and abaxial surfaces.*

Oxalis oculifera (Figure 3.18)

Project number: MO 295

Rhizome: covered with black-headed capitate trichomes, sheath absent, 0.5–9.0 mm (3.6 mm average) long, diameter decreasing gradually towards the bulb, clustered by tunics¹, bulbels absent.

Scales: leathery, some with black-headed capitate trichomes, dry, semi-amplexicaule, alternately arranged.

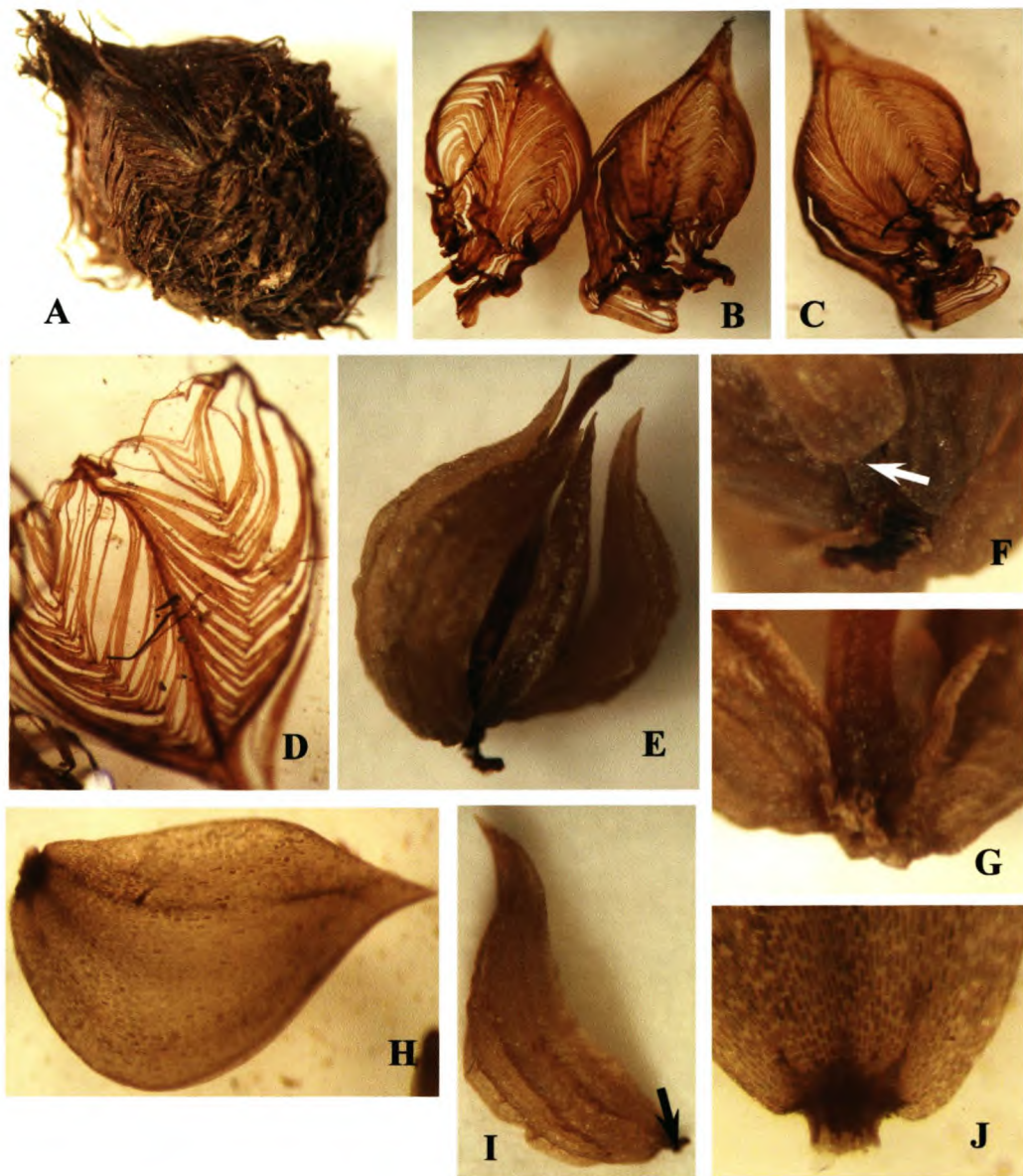


Figure 3.18 *Oxalis oculifera*: [A] Bulb with flaking, membranous tunics; [B], [C] & [D] Membranous tunics showing the characteristic inverted W-split pattern with wrinkled and split bases; [E] “Naked” bulb showing lingulate fleshy leaves attached to the basal plate from where the rhizome also extends; [F] The basal plate viewed from below, showing the shortly petiolated attachment of fleshy leaves (arrow); [G] Section through a naked bulb showing the cylindrical fleshy leaves surrounding a central rhizome; [H] Adaxial view of a single fleshy leaf; [I] Abaxial view of a single fleshy leaf, clearly showing the well-developed petiole (arrow); [J] Close-up of a short petiole at the base of a fleshy leaf

Bulb: solitary, 7.5–10.0 mm (8.6 mm average) long, 5.0–7.5 mm (6.1 mm average) wide in middle, spheroid, dark-brown, surface spongy or fibrous, apex not beaked, base usually round.

Tunics: membranous, dark-brown, surface dull, non-spotted, glabrous, non-sticky, open, aestivation imbricate, split in distinctive inverted W-pattern; with longitudinally ridged, non-splitting section along the middle; covering 40% of bulb width, most tunics split into fibers (except for the inner-most layers); margins not conspicuous; apex acute; adaxial surface ornamentation striate with large inverted W-patterns across the entire surface; abaxial surface ornamentation striate with large inverted W-patterns across the entire surface.

Fleshy leaves: 4–6, white, non-winged, shape lingulate, apex acute, base shortly attenuate.

Basal plate: wide

Contractile root: not seen

Root type: adventitious

Note:

1. *The rhizomes of the bulbs mostly grow through the tunics of another bulb. The specimen was collected from a dense colony, so this type of arrangement might not be genetically controlled, but could be a consequence of limited space in its specific habitat.*

Oxalis oligophylla (Figure 3.19 A & B)

Project number: MO 293

Rhizome: glabrous, sheath absent, 15.0–52.0 mm (37.3 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, semi-amplexicaule, alternately arranged.

Bulb: solitary, 17.0–27.0 mm (22.5 mm average) long, 4.0–15.0 mm (9.2 mm average) wide in middle, oblong or oval, black; surface gummy¹, apex attenuate, non-beaked; base usually depressed, intact bulb remains of previous years' growth enclose the current year's bulb.

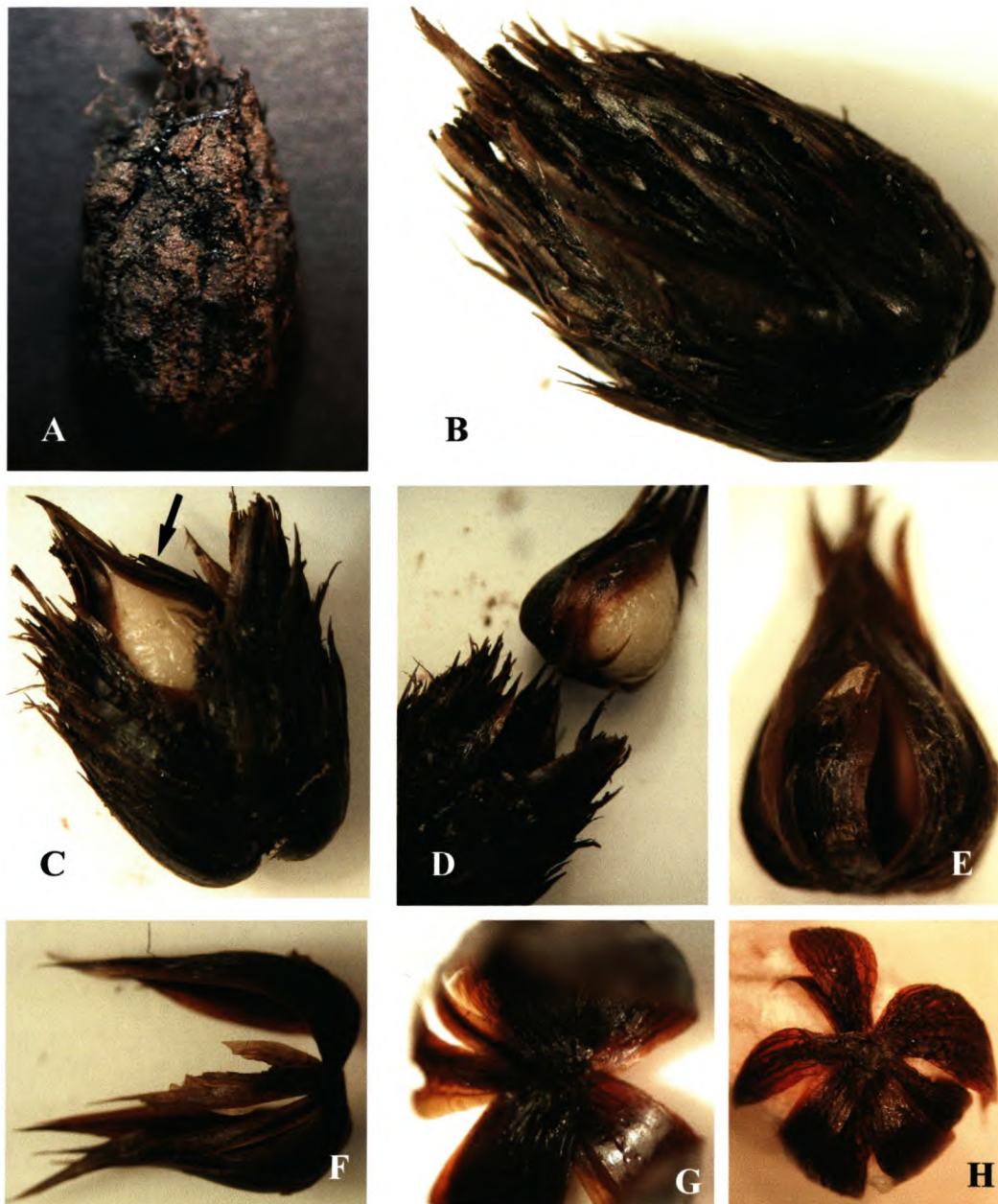


Figure 3.19 A *Oxalis oligophylla*: [A] Bulb with gummy tunics before soaking in benzene (sand grains stuck to bulb surface still visible); [B] Cleaned bulb that has been soaked in benzene; [C] & [D] Current year's bulb made visible (arrow) between remains of previous years' bulbs; [E] – [H] A single bulb tunic layer seen from the side (E and F), above (G) and below (H). These pictures clearly show how successive tunic layers remain attached to the basal plate, unlike the case in most other species

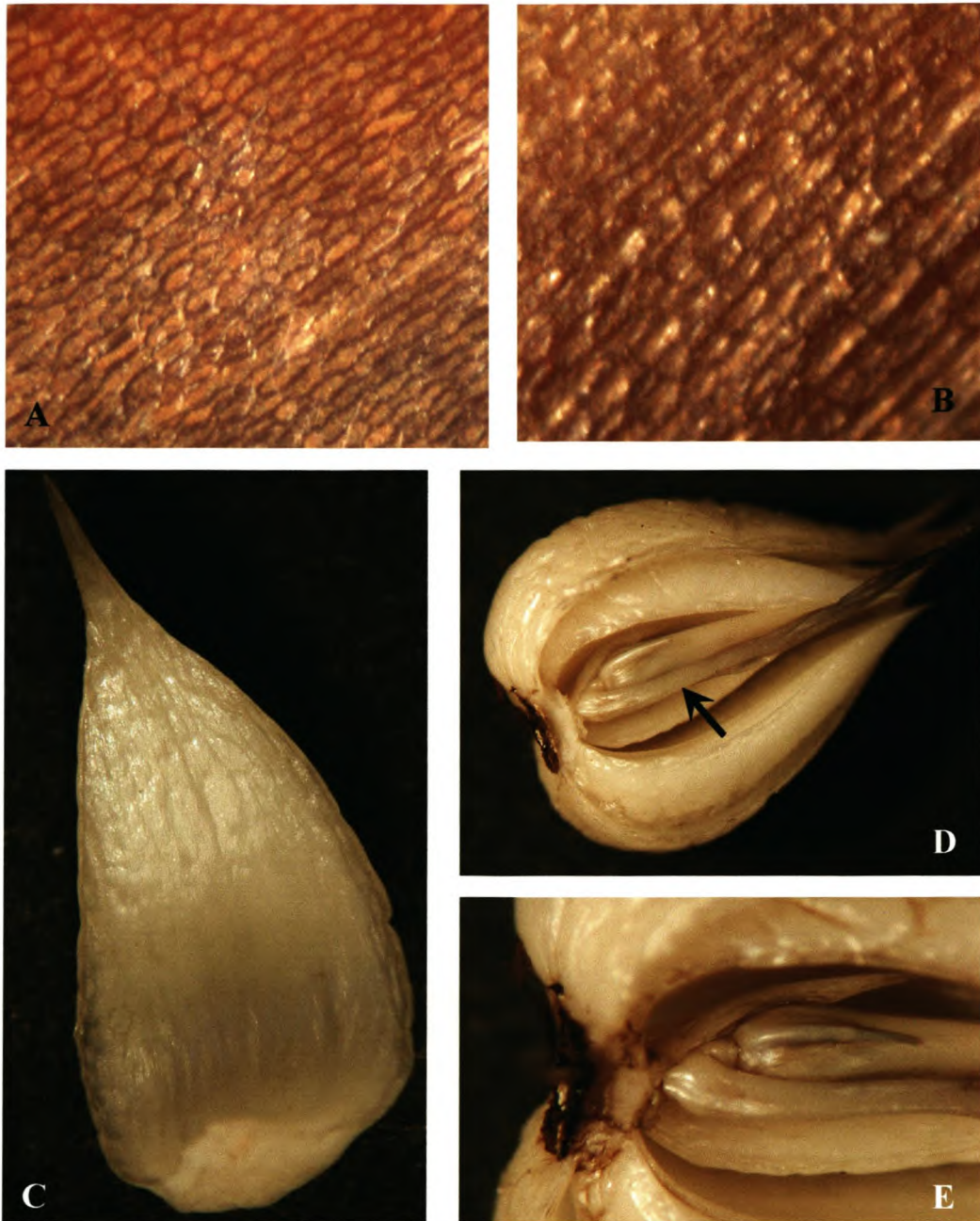


Figure 3.19 B *Oxalis oligophylla*: [A] Adaxial surface of tunic showing areolate surface ornamentation with elongated cells; [B] Abaxial surface of tunic showing scalariform-areolate surface ornamentation with elongated cells; [C] Adaxial view of a single fleshy leaf, clearly showing the distinctly beaked apex; [D] Cross-section through a naked bulb showing the lingulate fleshy leaves surrounding a central rhizome (arrow); [E] Closer view of the wide basal plate with fleshy leaves attached

Tunics: leathery, few inner ones membranous, open, aestivation imbricate, dark-brown to honey-brown, non-spotted, glabrous, sticky (gummy), narrow, covers less than 25% of the bulb width, margins membranous, apex beaked, base sessile; adaxial surface ornamentation areolate with elongated cells; abaxial surface ornamentation scalariform-areolate with elongated cells.

Fleshy leaves: 10, white, non-winged, shape lingulate, apex beaked, base sessile.

Basal plate: wide²

Contractile root: absent

Root type: absent

Note:

1. *The entire bulb is covered by soil due to the gummy abaxial surface of the bulb.*
2. *The basal plates of the previous years' bulbs do not disintegrate, so they stay intact with their dried fleshy leaves and tunics. The new bulb grows out on top of the previous years' growth, so that the remains of previous year's bulbs cup this new bulb.*

Oxalis oreophila (Figure 3.20)

Project number: M0 270

Rhizome: glabrous, sheath absent, 10.0–61.0 mm (35.3 mm average) long, of even diameter, not clustered by previous years' bulb tunics, bulbels absent.

Scale: membranous, transparent and delicate, cilia present along margins, amplexicaule, dry, alternately arranged.

Bulb: solitary, 14.0–19.0 mm (16.3 mm average) long, 7.5–12.0 mm (9.4 mm average) wide in middle, oval, deep honey-brown, surface smooth; apex non-beaked, acute or shortly attenuate; base widely cuneate, tunics tightly packed.

Tunics: leathery, lighter honey-brown, spotted with groups of creamy inflated cells, glabrous, non-sticky, open, aestivation equitant, clasping at base, all similar in size; margins membranous, apex acute, base longitudinally undulate; adaxial surface ornamentation scalariform; abaxial surface ornamentation scalariform, striate along veins.

Fleshy leaves: three, white¹, non-winged, shape lingulate, apex acute, base sessile.



Figure 3.20 *Oxalis oreophila*: [A] Oval bulb with leathery tunics, with old tunics at its apex; [B] Abaxial view of leathery tunic, note the diagnostic cream spots; [C] Adaxial view of leathery tunic showing the longitudinally undulate base and the clasping apical margins; [D] A close-up view of the longitudinally undulate tunic base; [E] Adaxial surface of a leathery tunic showing scalariform ornamentation; [F] Abaxial surface of a leathery tunic showing scalariform ornamentation and diagnostic groups of inflated cells; [G] A single lingulate fleshy leaf with a sessile base and an acute apex; [H] Adaxial view of fleshy leaves attached to a wide basal plate; note the central rhizome (black arrow) and the enclosed new bulb (white arrow)

Basal plate: wide

Contractile root: not seen

Root type: adventitious

Note:

1. *Apices of the fleshy leaves are brown. The colouration is not formed within the epidermal cells, but most probably by substances produced in the mesophyll cells.*

Oxalis pes-caprae (Figure 3.21)

Project number: O 367

Rhizome: with simple and short capitate trichomes intermixed, sheath absent, 122.5–218.0 mm (166.3 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous or with simple trichomes, dry, semi-amplexicaule, alternately arranged¹.

Bulb: solitary, 24.0–39.0 mm (30.3 mm average) long, 45.0–8.0 mm (6.5 mm average) wide in middle, conical, brown; surface dull, with longitudinal, non-raised ridges placed at intervals²; apex beaked, base rounded.

Tunics: rigid, leathery, brown, abaxial surface with longitudinal ridges, adaxial surface smooth, non-spotted, glabrous, non-sticky, open, aestivation imbricate, covering 50% of the bulb body, margins membranous; apex beaked, outermost tunic usually with bulged part³; base sessile; adaxial surface ornamentation undulate-ruminate; abaxial surface ornamentation areolate (faintly ornamented).

Fleshy leaves: six, white, narrowly winged, shape lingulate, apex acuminate, base sessile.

Basal plate: wide

Contractile root: not seen

Root type: not seen

Note:

1. *Some nodes had already shed their scales so that only scars are left. Some scales are brown, while others are very transparent.*



Figure 3.21 *Oxalis pes-caprae*: [A] Bulb with ridged leathery tunics; [B] Ridged leathery tunics showing the characteristic non-raised longitudinal ridges; [C] A bulb from a young plant; [D] Adaxial surface of leathery tunic showing undulate-ruminate ornamentation; [E] Abaxial surface of leathery tunic showing finely areolate ornamentation, with arrow pointing to a longitudinal ridge; [F] "Naked" bulb showing imbricate fleshy leaves with narrow membranous margins (arrow); [G] & [H] Adaxial view of a single fleshy leaf, a rhizome (white arrow) and young bulb (black arrow) attached to a wide basal plate (white circle)

2. *Some outer tunics have lost their epidermal layers, exposing the ridges within.*
3. *This bulged apical part of the tunic could be filled with soil or just be empty with a deteriorated cover.*

Oxalis pulchella (Figure 3.22 A-C)

Project number: MO 116

Rhizome: with dense capitate trichomes¹, sheath absent, 7.0–42.0 mm (18.8 mm average) long, diameter decreasing gradually towards the bulb, usually clustered by old tunics, bulbels absent.

Scales: membranous, with capitate trichomes, sometimes metabolically active, with apex acute or obtuse, amplexicaule, alternately arranged.

Bulb: clustered together by the presence of old tunics², 21.0–29.0 mm (24.2 mm average) long, 2.0–2.5 mm (2.3 mm average) wide in middle, narrowly ovate, pale to dark-brown, surface sticky and wrinkled, apex beaked, base cuneate, older bulbs with reticulate ridges.

Tunics: consist of two textures namely membranous and leathery. **Membranous tunics:** layered alternately with leathery tunics, honey-brown; surface interlocking³ with leathery tunics beneath, usually irregularly shaped; open, aestivation convolute, margins not conspicuous; apex long, narrowly convolute; base split, wide open; adaxial surface ornamentation a complex mosaic of striate bunches; abaxial surface ornamentation a complex mosaic of striate bunches overlaid on an areolate surface. **Leathery tunics:** layered alternately with membranous tunic, dark-brown; surface abaxial usually with rough reticulate ridges exposed in older bulbs, adaxial smooth; non-spotted, glabrous, open, aestivation convolute, margins membranous, apex long, narrowly convolute; base split wide open; adaxial surface ornamentation with fine striate lines overlaid on scalariform cells; abaxial surface ornamentation unevenly reticulate with elevated elements raised to different heights, with rounded concave sunken areas in between.

Fleshy leaves: usually single, white, narrow, non-winged, shape lingulate, apex acuminate, base sessile, sheathing.

Basal plate: narrow

Contractile root: not seen

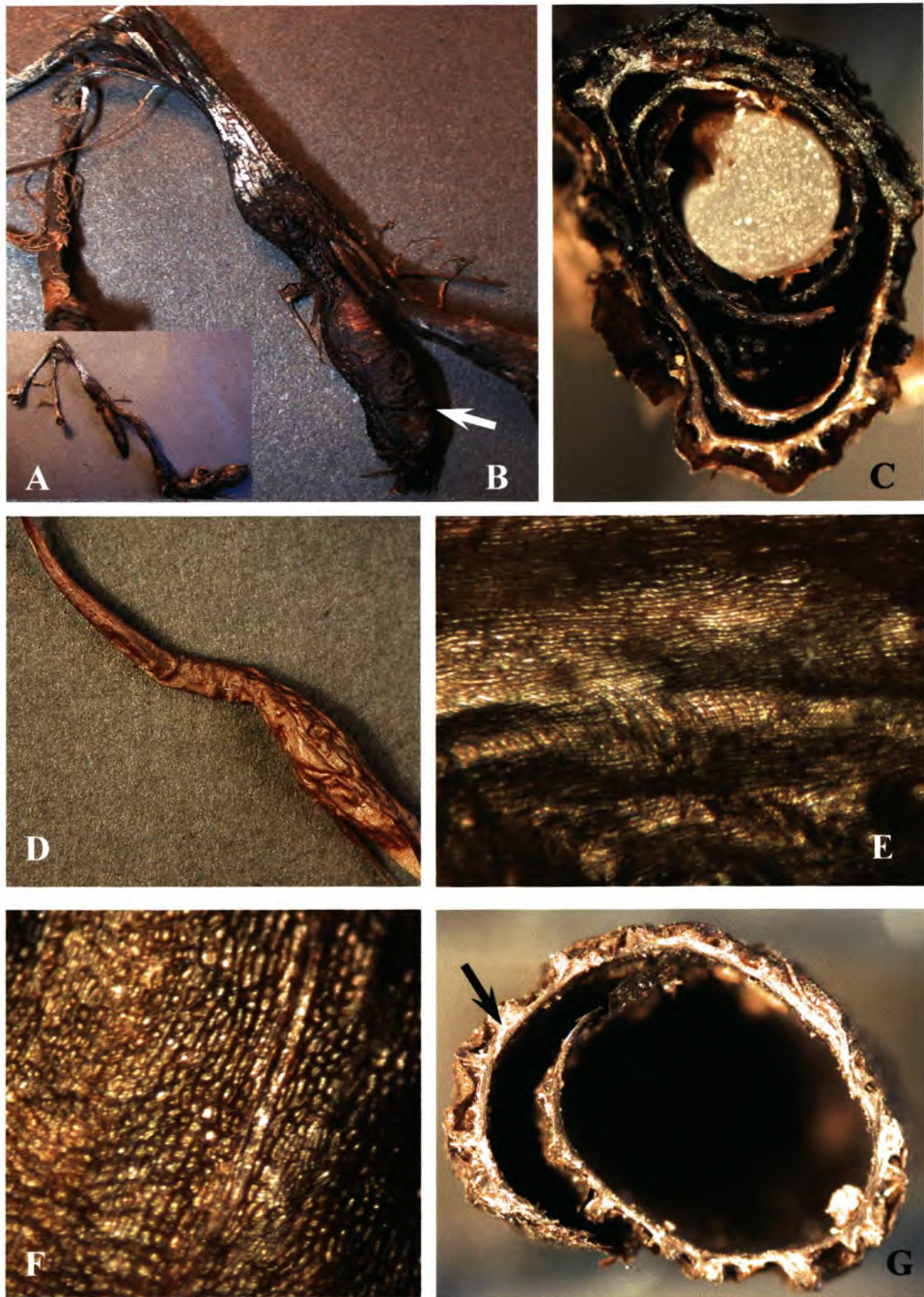


Figure 3.22 *Oxalis pulchella*: [A] Bulb organization showing bulbs of subsequent years dovetailed with the youngest bulb right at the bottom; [B] Close up the current year's bulb (arrow), along with tunic remains of previous years; [C] Cross-section through a mature bulb; [D] Membranous outer tunic; [E] Adaxial surface of membranous tunic showing surface ornamentation of striate bunches in a complex mosaic; [F] Abaxial surface of membranous tunic showing areolate surface ornamentation; [G] Cross-section through a single leathery tunic showing convolute arrangement and the prominent ridges (arrow)

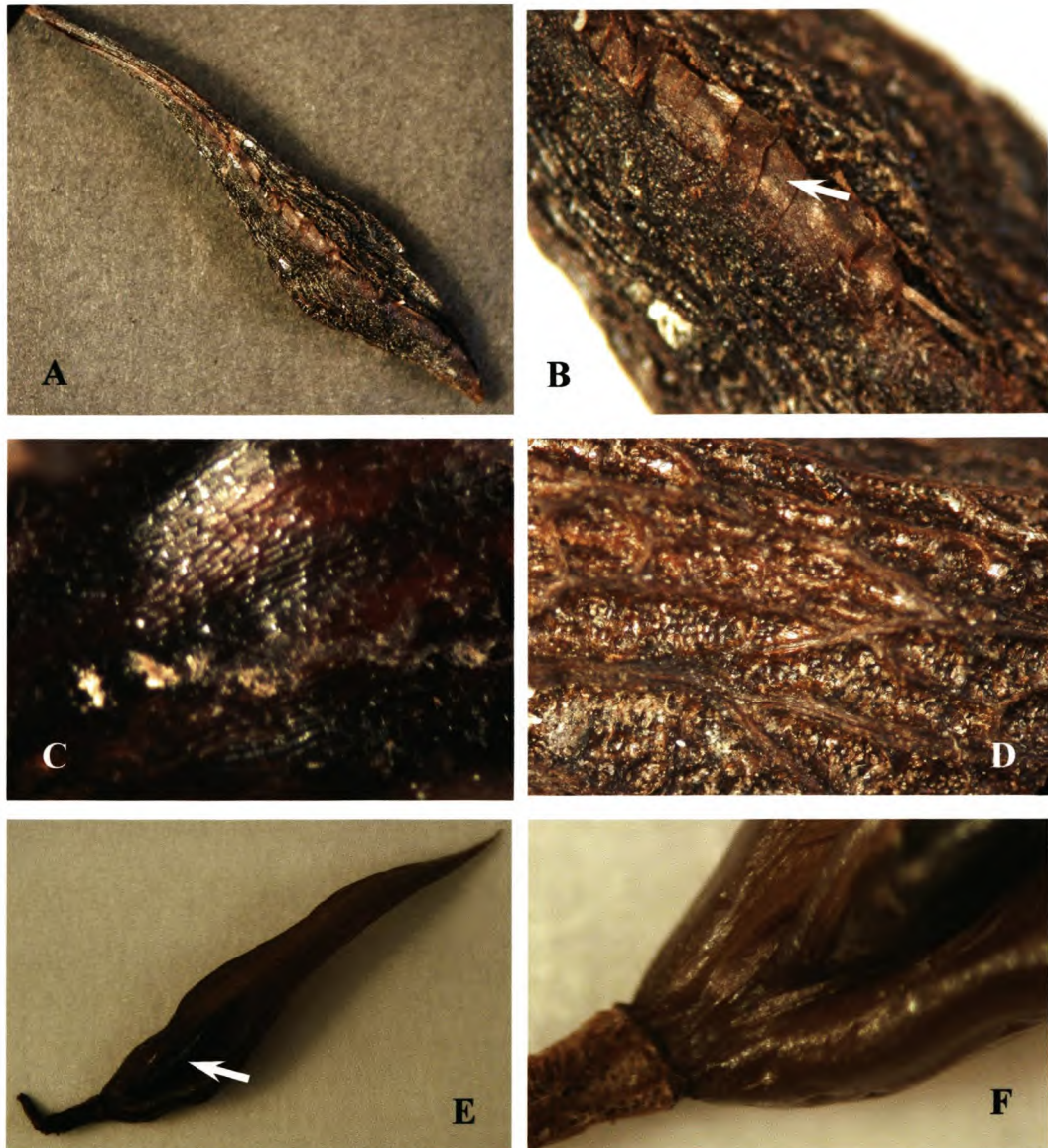


Figure 3.22 B *Oxalis pulchella*: [A] A single, closed leathery tunic; [B] Closer view of the overlapping, membranous margin (arrow) of the leathery tunic; [C] Adaxial surface of leathery tunic showing scalariform surface ornamentation; [D] Abaxial surface of leathery tunic showing unevenly reticulate surface ornamentation with individually raised elements; [E] Adaxial view of the single fleshy leaf showing a rhizome attached to the basal plate and a black young bulb (arrow); [F] Close-up view of the basal plate and the point of attachment of the fleshy leaf

Root type: not seen

Note:

1. Some trichomes have black glandular heads.
2. Bulbs are clustered exists due to the previous years' bulb remains. Therefore, as shown in the figure below, the current year's rhizome grows through successively dovetailed remains of previous years' bulbs. When two or more of these similar bulbs join together, they form clusters.
3. Not all membranous tunics are necessarily independent tunics, but they could be epidermal tissue layers of the leathery tunics, which get exposed with age.

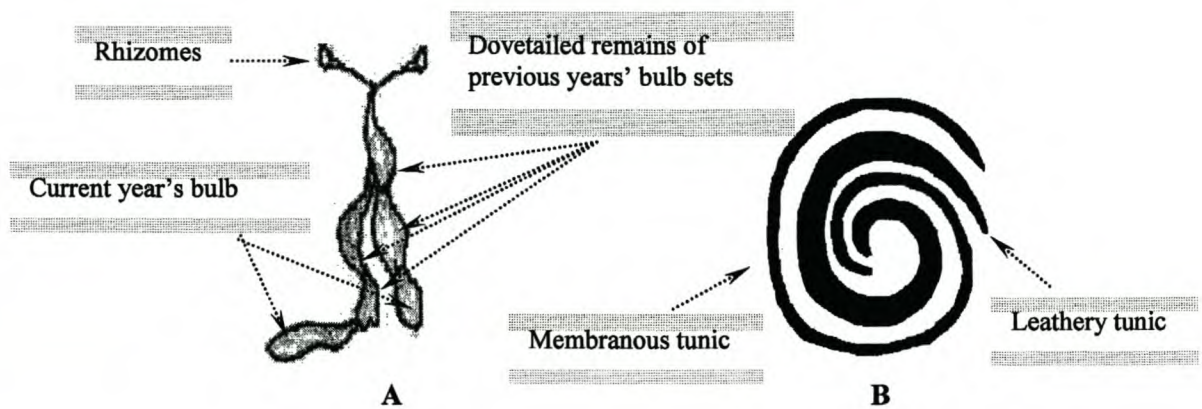


Figure 3.22 C *O. pulchella* [A] Bulb organization: bulb remains of previous years' bulb sets dovetail with each other, and current year's bulb set always sits at the bottom. As a result their rhizomes pass through the dovetailed bulb clusters. [B] Tunic layers demonstrating convolute tunic aestivation and arrangement of the membranous tunic (thin) and leathery tunic (bold).

Oxalis purpurea (Figure 3.23)

Project number: O 283

Rhizomes: with capitate trichomes¹, sheath absent, 9.0–39.0 mm (23.9 mm in average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, semi-amplexicaule, alternately arranged.

Bulb: usually solitary, some clustered by previous years' bulb tunics, 11.0–33.0 mm (23.0 mm average) long, 4.0–14.0 mm (8.4 mm average) wide in middle, fusiform, dark-brown, surface smooth, apex beaked, base usually cuneate.

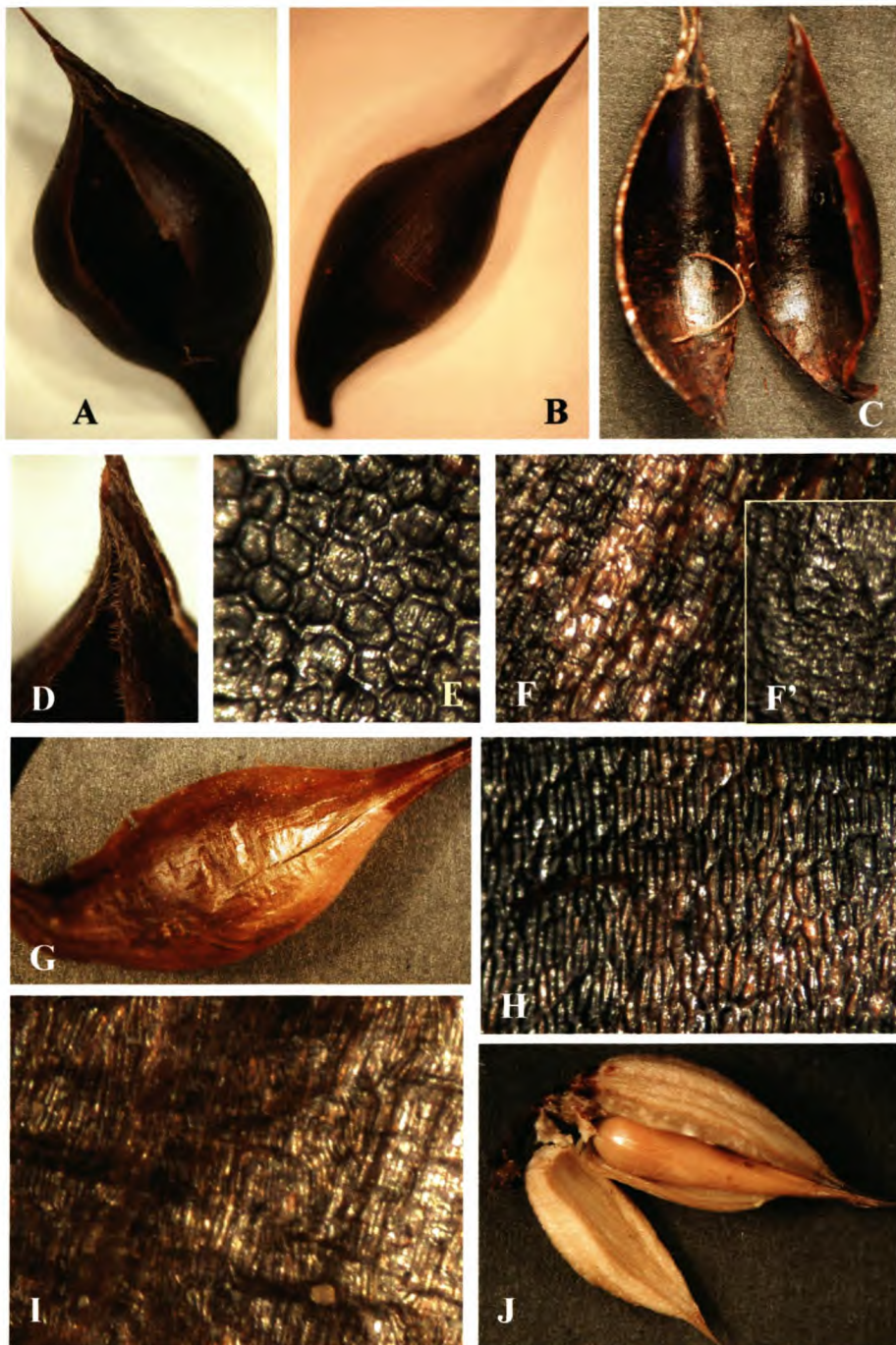


Figure 3.23 *Oxalis purpurea*: [A] Adaxial view of leathery tunic; [B] Abaxial view of leathery tunic; [C] Split leathery tunic; [D] Adaxial view of leathery tunic apex showing apical trichomes and ciliate margins; [E] Adaxial surface of leathery tunic showing wavy-striations overlying an alveolate surface ornamentation; [F] Variable abaxial surface of leathery tunic showing ornamentation variation in different parts of the same structure (F = areolate; F' = uneven); [G] Abaxial view of beaked outer membranous tunic; [H] & [I] Adaxial surface ornamentation of membranous tunics showing intra-specific variation (H = rows of flattened cells; I = complex mosaic of striate bunches); [J] Fleshy leaves surrounding a central rhizome and an enclosed new bulb

Tunics: consist of two textures namely membranous and leathery. **Membranous tunics:** restricted to outer layers, golden-brown, surface smooth, non-spotted, apical margins and abaxial surfaces covered by simple trichomes, inner layers sticky, open, aestivation equitant, cover almost entire bulb body, margins membranous; apex beaked, with longitudinal ridges; base cuneate, amplexicaule, with longitudinal ridges; adaxial surface ornamentation with a complex mosaic of striate bunches; abaxial surface ornamentation areolate overlaid on fine vertically-striate lines. **Leathery tunics:** restricted to inner layers, honey-brown; surface smooth, apical margins and abaxial surfaces covered by simple trichomes; non-spotted, some sticky, open, aestivation equitant, cover almost 100% of bulb's body; margins membranous, ciliate; apex beaked with longitudinal ridges; base cuneate, amplexicaule, with longitudinal ridges; adaxial surface ornamentation wavy-striate² overlaid on an areolate under surface; abaxial surface ornamentation areolate.

Fleshy leaves: two, white, non-winged, shape lingulate³, apex acuminate base amplexicaule (sheathing).

Basal plate: narrow

Contractile root: present

Root type: adventitious

Note:

1. *Trichomes are abundant on the lower part of the rhizome.*
2. *The wavy-striate lines might appear as a complex mosaic of striate bunches, but it is continuously striate and wavy.*
3. *Only the bigger fleshy leaf has a membranous margin.*

Oxalis purpurea (Figure 3.23)

Project number: O 291

Rhizome: glabrous, sheath absent, 34.0–103.0 mm (51.9 mm average) long, diameter gradually decreasing towards the bulb, non-clustered, bulbels absent.

Scales: membranous, glabrous, dry, semi-amplexicaule, alternately arranged.

Bulb: solitary, 25.0–54.0 mm (38.9 mm average) long, 2.0–11.0 mm (5.3 mm average) wide in middle, fusiform, dark-brown, surface smooth but sticky; usually with long¹ beak, apical beak comprises more than 40% of bulb's length; base cuneate.

Tunics: consist of two textures, membranous and leathery. **Membranous tunics:** represents the outer layers, honey-brown, surface smooth, abaxial surface of apex (upper quarter) covered with simple trichomes², non-spotted, sticky, open, aestivation equitant, covers 75–90% of bulb's body, margins not conspicuous, apical margin ciliate; adaxial surface ornamentation wavy-striate; abaxial surface ornamentation scalariform.

Leathery tunics: restricted to the inner layers, honey-brown, surface smooth, abaxial surface of apex (upper quarter) covered with simple trichomes², non-spotted, sticky, open, aestivation equitant, covers 75–90% of bulb's body; margins narrow, membranous, ciliate from apex to middle; apex beaked, base cuneate; adaxial surface ornamentation variable, either rows of flattened cells or complex mosaic of striate bunches, areolate at base; abaxial surface ornamentation areolate.

Fleshy leaves: two or three, white, non-winged, shape lingulate³, apex beaked, base amplexicaule.

Basal plate: narrow

Contractile root: not seen

Root type: adventitious

Note:

1. *This long apical beak is as long as the main bulb.*
2. *Trichomes present only on the abaxial surface of the tunics.*
3. *The largest of the fleshy leaves always has narrow membranous margins.*

Oxalis salteri (Figure 3.24)

Project number: MO 280

Rhizome: ¹ glabrous, sheath absent, with bark-like cover ², diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, amplexicaule, alternately arranged, usually short where rhizome is covered by bark-like structure.

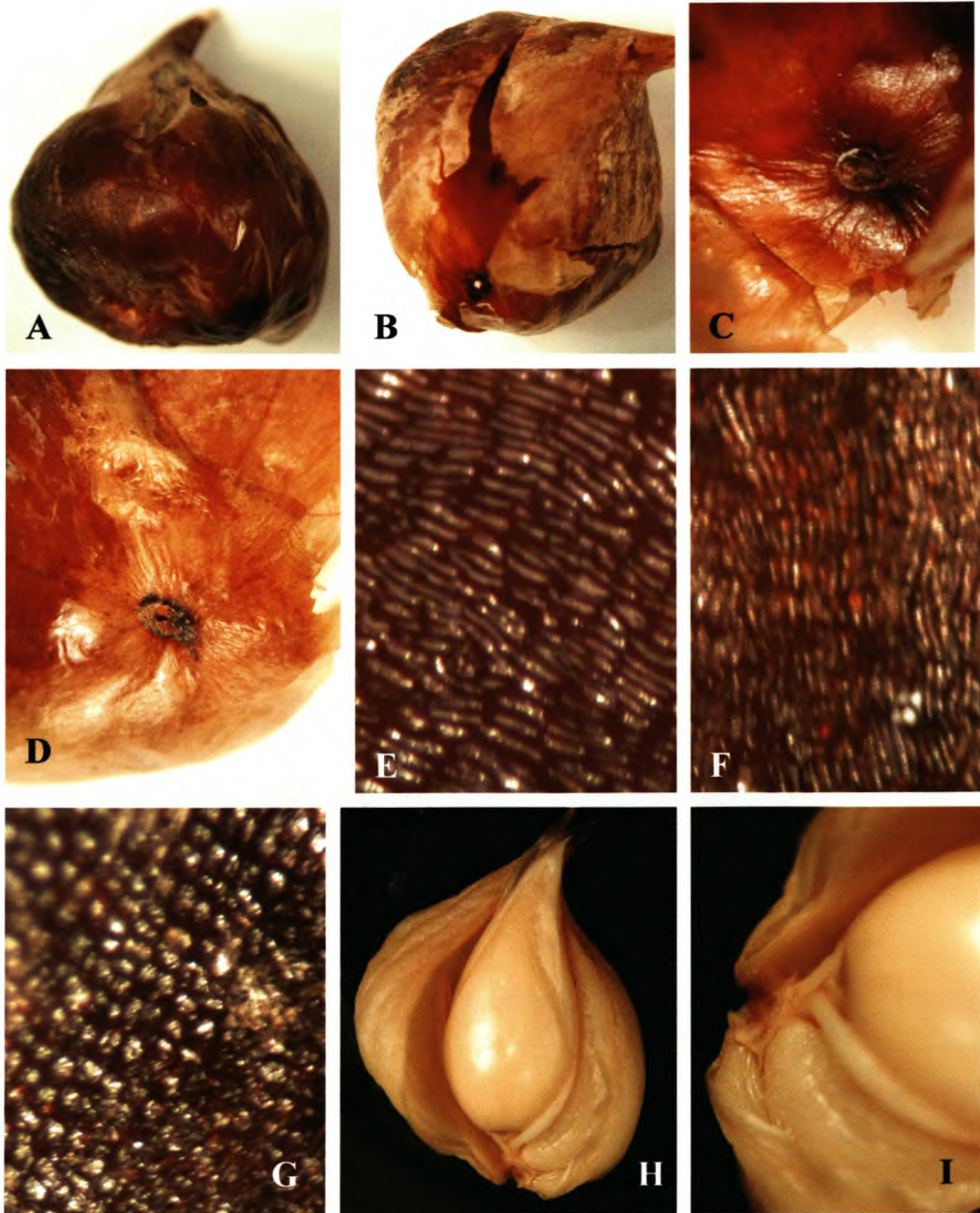


Figure 3.24 *Oxalis salteri*: [A] Bulb with membranous tunics and distinct apical beak; [B] Enclosing outer tunic viewed from the bottom up; [C] Adaxial view of the perfoliate base of the outer tunic; [D] Abaxial view of the perfoliate base of the outer tunic; [E] & [F] Adaxial views of the variable tunic surfaces showing both areolate surface ornamentation with elongated cells (E) and vertical striate ornamentation (F); [G] Abaxial view of tunic showing areolate surface ornamentation; [H] Section through a naked bulb showing lingulate fleshy leaves and a new bulb; [I] Closer view of the narrow basal plate with fleshy leaves attached

Bulb: solitary, 13.0–19.0 mm (15.8 mm average) long, 5.0–17.0 mm (8.8 mm average) wide in middle, shape ranges from conical to widely oval, honey-brown, surface smooth, apex shortly beaked, with membranous tunics.

Tunics: membranous, honey-brown, non-spotted, glabrous, non-sticky, abaxial surface dull, adaxial surface shiny and smooth, open, aestivation equitant, covering more than 75% of bulb's body, margins not conspicuous, apex embracing and acute, base perfoliate; adaxial surface ornamentation variable, some areolate others with vertical striations; abaxial surface ornamentation without clear sculpture, some areolate with small cells.

Fleshy leaves: two or three³, white, non-winged, shape lingulate, apex mucronate, base amplexicaule.

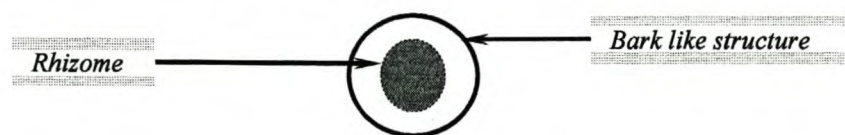
Basal plate: narrow

Contractile root: not seen⁴

Root type: not seen⁴

Note:

1. *The parts of the specimen were detached; therefore no rhizome length measurements could be taken.*
2. *This bark-like structure circularly encloses the rhizome and does not have any openings except where it was torn. This structure has nodes and internodes with scales at each node. Actually it seems as if the active rhizome grows through an old, dried, earlier rhizome. Removing this thick membranous structure revealed buds that are directed downwards. These could be root buds or droppers that may produce bulbels at their ends.*



3. *Inside the bulb there is a new bulb, which is bigger than the fleshy leaves. This new bulb is larger than the new bulbs included in other species studied.*
4. *Roots and contractile roots were not observed because of difficulties encountered during collection. The rhizome is deep and the bulb is wedged in between stones.*

Oxalis stenopetala (Figure 3.25)

Project Number: M0 106

Rhizome: with simple trichomes on upper part, sheath absent, 22.0–45.0 mm (33.8 mm average) long, diameter decreasing gradually towards the bulb, sometimes clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, some ciliate with simple trichomes, others glabrous, dry, semi-amplexicaule, alternately arranged.

Bulb: surrounded by a cluster of small, mature, additional bulbs¹, 18-40 mm (27.25 mm average) long, 5.5–7.0 mm (6.4 mm average) wide in middle, fusiform, dark-brown, surface smooth, non-shiny, non-sticky, apex beaked; base shortly tapering, some flattened; older bulb tunics positioned at apex of tunics of the new bulb.

Tunics: consist of two textures namely membranous and leathery. **Membranous tunics:** present as innermost layer and outermost layers, honey-brown, surface with flat longitudinal ridges, non-spotted, glabrous, non-sticky, open, aestivation equitant, innermost one covers 75% of the bulb's body, outer layers only cover 25% of the width, some shorter than others, margins membranous, apex beaked, base shortly attenuate amplexicaule; adaxial surface ornamentation scalariform; abaxial surface ornamentation scalariform. **Leathery tunics:** restricted to middle layers, honey-brown, glabrous, non-spotted, non-sticky, open, aestivation equitant, cover 100% of the bulb, with flat longitudinal ridges, apex beaked, base shortly attenuate amplexicaule²; margins not-membranous; both inner and abaxial surface ornamentation scalariform.

Fleshy leaves: two, white, non-winged, shape lingulate³, apex acuminate, base amplexicaule.

Basal plate: narrow

Contractile root: not seen

Root type: taproot

Note:

1. *These small bulbs (2–3) are distinguished from bulbels because of their dried tunics, which are already specialized, unlike the tunics of normal bulbels.*
2. *The leathery tunics of old bulbs are split and wide open at the base.*
3. *Only the largest one has narrow membranous margins.*

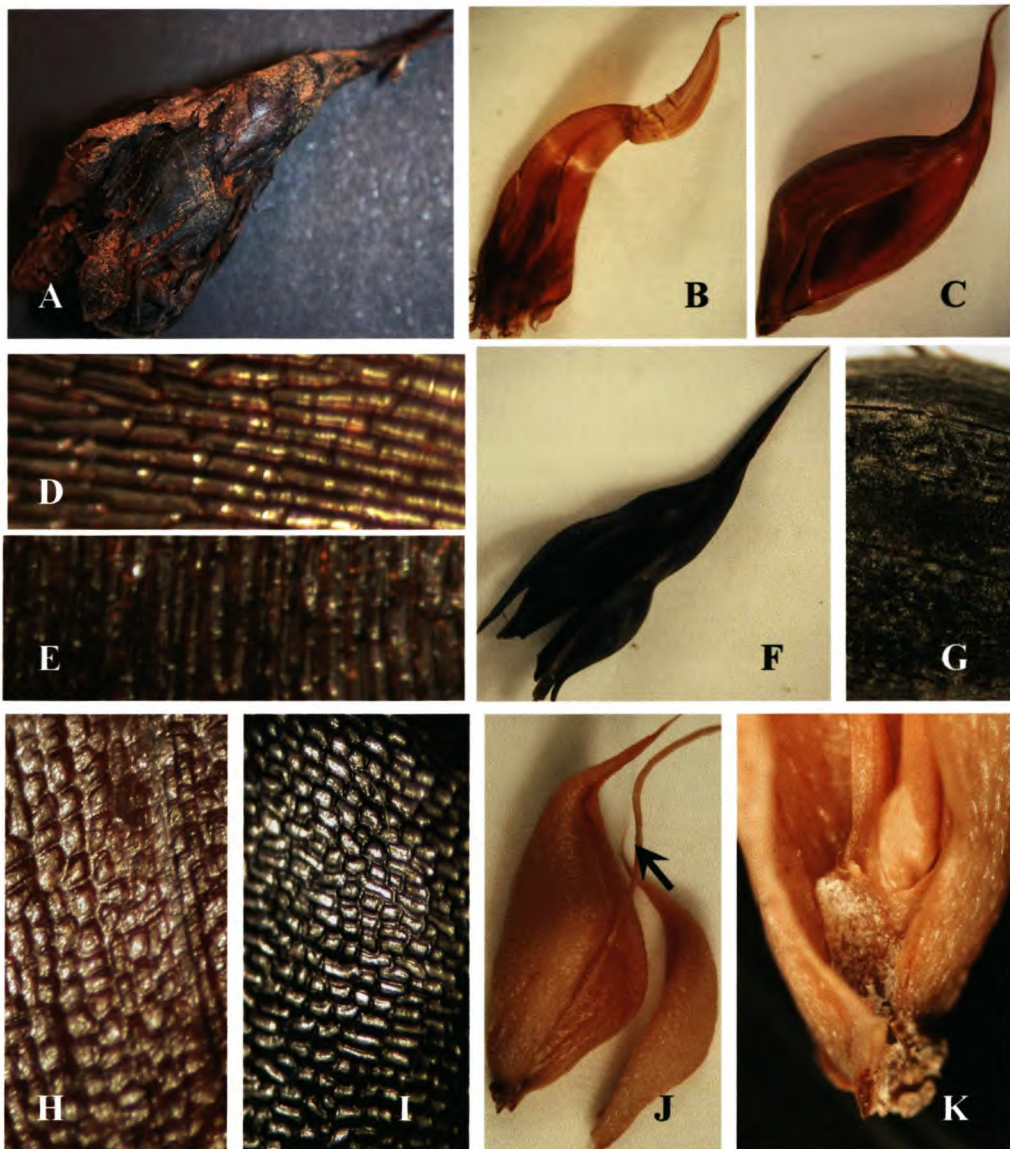


Figure 3.25 *Oxalis stenopetala*: [A] Bulb with both leathery and membranous tunics; [B] A single outer membranous tunic with a beaked apex; [C] Innermost membranous tunics that extend over a far greater surface of the bulb body; [D] Adaxial surface of a membranous tunic showing scalariform ornamentation; [E] Abaxial surface of a membranous tunic showing scalariform ornamentation with narrower cells; [F] A single, apically beaked leathery tunic with flat longitudinal ridges; [G] A closer view of flat longitudinal tunic ridges; [H] Adaxial surface of a leathery tunic showing scalariform ornamentation; [I] Abaxial surface of a leathery tunic showing scalariform ornamentation; [J] Fleshy leaves attached to a narrow basal plate; note the central rhizome (arrow); [K] Adaxial view of fleshy leaves attached to a narrow basal plate

Oxalis tenella (Figure 3.26 A & B)

Project number: MO 70

Rhizome: glabrous, sheathed by a brown tunic-like structure¹, 20.0–40.0 mm (31.0 mm) long, diameter decreasing gradually towards the bulb, not clustered by previous years' tunics, bulbels absent.

Scales: membranous, glabrous, dry, semi-amplexicaule, alternately arranged, apex obtuse.

Bulb: solitary, 6.0–17.0 mm (10.5 mm average) long, 3.0–10.0 mm (6.5 mm average) wide in middle, oval to fusiform, apex not beaked, reddish-brown, surface smooth, vertically orientated in the substrate.

Tunics: consist of two textures namely membranous and leathery. **Membranous tunics:** restricted to outer layers, golden-brown, surface smooth, spotted by creamy groups of inflated cell(s), glabrous, non-sticky, single closed circular unit², aestivation concentric, all similar in size, margins not conspicuous, apex acute, base amplexicaule; adaxial surface ornamentation wavy-striate overlaid on a complex mosaic of striate bunches; abaxial surface ornamentation areolate, striate along veins. **Leathery tunics:** restricted to inner layers, glabrous, single closed circular unit², aestivation concentric, non-sticky, reddish-brown, all similar in size, spotted by creamy groups of inflated cell(s), apex acute, base with longitudinal undulations; adaxial surface ornamentation with rows of flattened cells; abaxial surface ornamentation areolate.

Fleshy leaves: two, brown, non-winged, shape lingulate, apex acute, dark-brown, base sessile.

Basal plate: wide

Contractile root: not seen

Root types: adventitious

Note:

1. *The sheathing structure is usually only found in young plants.*
2. *Only old outer tunic layers are split (open) at the base.*

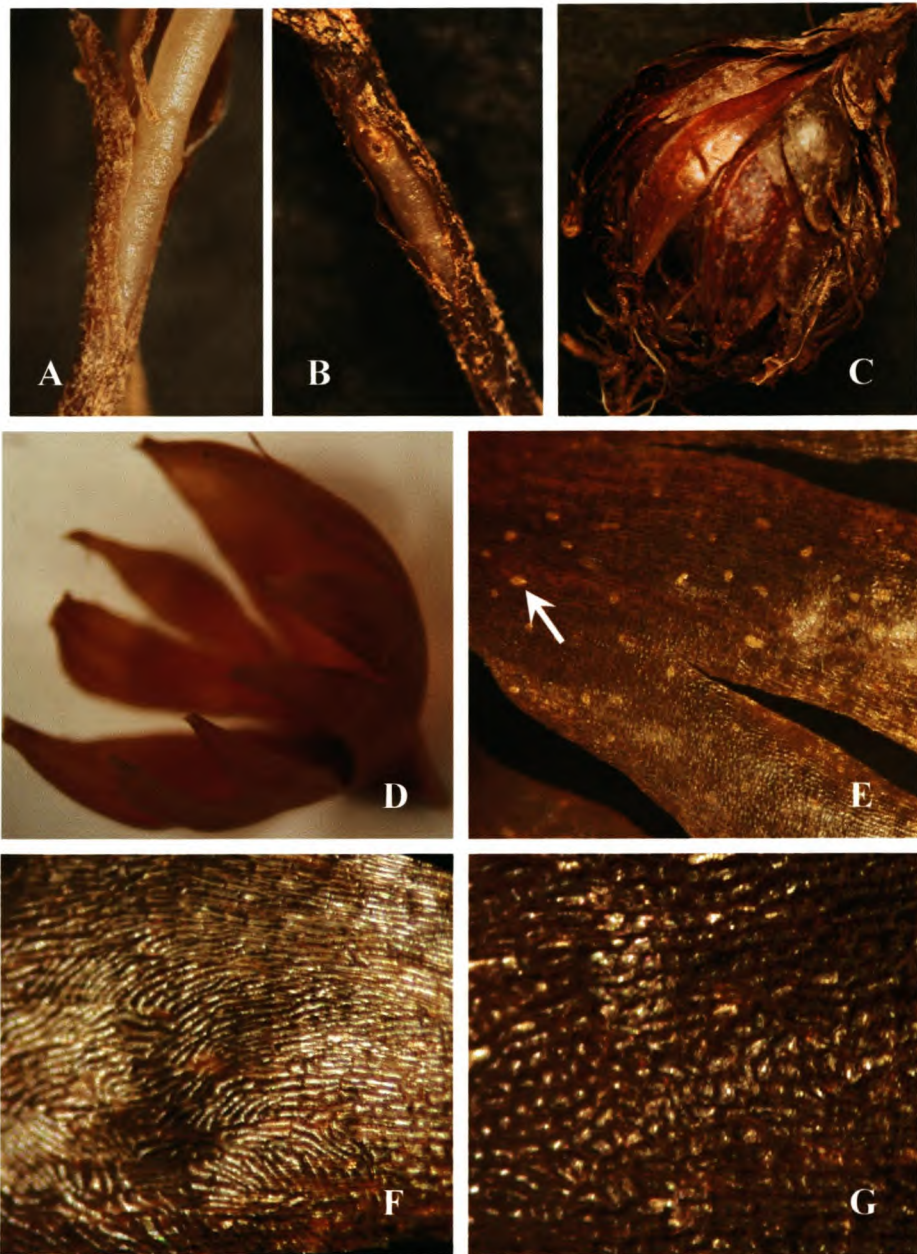


Figure 3.26 A *Oxalis tenella*: [A] & [B] Rhizomes covered by brown tunic-like sheaths; [C] Bulb covered with membranous outer tunic layers; [D] A single membranous tunic forming a closed circular unit that results in circular aestivation; [E] A close-up view of a membranous tunic to show the characteristic spots formed by groups of inflated cells (arrow); [F] Adaxial surface of membranous tunic showing surface ornamentation of striate bunches in a complex mosaic; [G] Abaxial surface of membranous tunic showing areolate ornamentation

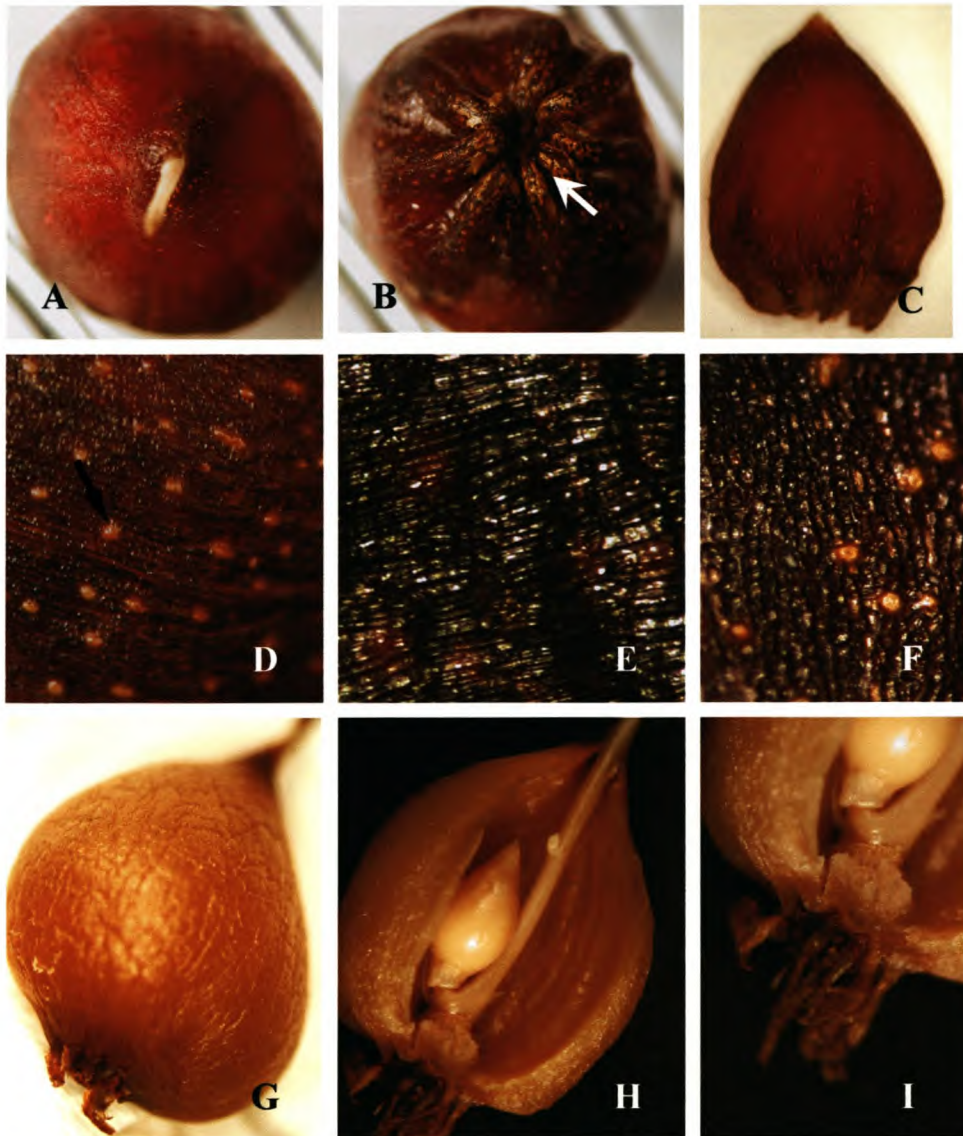


Figure 3.26 B *Oxalis tenella*: [A] Top view of a bulb with leathery tunics after the outer membranous tunics have been removed, note that it forms a single, continuous structure; [B] A bottom view of a bulb with leathery tunics after the outer membranous tunics have been removed, note the longitudinal basal undulations (arrow); [C] A leathery tunic viewed from the side; [D] A closer view of the abaxial surface of a leathery tunic to show the groups of inflated cells (arrow); [E] Adaxial surface of a leathery tunic showing rows of flattened cells; [F] Abaxial surface of a leathery tunic showing areolate ornamentation; [G] Abaxial view of a single fleshy leaf with basal undulations from which adventitious roots originate; [H] Section through the naked bulb showing fleshy leaves attached to a wide basal plate, also note the rhizome and the enclosed new bulb; [I] Closer view of the wide basal plate and adventitious roots arising from the fleshy leaf bases

Oxalis urbaniana (Figure 3.27 A-E)**Project number:** MO 305**Rhizome:** glabrous, sheath absent, 7.0–19.0 mm (10.3 mm average) long, of even diameter, clustered by adventitious roots, horizontally orientated, bulbels present.**Bulbels:** produced at tips of vertical dropper/stolon, cupped successively by conical calyprate scales originating from the nodes of the dropper.**Scales:** membranous, glabrous, dry, amplexicaule, alternately arranged.**Bulb:** solitary, 17.0–21.0 mm (20.3 mm average) long, 5.0–8.0 mm (6.9 mm average) wide in middle, fusiform, apex long-beaked, surface smooth, dull brown, with angular ridge bulging out from the inside, horizontally orientated in substrate.**Tunics:** with three types of textures present: normal membranous, a corky one and membranous with a longitudinally hardened section along centre. **Membranous tunics:** restricted to outer two layers, one or two, closed circular units without lateral margins, aestivation concentric, dark-brown, glabrous, non-spotted, smooth, adaxial surface sticky¹, covering entire bulb body, apex beaked, base shortly attenuate, adaxial surface with fungal hyphae; adaxial surface ornamentation with rows of flattened cells²; abaxial surface ornamentation areolate, striate (with thick ridges) along veins. **Corky tunic:** restricted to middle layer, single, closed circular unit without lateral margins, aestivation concentric, reddish-brown, non-spotted, apex beaked, base shortly attenuate; adaxial surface non-sticky, smooth, with concave longitudinal corners that correspond to wings/angles of the abaxial surface, ornamentation with rows of flattened cells³; abaxial surface with seven prominent ridges, two ridges extend from the base to the upper quarter of the bulb, these ridges alternate with two long ridges that extend from the base to the apex, a third ridge type on the opposite side of the bulb extends from the base to the lower quarter, where it then fork to form two ridges, which extend to the apex of the bulb⁴, ridges are apically flattened with convolute sides, surface ornamentation of ridge-tops areolate; spaces between the ridges form U-shaped furrows covered, with dark and sticky glandular trichome-like spikes interconnected by fungal hyphae⁵, surface ornamentation between ridges horizontally striate. **Membranous tunics with longitudinally hardened section along the centre:** confined to the innermost layer, single, open, golden-brown, non-spotted, covering 75% of bulb body, apex beaked, base attenuate; abaxial surface with single, dark-brown, slightly raised longitudinal section

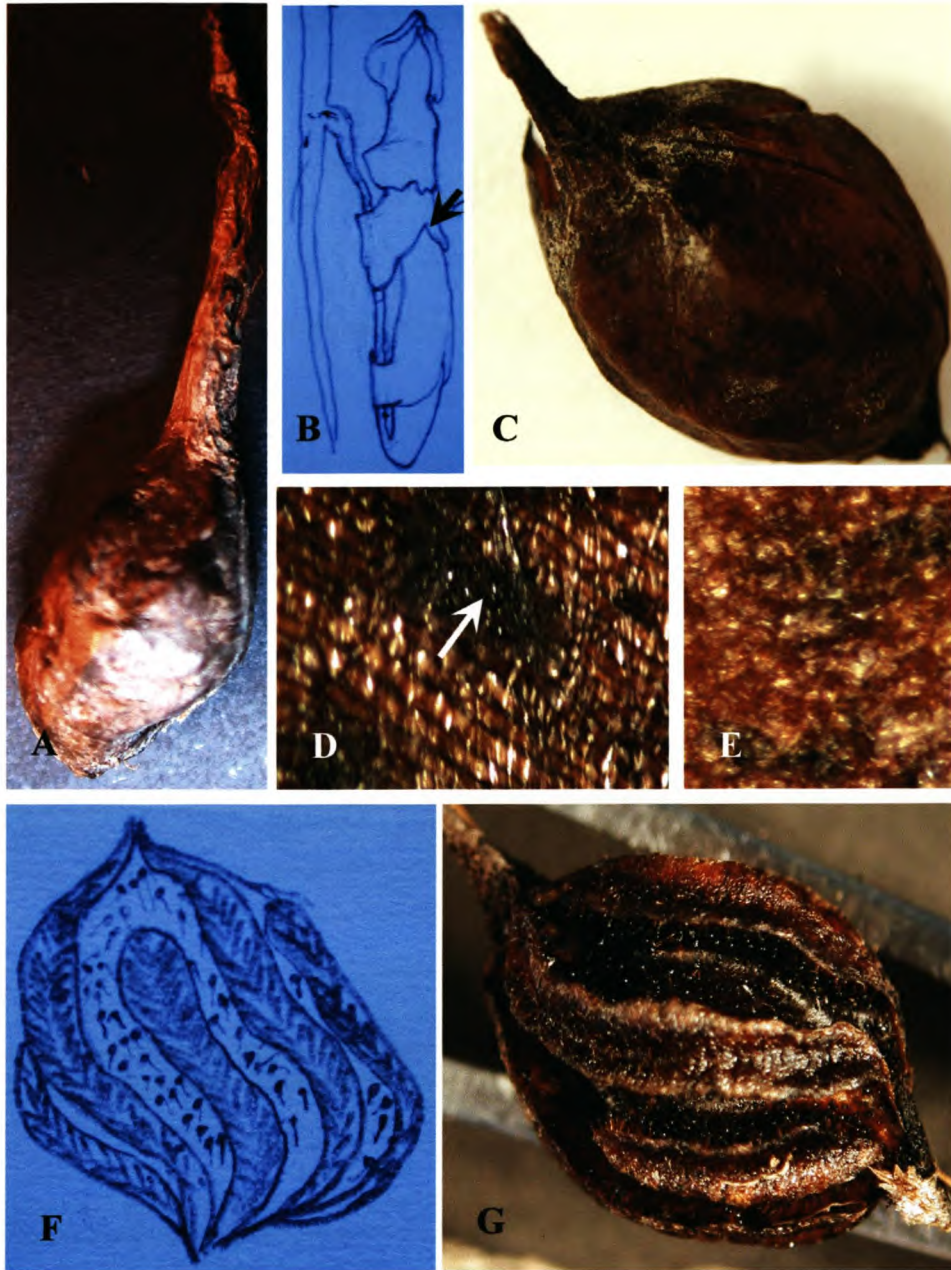


Figure 3.27 *Oxalis urbaniana*: [A] Bulb with outer membranous tunics and a distinct apical beak; [B] Drawing of a bulbel attached to the rhizome via a dropper; note the distinct calyptrate scales covering the bulbel (arrow); [C] Abaxial view of a single membranous tunic revealing a faint angular structure caused by angular deeper layers; [D] Adaxial surface of membranous tunic showing areolate ornamentation, note the patches of sticky substance (arrow); [E] Abaxial surface of membranous tunic showing areolate surface ornamentation; [F] Drawing of the angular middle corky tunic layer; [G] Middle corky tunic layer with distinct angular ridges and deep furrows between



Figure 3.27 B *Oxalis urbaniana*: [A], [B] & [C] Different sides of the angular, corky middle tunic layer (rotating from A to C); [D] Top view of the angular, corky middle tunic layer; [E] Bottom view of the angular, corky middle tunic layer; [F] Black-headed trichome-like structures in the furrows between the angular ridges; [G] Fungal hyphae interconnecting the sticky black-headed trichome-like structures (arrow); [H] A close-up view of the sticky black-headed trichome-like structures; [I] Flattened ridged apex of one of the prominent angular ridges

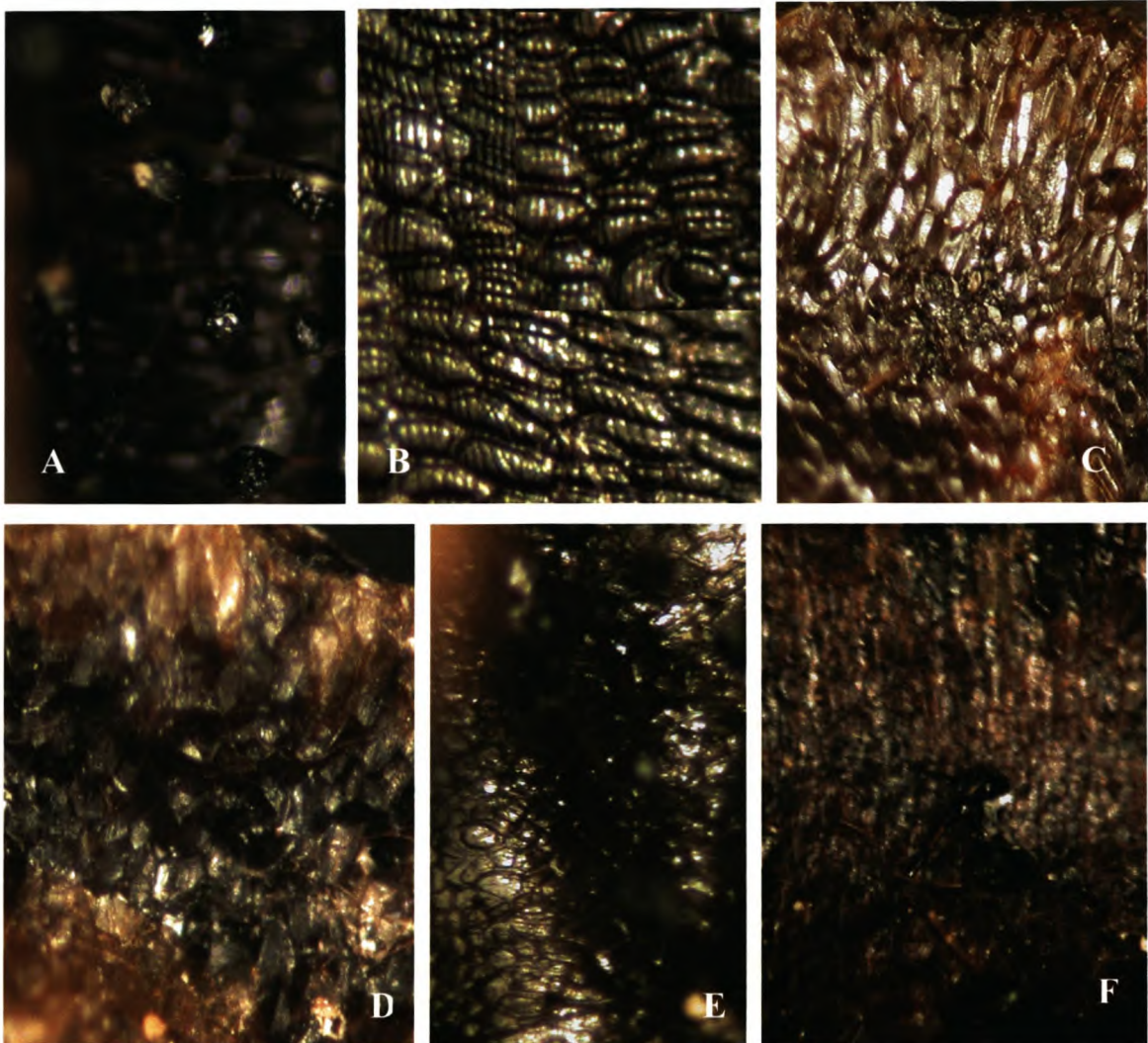


Figure 3.27 C *Oxalis urbaniana*: [A] A close-up view of the sticky black-headed trichome-like structures; [B] Adaxial surface of middle corky tunic with rows of flattened cells overlaid by a vertical striation pattern; [C] & [D] Abaxial surface of ridge-tops of the middle corky tunic showing areolate ornamentation; [E] Abaxial surface of middle corky tunic along the side of ridges showing areolate ornamentation; [F] Abaxial surface of middle corky tunic in the furrows between the ridges showing striate ornamentation

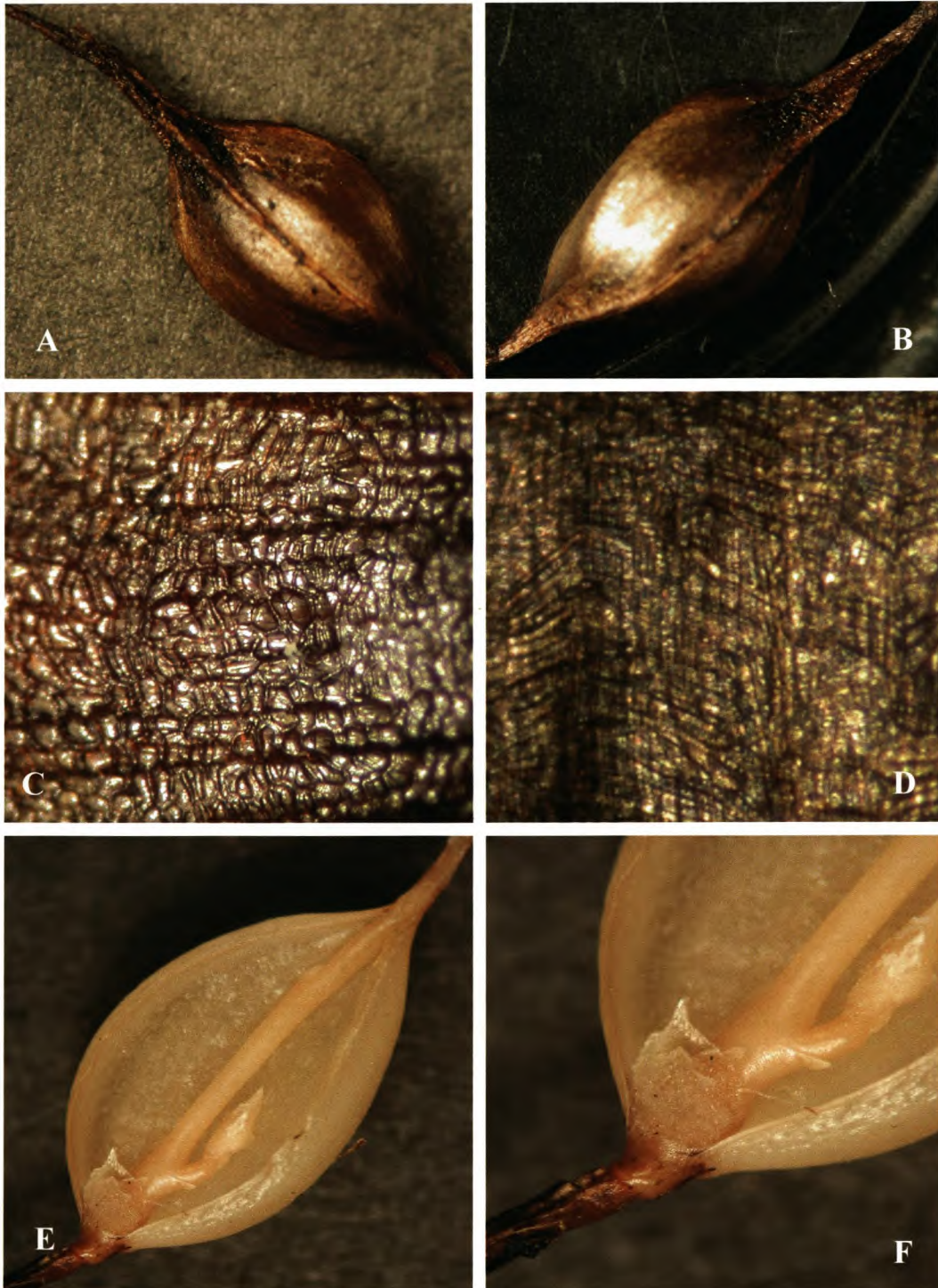


Figure 3.27 D *Oxalis urbaniana*: [A] & [B] Inner membranous tunic with longitudinal ridges extending over the entire tunic length, also note the prominent apical beak; [C] Adaxial surface of inner membranous tunic showing areolate ornamentation with flattened cells; [D] Abaxial surface of inner membranous tunic showing wavy-striate (zig-zag) ornamentation; [E] Adaxial view of a fleshy leaf attached to a narrow basal plate, also showing the rhizome and the enclosed new bulb; [F] A closer view of the narrow basal plate and the amplexicaul fleshy leaf base folded around the basal plate

along the centre, apex with black-headed sticky trichomes; margins membranous; adaxial surface ornamentation areolate with flattened cells (fungal hyphae common); abaxial surface ornamentation wavy-striate, longitudinally striate along veins.

Fleshy leaves: two, white to colourless, non-winged, shape lingulate, apex acute, base sessile, alternately attached to the rhizome.

Basal plate: narrow

Contractile root: not seen

Root type: adventitious

Note:

1. *The adaxial surfaces might be covered by a sticky substance here and there. This substance may be produced by the trichome-like spikes on the middle corky tunic or by fungi occurring between the tunic layers.*
2. *The flattened surface ornamentation is overlaid on a vertical striation pattern.*
3. *Usually the zigzag lines between the rows of flattened cells have very short oscillations.*

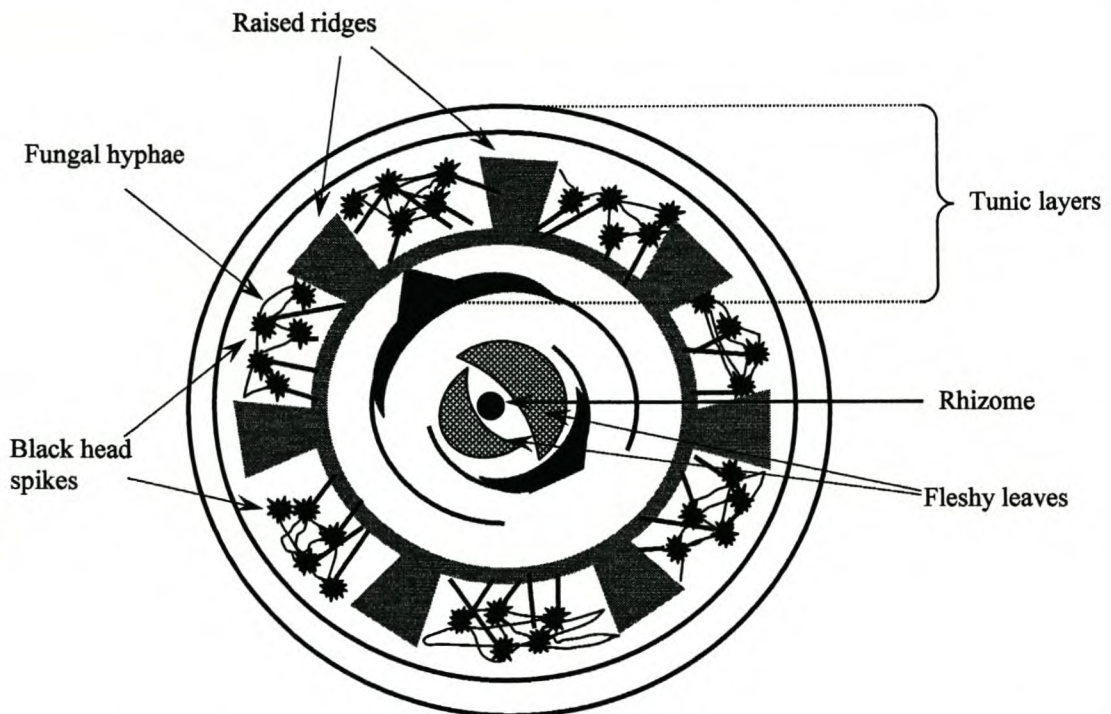


Figure 3. 27 E A cross-sectional diagram through the bulb of *O. urbaniana*. The bulb has two outer membranous tunic layers, a central, winged corky tunic layer and an inner membranous tunic with a hardened central part. Between the raised ridges there are trichome-like spikes have black sticky heads, which are interconnected to one another by fungal hyphae. Each raised ridge is apically flattened and the flat part has an areolate surface ornamentation.

4. *There is a trace of an opening near the apex of the ridge that splits in the lower quarter of the bulb. This might have been the fusion point of previously open tunics.*
5. *These spikes may be fungi growing between the ridges, or it may be part of the tunic. Detailed anatomical studies are required before they could be interpreted fully.*

Oxalis versicolor (Figure 3.28)

Project Number: MO 307

Rhizome: mostly glabrous, some times with simple trichomes, sheath absent, 17–38 mm (25.5 mm average) long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, sometimes ciliate, dry, semi-amplexicaule, alternately arranged.

Bulb: usually solitary, some clustered by previous years bulb tunics, 12–18 mm (14.5 mm average) long, 4–11 mm (7.75 mm average) wide in middle, fusiform, black; surface smooth, not shiny; apex not beaked, base cuneate; bulb orientated perpendicular to rhizome.

Tunics: two textures: leathery and membranous. **Leathery tunics:** restricted to outer two layers, blackish brown, glabrous, non-spotted, outer surface with globular balloon-like structures¹, sticky, open, aestivation equitant, cover 80% of bulb body; margins overlapping along the lower half of bulb's body, base shortly attenuate, amplexicaule; adaxial surface ornamentation areolate with some flattened cells; abaxial surface ornamentation colliculate and areolate. **Membranous tunics:** present as innermost layers and the outermost basal tunic; innermost layers covering more than 75% of bulb width; margins membranous; inner surface ornamentation ruminant; outer surface ornamentation scalariform; outermost tunic single, basal, amplexicaule, with overlapping margins, apex extend to upper quarter of bulb length; adaxial surface ornamentation scalariform; abaxial surface ornamentation scalariform.

Fleshy leaves: two, white, non-winged, shape lingulate, apex acute; base semi-amplexicaule, sessile.

Basal plate: narrow

Contractile root: not seen

Root type: taproot

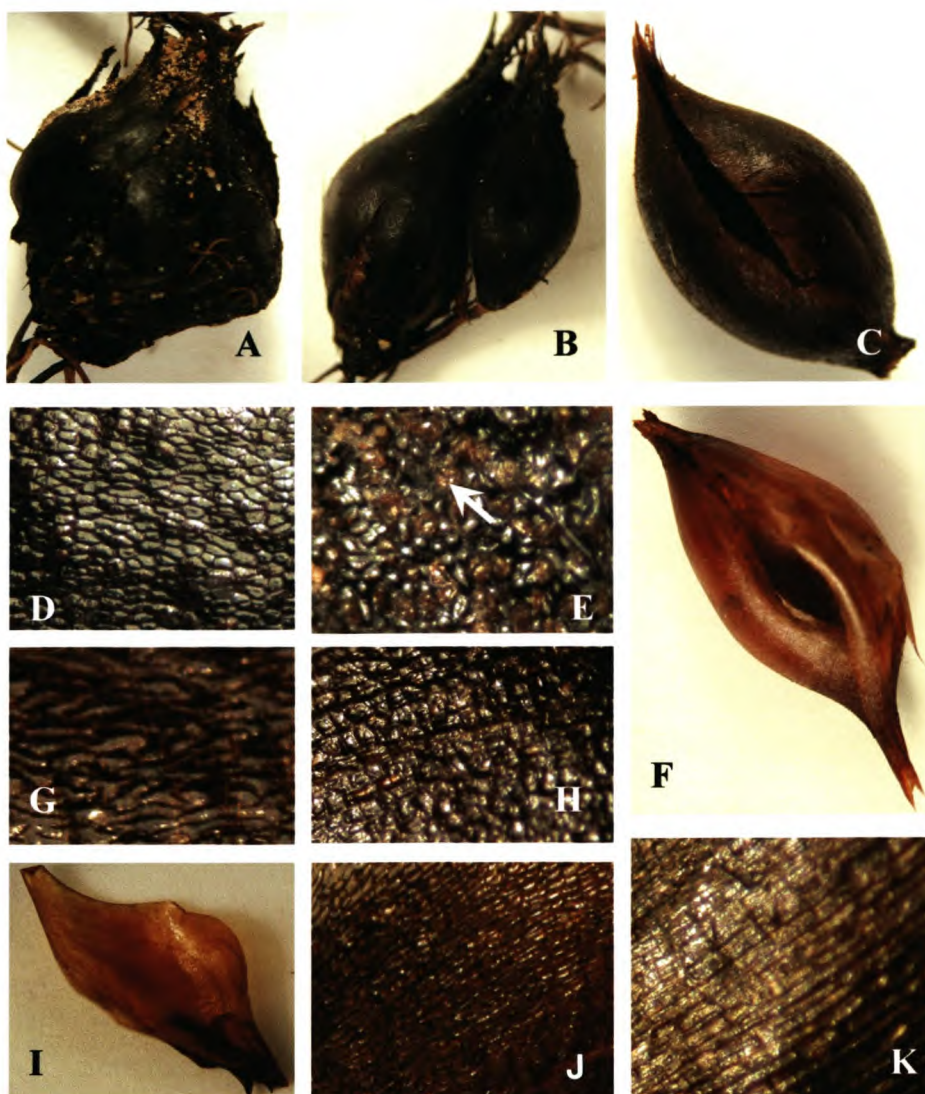


Figure 3.28 *Oxalis versicolor*: [A] Solitary bulb with leathery tunics; [B] Two clustered bulbs; [C] Outer leathery tunic with overlapping lower margins; [D] Adaxial surface of leathery tunic showing areolate ornamentation with flattened cells; [E] Abaxial surface of leathery tunic showing colliculate and areolate ornamentation and large, orange, balloon-like secreting cells (arrow); [F] Inner membranous tunic; [G] Adaxial surface of innermost membranous tunic showing ruminant ornamentation; [H] Abaxial surface of innermost membranous tunic showing scalariform ornamentation; [I] Outermost basal tunic with clasping lower margins; [J] Adaxial surface of outermost basal tunic showing scalariform ornamentation; [K] Abaxial surface of outermost basal tunic showing scalariform ornamentation

Note:

1. *These surface structures could be secreting cells that produce the sticky substances on the tunics.*

Oxalis viscosa (Figure 3.29)

Project Number: MO 260

Rhizome: with capitate trichomes, sheath absent, 9–20 mm (15.75 mm average) long, abruptly decreasing in diameter near bulb, not clustered by previous years' bulb tunics¹, bulbels absent.

Scales: membranous, with capitate trichomes, trichomes also present along margins², dry, amplexicaule, alternately arranged.

Bulb: solitary, 8–12 mm (10 mm average) long, 4–5.5 mm (4.4 mm average) wide in middle, variable in shape ranging from elliptical to obovate, usually oval, brown, surface irregularly wrinkled, non-sticky; apex obtuse-apiculate, non-beaked.

Tunics: membranous, honey-brown, irregularly wrinkled, non-sticky, outer two layers mostly closed, aestivation concentric, apex closed; inner two layers open from apex to mid-length, aestivation equitant, margins ciliate with capitate trichomes, apex embracing, acute, base with abundant capitate trichomes on both surfaces, amplexicaule; adaxial surface ornamentation ruminant and scalariform intermixed; abaxial surface ornamentation scalariform.

Fleshy leaves: two, brown, shrivelled³, shape lingulate, winged in lower half, apex acuminate, base amplexicaule.

Basal plate: wide

Contractile root: not seen

Root type: not seen

Note:

1. *Adventitious roots growing from them clusters rhizomes together.*
2. *Lower scales are glabrous.*
3. *Fleshy leaves are shriveled and brown when the plant is in flower.*

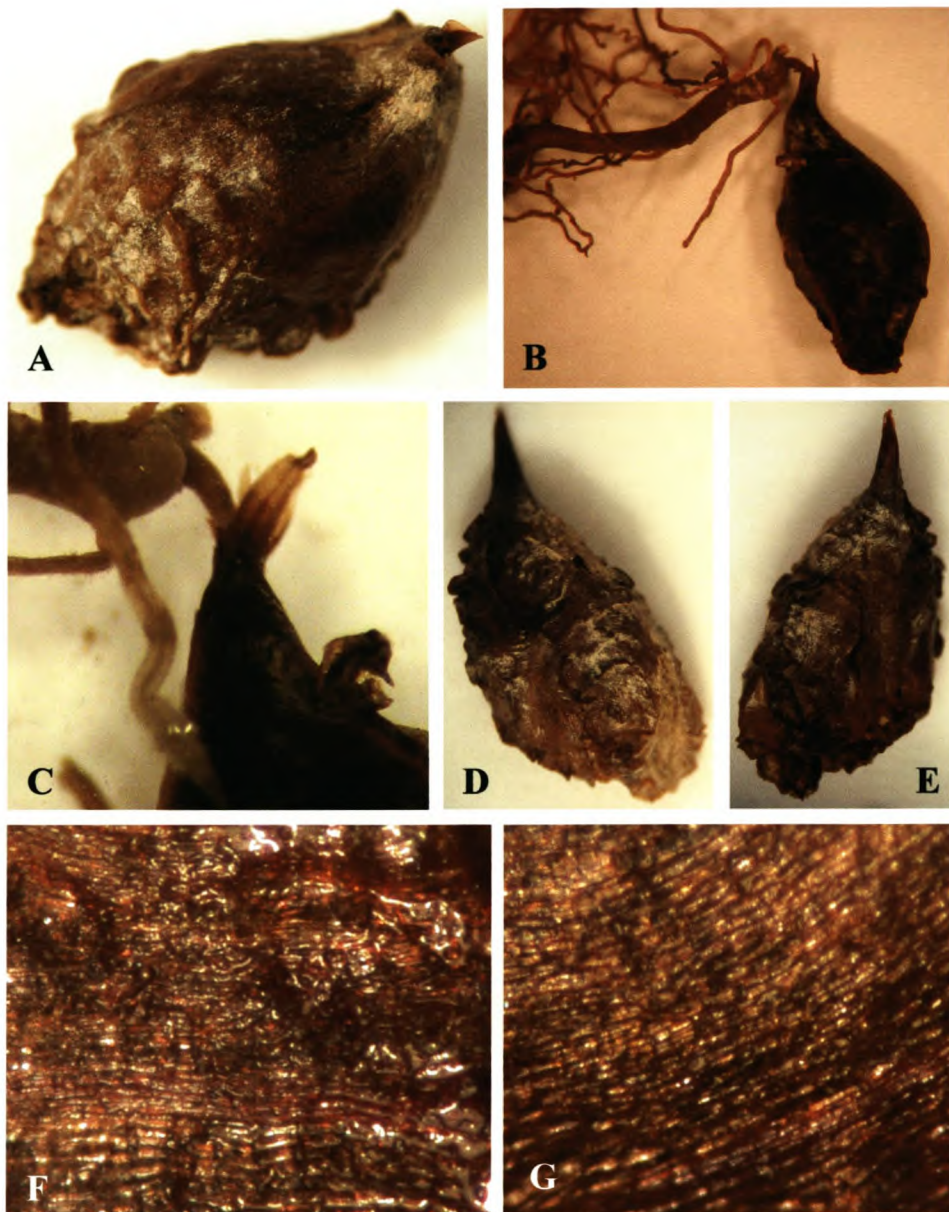


Figure 3.29 *Oxalis viscosa*: [A] Bulb with wrinkled membranous tunics; [B] Bulb attached to a rhizome showing the abrupt thinning of the rhizome just above the bulb; [C] Closer view of the thin rhizome section and the bulb apex; [D] & [E] Abaxial view of wrinkled membranous tunics; [F] Adaxial surface of membranous tunic showing mixed ruminant and scalariform ornamentation; [G] Abaxial surface of membranous tunic showing scalariform ornamentation

Oxalis xantha (Figure 3.30)

Project number: MO 102

Rhizome: glabrous, sheathed by a tunic-like coating, 21 mm long, diameter decreasing gradually towards the bulb, not clustered by previous years' bulb tunics, bulbels absent.

Scales: membranous, glabrous, dry, amplexicaule, alternate, size decreases towards the bulb.

Bulb: solitary, 14 mm long, 8 mm wide in middle, fusiform, honey-brown, surface smooth, apex sharply acute, base acute, tunics tightly packed.

Tunics: leathery, honey-brown, non-spotted, glabrous, non-sticky, open, aestivation equitant, covering more than 50% of bulb body, all similar in size; margins membranous, split towards the centre; base with finger-like projections, apex acute; adaxial surface ornamentation with rows of flattened cells, with widely oscillating longitudinal zigzag lines between rows; abaxial surface ornamentation colliculate-pusticulate, smooth along veins¹

Fleshy leaves: four, white, non-winged, shape lingulate², apex acute, base sessile, conspicuous brown tannins present in most epidermal cells.

Basal plate: narrow

Contractile root: not seen

Root type: not seen

Note:

1. *There is no ornamentation along the veins.*
2. *Only the outer big fleshy leaf has narrow membranous margins.*

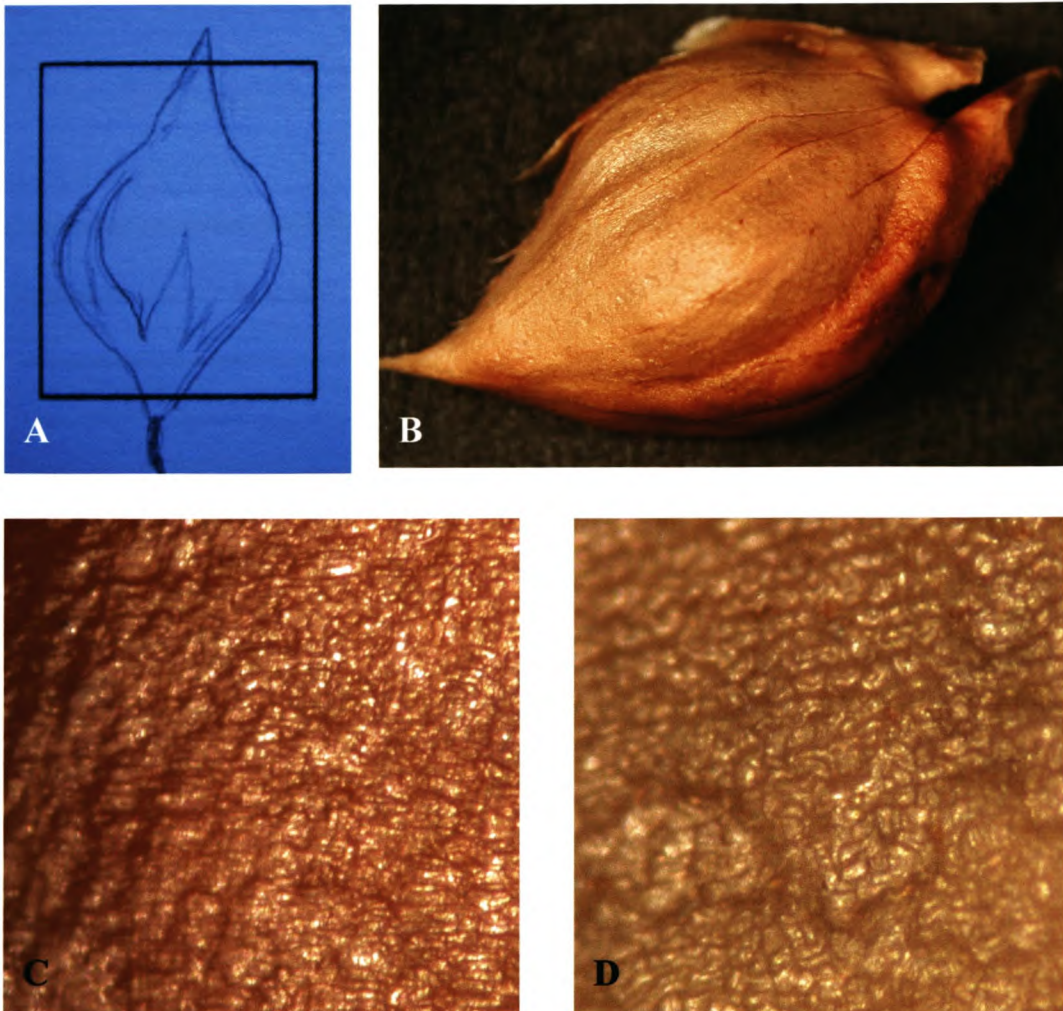


Figure 3.30 *Oxalis xantha*: [A] Drawing of the bulb outline to illustrate the bulb shape; [B] Abaxial view of a leathery tunic showing the finger-like projections at the base; [C] Adaxial surface of leathery tunic showing rows of flattened cells with wide oscillating longitudinal zigzag lines; [D] Abaxial surface of leathery tunic showing colliculate-pusticulate surface ornamentation

CHAPTER FOUR: DISCUSSION

4.1. Introduction

Morphological examination of the underground structures revealed major variation between the different *Oxalis* species. One binding similarity seen in all the specimens studied is the presence of underground stems (rhizomes), bulbs and roots. In addition, the bulbs of all examined specimens have fleshy leaves or nutritive scales beneath layers of protective scales or covers. All of these parts, as well as the rhizome, originate from the base of the bulb, called the basal plate. As illustrated in previous morphological and anatomical studies (Gebregziabher, 2001) the subterranean structures of all *Oxalis* species are homologous. According to the definition given by Rees (1992), the subterranean structures in *Oxalis* are all true bulbs. Despite this basic similarity in structure, major phenotypic variation is present between the different species in the genus.

Similarities that link some species together or differences that distinguish between species are taxonomically important to reveal natural relationships. Such characters are regarded as being taxonomically informative. Based on the descriptions in the previous chapter, informative characters were recorded and summarized in Tables 3.1 and 3.2. As reflected in these tables, the bulb is the underground part that contributes most of the variable characters. Within the bulbs, the tunics and fleshy leaves contribute the most important informative characters, e.g. tunic texture, tunic base modifications and the aestivation of the tunics. Similarly, the attachment of the fleshy leaf to the base and the shape and colour of the fleshy leaves are also very informative. In contrast, the tunic surface ornamentation also displays major variation, but this seems to be taxonomically less informative, as it is highly variable within a single species.

Some informative characters were also detected for other parts of the underground structure. For example, the presence or absence of roots or the type of roots arising from or at the base of the bulb can be of taxonomic importance. The relative rhizome length and indumentums link a few species together (Salter, 1944). Characters of the rhizome are, however, few and they are less variable than true bulb characters.

Although bulb shape and stickiness seem to be good and informative characters, they are, to some extent, affected by the environment. Bulbs growing in rocky areas are often deformed, but specimens from the same locality (or same population) collected in softer soil yield a better overall idea of the shape of the bulb. Salter (1944) similarly ascribed the sticky nature of the bulbs of *O. polyphylla* Jacq. as being affected by soil type. He regarded the bulbs of specimens growing in sandy soil as sticky and those growing in other soil types as non-sticky. The current study revealed a variation in the production of the sticky substance in two specimens of *O. purpurea*. It is present in the one specimen and absent from the other. This is probably an indication that the potential for producing this substance is always present. Ultimately, a population level study will be necessary to test which characters are affected by environmental conditions and which are not.

Salter (1944) described the scales of some species as amplexicaule or semi-amplexicaule based on the way they are attached to the rhizome. Since single rhizomes were observed to have both states (*O. lichenoides*, *O. monophylla* and *O. ebracteata*), the current study considers the attachment of scales as an unreliable character. Similarly, Salter (1944) also described the shape of the scale apex as important, but the current study found this to be unreliable, because variation in this character was observed in the scales of a single rhizome in many species.

Based on the morphological descriptions provided in Chapter 3 and giving weight to what I believe to be potentially informative characters, ten bulb types were identified. Each bulb-type has its own diagnostic characters and is named after one of the typical included species displaying the particular set of diagnostic characters. These bulb types are discussed in some detail below:

4. 2. Delimitation and description of bulb-types

4. 2. 1 Bulb-type 1 (*O. monophylla* type):

Included taxa: *O. monophylla*, *O. oculifera*

The diagnostic characters for this bulb type are the presence of a soft and spongy bulb surface (formed by interwoven split pieces of soft outer tunic layers) and the shortly petiolate fleshy

leaves. The pattern in which the tunic splits into inverted V's or W's, is also diagnostic for this bulb-type. The splitting pattern of the tunics of *O. monophylla* is an inverted V, while outer tunics of *O. oculifera* split as an inverted W with a rigid median vein (Figure 4.1). This difference seems not to be that important, since the tunics of the type specimen of *O. oculifera* were described as having an inverted V splitting pattern (Oliver, 1993) like in *O. monophylla*.

There are other shared characters that also link the species included in this bulb-type, but they are not unique to these two species or this bulb-type. Both species have bulbs with wide basal plates, imbricate tunic aestivation and rhizomes that are covered by capitate trichomes. Due to the many shared characters, this appears to be a natural bulb-type. However, there are a few differences that can be used to distinguish between the two species. These include the number and shape of the fleshy leaves in the bulbs. *O. monophylla* usually has more than 20 (up to 60–80), mostly columnar fleshy leaves, whereas *O. oculifera* has only 4–6 broader and lingulate fleshy leaves. Additionally, the tunic bases are wrinkled in *O. monophylla* and not in *O. oculifera*.

4. 2. 2 Bulb-type 2 (*O. hirta* var. *tubiflora* type):

Included taxa: *O. cf. callosa*, *O. hirta* var. *tubiflora*, *O. linearis* and *O. cf. helicoides* var. *helicoides*

This bulb-type has brown, winged and sessile fleshy leaves, wide and usually flattened conical basal plates and membranous tunics (Figure 4.2). In addition, all included species usually have more than six fleshy leaves per bulb and all shares an imbricate aestivation of the fleshy leaves. With the exception of *O. cf. callosa*, the fleshy leaves of all the other included taxa contain a creamy substance in a continuous or irregular distribution pattern within their canals. *O. cf. helicoides* var. *helicoides* and *O. hirta* var. *tubiflora* are further grouped together by the presence of spots on the tunic surfaces that are formed by groups of inflated hypodermal cells.

O. engleriana and *O. adpersa* both show close affinities to bulb-type 2 in having membranous tunics and narrowly winged fleshy leaves. *O. engleriana* also has a wide basal plate and longitudinally undulate tunic bases, similar to *O. linearis*. Both *O. engleriana* and *O. adpersa* display wrinkled tunic bases similar to those found in *O. cf. helicoides* var. *helicoides*. However, neither of these two species have brown fleshy leaves like those found

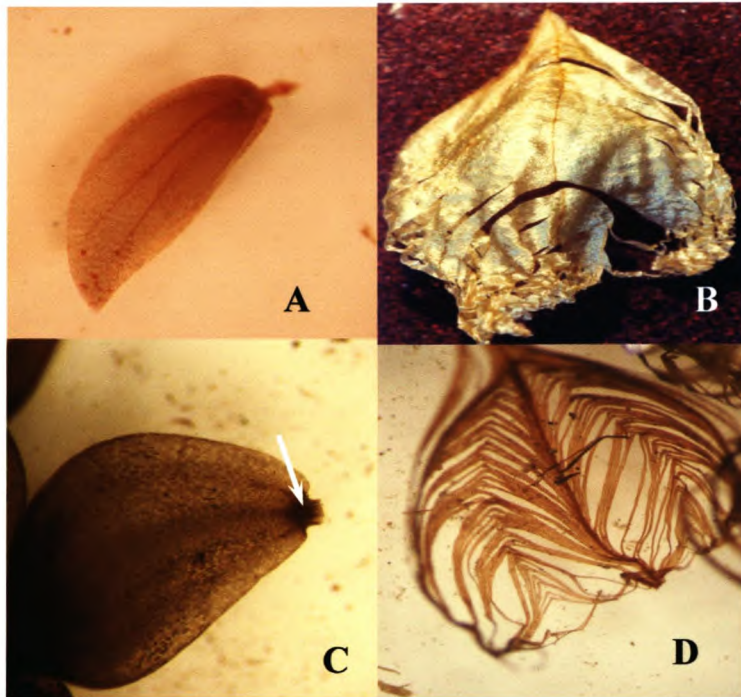


Figure 4. 1 Diagnostic characters of bulb-type 1. *O. monophylla*: [A] petiolated fleshy leaf and [B] tunic with inverted V splitting pattern. *O. oculifera*: [C] petiolated fleshy leaf (arrow) and [D] inverted W splitting pattern.



Figure 4. 2 Diagnostic characters of bulb-type 2. *O. hirta* var. *tubiflora*: [A] Tunic, spotted with groups of inflated hypodermal cells and [B] brown fleshy leaves with membranous margin (arrow). *O. hirta* var. *hirta*: [C] tunic and [D] brown fleshy leaf with membranous margin (arrow).

in other members of this group. *O. adspersa* also lacks a wide basal plate. Due to the similarities outlined above, *O. engleriana* and *O. adspersa* are included in bulb-type 2, but because of the clearly visible differences they are included as a subtype, namely subtype B.

Members of bulb-type 2 show affinities to members of bulb-type 1 in having wide basal plates and an imbricate aestivation of the fleshy leaves. The large number of fleshy leaves in *O. monophylla* is also congruent with the larger number of fleshy leaves found in the bulbs of some members of bulb-type 2 (e.g. *O. cf. callosa* and *O. helicoides*).

4. 2. 3 Bulb-type 3 (*O. aridicola* type):

Included taxa: *O. eckloniana*, *O. xantha*, *O. aridicola*, *O. oreophila*, *O. tenella*

The diagnostic character of this bulb type is the modified nature of the tunic base. The base either forms longitudinal undulations or finger-like projections (Figure 4.3). The majority of the included taxa have finger-like projections at the bases of their tunics. The exceptions are *O. tenella* and *O. oreophila*, which have tunics with longitudinally undulated bases (Figure 4.3). Other characters also link these species together. For instance, all of them have leathery tunics and glabrous rhizomes. All members have white fleshy leaves, although in *O. oreophila* and *O. tenella* the apices of the fleshy leaves are brown. The latter two species also share the presence of a wide basal plate. With the exception of *O. eckloniana* and *O. xantha*, all the other species have spotted tunic surfaces (Figure 4.3). With regard to tunic aestivation, the included species show a diversity of all the types of aestivations observed in this study. Similarly, the number of fleshy leaves also varies, ranging from two to four.

The presence of finger-like projections at the tunic bases and the spotted tunic surfaces are unique to a few members belonging to this bulb-type. However, similar characters are observed in other species belonging to other bulb types. For example, the creamy groups of inflated hypodermal cells that cause the spots on the tunic surface are observed in a similar pattern on the membranous tunics of *O. hirta* var. *tubiflora*, *O. cf. helicoids* var. *helicoids* and *O. monophylla*, but with a dark grayish colour. Similarly, longitudinally undulated tunic bases are regarded as tunic base modifications similar to the finger-like projections.

O. campylorrhiza has some characters that resemble those of bulb-type 3. The species has a limited number of bulb tunics with closed concentric aestivation and projected folding at the

base. It also possesses two types of tunics (membranous and leathery) in a single bulb, similar to the tunics in *O. tenella*.

Although fleshy leaf colouration is obvious in bulb-type 2, it is also observed in the bulbs of *O. tenella* and *O. oreophila*, indicating an affinity between these two species and members of bulb-type 2. Also, the presence of a wide basal plate and longitudinally undulate tunic bases in *O. tenella* and *O. oreophila* resemble those observed in *O. linearis* and *O. engleriana* (members of bulb-type 2). Therefore, it is evident that bulb-type 3 has a close affinity to bulb-type 2.

4. 2. 4 Bulb-type 4 (*O. purpurea* type):

Included taxa: *O. purpurea*, *O. versicolor*, *O. stenopetala*, *O. ebracteata*

The presence of a fusiform bulb shape, narrow basal plate and two types of tunics (membranous and leathery) per bulb diagnose bulb-type 4 (Figure 4.4). The included species also share an equitant aestivation of the fleshy leaves. All included species, except for *O. stenopetala*, also have sticky bulb tunics. All bulbs with sticky tunics have microscopic globular balloons (or secreting cells) on the lower half of the outer tunic surface, but they are revealed only after soaking the tunics in benzene. With the exception of *O. versicolor*, all the members share the presence of beaked bulb apices and in all taxa the biggest fleshy leaf has narrow membranous margins. All included species, except *O. ebracteata*, also have trichomes on their rhizomes. However, in *O. purpurea* this is a variable character. Since this species is regarded as a group species (Salter, 1944) variations like these may be expected.

The layering pattern of the membranous and leathery tunics differs between the included taxa. The bulbs of *O. purpurea* and *O. ebracteata* have their membranous tunics as the outermost layers and leathery tunics as the inner layers. In *O. versicolor* the reverse is true. *O. stenopetala* have membranous tunics in both the outermost and innermost layers and the leathery tunics in between.

Although the combination of these characters defines bulb-type 4, species belonging to other bulb-types may also share some of these individual characters. For example, *O. tenella* (bulb-type 3) has a fusiform bulb shape as well as membranous and leathery tunics in the same bulb. Different kinds of tunics in a single bulb were also observed in *O. urbaniana*, *O. pulchella*

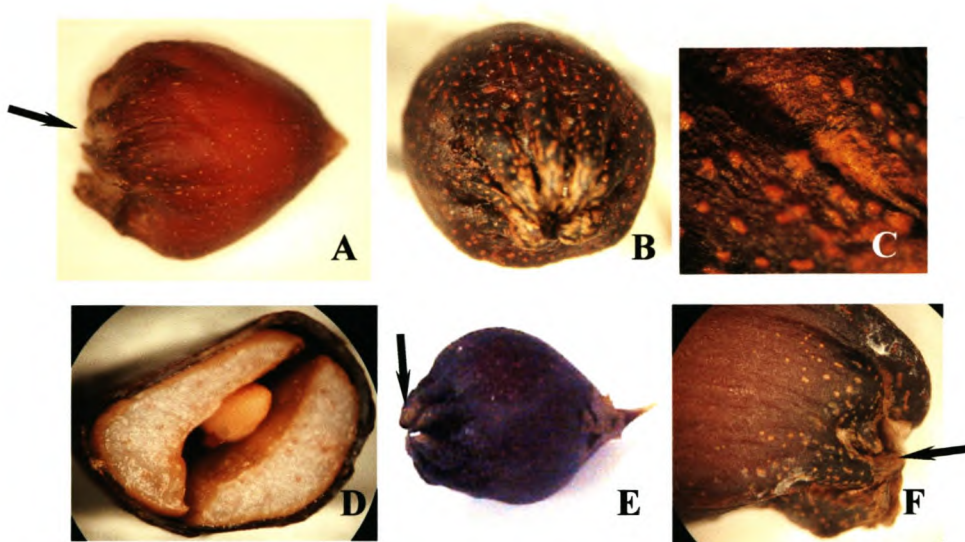


Figure 4. 3 Diagnostic characters of bulb-type 3. *O. tenella*: [A] spotted tunic with undulated base (arrow). *O. aridicola*: [B] bottom view of bulb showing finger-like projections of the tunic base; [C] a closer view of the spotted tunic surface (groups of inflated hypodermal cells); [D] a cross section through the bulb to illustrate the circular tunic aestivation and the two white fleshy leaves; [E] & [F] side view of the finger-like projections (arrows).

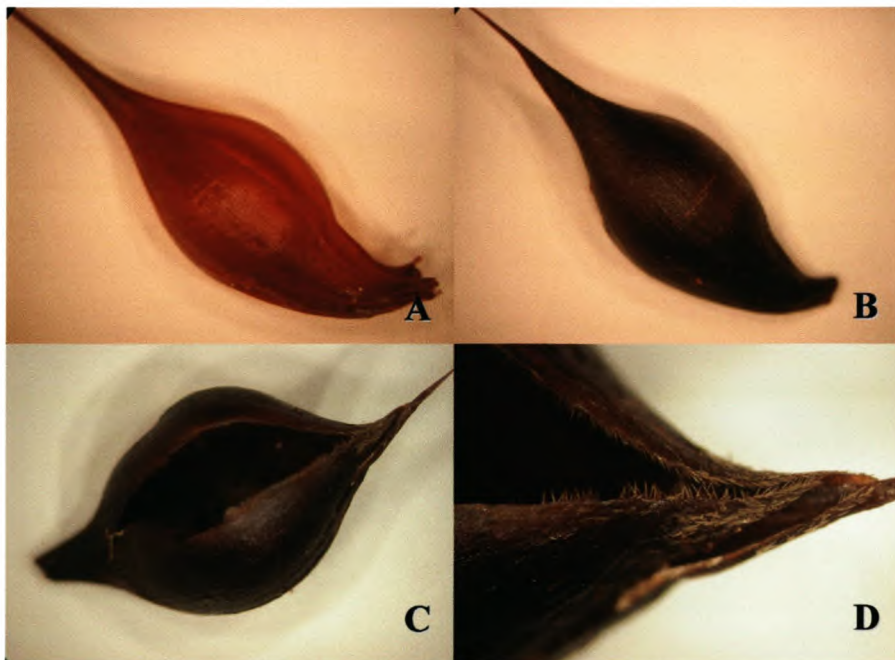


Figure 4. 4 Diagnostic characters of bulb-type 4. *O. purpurea*: [A] membranous tunic, [B] & [C] leathery tunics and [D] Upper part of leathery tunic with ciliate apex and abaxial trichomes.

and *O. campylorrhiza*. In addition, the fusiform bulb shape is also shared with *O. xantha* (bulb-type 3), *O. urbaniana* (bulb-type 5) and *O. obtusa* (bulb-type 5). Based on the total evidence bulb-type 4 has a strong affinity to both bulb-type 3 and bulb-type 5.

4. 2. 5 Bulb-type 5 (*O. lichenoides* type):

Included taxa: *O. lichenoides*, *O. urbaniana*, *O. obtusa*, *O. pulchella*, *O. dregei*

The diagnostic characters of this bulb-type are a narrow basal plate and the presence of either angular tunics or a single dominant fleshy leaf per bulb (Figure 4.5). This bulb-type thus links two groups of species with overlapping bulb characters. The first group has bulbs with a single dominant fleshy leaf, whereas the second group of bulbs has angular/winged tunics. *O. lichenoides* is the only species with both of these characters. *O. lichenoides*, *O. urbaniana* and *O. obtusa* share the presence of angular / winged tunics. Conversely, *O. lichenoides*, *O. pulchella* and *O. dregei* share the presence of a single dominant fleshy leaf per bulb (the second fleshy leaf in *O. dregei* is underdeveloped and less functional as storage leaf). With the exception of *O. obtusa*, the bulbs of all the included species also have a beaked apex (sometimes very short), and all (except *O. pulchella*) have bulbels attached to the rhizome.

Most of the specimens examined in this study have two fleshy leaves per bulb and a few have more than three. Having a single dominant fleshy leaf is therefore unique within the genus. This bulb type displays a diverse range of tunics aestivation. A unique convolute aestivation of the tunics was observed in *O. pulchella*. *O. urbaniana* has a concentric aestivation, whereas the other members have an equitant aestivation of the tunics.

From morphological observations, angular tunics appear to be formed in different ways in the species that share this character. Outward folding and excessive growth in specific longitudinal regions of the leathery tunics form the angular wings of *O. lichenoides*. Tunics of *O. obtusa* are different in having a deeply pitted texture with longitudinally angled wings (Figure 4.5). The wings of *O. obtusa* are not raised as high as in *O. lichenoides*. *O. urbaniana* differs from both of the above-mentioned species in having both a membranous tunic and an angular tunic in the same bulb and the latter has a corky texture (see description in chapter 3).

As mentioned almost all of the members of this group, except *O. pulchella*, have bulbels attached to their rhizomes. *O. adpersa* is the only species outside of this bulb type that

displays this character. The bulbels produced by *O. adspersa* and *O. urbaniana* are organized in an identical way. They are produced on vertical stolons or droppers. Each node of the dropper produces conical calyptrate scales that cover the apex of the bulbels successively. Although *O. adspersa* thus shows an affinity to this group (based on the presence of the bulbels), it differs considerably in having a different tunic structure and a different number of fleshy leaves per bulb.

There is probably an affinity between bulb-type 4 and 5, as was outlined in the discussion of bulb type 4.

4. 2. 6 Bulb-type 6 (*O. salteri* type):

Included taxa: *O. salteri*

This bulb type is characterized by perfoliate tunics (Figure 4.6).

The closed tunic bases found in *O. salteri* are similar to the closed concentric tunic aestivation found in *O. viscosa*, *O. tenella* and *O. aridicola*. Likewise, the presence of membranous tunics is shared with members of bulb-type 2 (*O. adspersa*) and bulb-type 10 (*O. viscosa*). This bulb-type thus seems to be most closely related to bulb-types 2 and 10.

4. 2. 7 Bulb-type 7 (*O. oligophylla* type):

Included taxa: *O. oligophylla*

This bulb-type has an intact set of the previous years' dried bulb remains at the base, covered by the present year's bulb tunics (Figure 4.7). Due to this character, the bulb creeps closer to the ground level every year. In addition, the tunics are very narrow, covering only about 15% of the width of the bulb. This type of bulb covering is also observed in other species, but then only after the tunic has split. This bulb-type is also sticky, as in most members of bulb-type 4. But, unlike in the case of members of bulb-type 4, the globular balloons (secreting cells) cannot be observed after soaking the tunic in benzene. This treatment revealed the presence of these cells on the tunics of bulb-type 4.

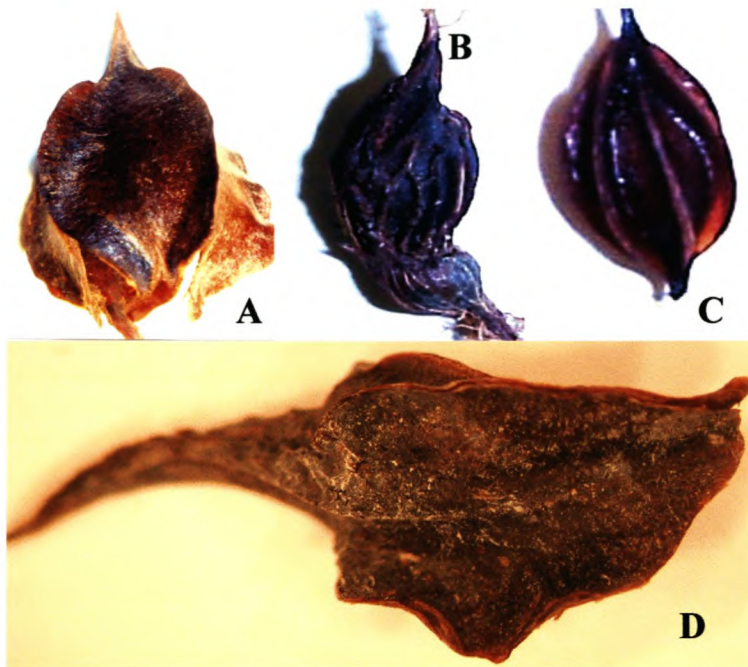


Figure 4.5 Diagnostic characters of bulb-type 4. [A] *O. pocockiae*: angular tunic, [B] *O. obtuse*: irregularly angular tunic [C] *O. urbaniana*: inner angular tunic and [D] *O. lichenoides*: angular tunic.

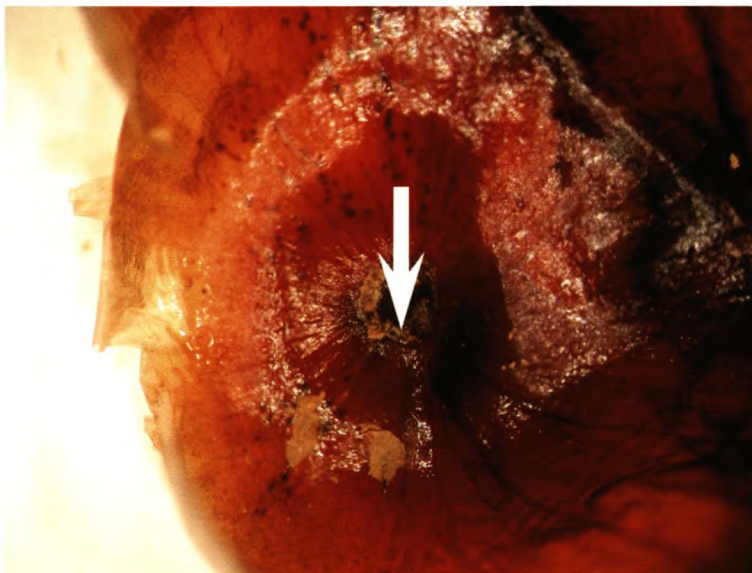


Figure 4.6 Diagnostic characters of bulb-type 6. *O. salteri*: perfoliated tunic base, showing the attachment to the bulb axis. The arrow shows the position of the basal plate.

4. 2. 8 Bulb-type 8 (*O. pes-caprae* type):

Included taxa: *O. commutata*, *O. pes-caprae*, *O. caprina*

The diagnostic characters of this bulb-type are the presence of non-raised longitudinal ridges on the outer surface of the tunics, membranous tunic margins and a wide basal plate (Figure 4.8).

All three species have longitudinally ridged tunics. *O. caprina* and *O. commutata* specifically share the presence of short outermost tunic layers and the presence of a wavy reticulate surface ornamentation between the non-raised longitudinal ridges of the outer tunics. However, the latter character is not observed in *O. pes-caprae*, as the surface ornamentation is unclear in this species. There is also a difference between the tunics of *O. commutata* and those of the other two species. The ridges of *O. commutata* are spaced more widely apart.

This bulb-type comprises different bulb shapes. *O. pes-caprae* has a conical bulb, *O. caprina* an oval one, while *O. commutata* has an oblong bulb.

The number of fleshy leaves present in the bulb also differs. *O. caprina* and *O. commutata* have two fleshy leaves per bulb, whereas *O. pes-caprae* has six. Six is also the minimum number of fleshy leaves per bulb for members of bulb-type 2. Bulb-type 8 also shares the presence of a wide basal plate with bulb-type 2. This suggests affinities between bulb-types 2 and 8.

4. 2. 9 Bulb-type 9 (*O. grammophylla* type):

Included taxa: *O. grammophylla*

Bulbs are covered with numerous split tunics with reversed, strigose, thorny hairs on the outer surface (Figure 4.9).

4. 2. 10 Bulb-type 10 (*O. viscosa* type):

Included taxa: *O. viscosa*

Bulbs are covered with wrinkled tunics (Figure 4.10).



Figure 4. 7 Diagnostic characters of bulb-type 7. *O. oligophylla*: [A] bulb showing successive tunic layers consisting of tunics and dried fleshy leaves of a previous year and [B], [C] and [D] are single tunic layers seen from the side, top and bottom respectively.



Figure 4. 8 Diagnostic characters of bulb-type 8. [A] *O. pes-caprae*: tunic with longitudinally ridged outer surface. *O. commutata*: [B] tunic showing similar surface ridges, and widely spaced reticulated ornamentation; [C] tunics showing membranous margin and different tunic sizes.



Figure 4. 9 Diagnostic characters of bulb-type 9. *O. grammophylla*: [A] split tunic and [B] reversed strigose trichomes on the outer surface of the leathery tunic.



Figure 4. 10 Diagnostic characters of bulb-type 10. *O. viscosa*: wrinkled membranous tunic.

Wrinkled tunics also occur in *O. monophylla* (bulb-type 1) and *O. cf. helicoides* var. *helicoides* (bulb-type 2), but in these two species only the basal parts of the tunics are wrinkled. Bulb-type 10 shares a concentric aestivation of the fleshy leaves with some members of bulb-type 3. The presence of narrow membranous margins to the fleshy leaves is also shared with *O. engleriana* and *O. adspersa* of bulb-type 2 subtype B.

4. 3. Comparison of bulb-types to the results of Gebregziabher (2001)

With the bulb-types proposed here used as a basis, the descriptions of the bulbs proposed by Gebregziabher (2001) are re-evaluated to assess their affinities. *O. monophylla*, *O. commutata*, *O. eckloniana* var. *sonderi* and *O. purpurea* were included in the present study, and have thus already been discussed, but *O. tenuifolia* Jacq., *O. dentata* Jacq., *O. truncatula* Jacq., *O. bifida* Thunb., *O. luteola* Jacq., *O. hirta* L. var. *hirta* L. and *O. pocockiae* L. Bolus were only considered in 2001, and need to be incorporated into the proposed system of bulb types.

O. tenuifolia has fusiform bulbs with narrow basal plates and membranous and leathery tunics in the same bulb. These characters match the diagnosis of bulb-type 4. Like in most members of bulb-type 4, the tunics of *O. tenuifolia* are also sticky. However, the tunic layering pattern of *O. tenuifolia* differs from that of members of bulb-type 4. The inner layers of the bulb of *O. tenuifolia* have a membranous texture, while the outer layers have alternately arranged leathery and membranous tunics.

O. dentata has spheroid bulbs with narrow basal plates, longitudinally ridged tunics with wide membranous margins, and six to nine fleshy leaves per bulb, each with narrow membranous margins. These bulb characters match the bulb characters of bulb-type 8 species, except for the narrow basal plates.

The bulbs of *O. truncatula* have smooth, non-sticky membranous tunics with sessile bases and an equitant aestivation, five fleshy leaves with sessile bases and narrow membranous margins and wide basal plates. These bulb characters resemble those of bulb-type 2. Although the bulb of *O. truncatula* is different in its tunic aestivation, it is assigned to bulb-type 2, subtype B.

O. bifida has spheroid bulbs, with loose membranous tunics that are covered with capitate and setose trichomes, and arranged in an equitant aestivation. The three to five fleshy leaves present have orange apices and narrow membranous margins. The basal plate is wide. The presence of trichomes on the tunics of *O. bifida* shows a resemblance to bulb-type 9, although the type of trichomes differs. Most characters of *O. bifida* bulb are similar to the characters of bulb-type 2 sub-type B. So it is placed within this latter type. The coloured apices of the fleshy leaves are similar to the fleshy leaves of *O. tenella* and *O. oreophila* (bulb-type 3). This again highlights an affinity between bulb-types 2 and 3.

The sticky bulb of *O. luteola* has an oval to spheroid shape, with both membranous and leathery tunics arranged in alternate layers. The tunic layers have trichomes at their apices and an equitant aestivation. The two fleshy leaves present lack membranous margins and the basal plate is narrow. Ignoring the tunic arrangement, the bulb of *O. luteola* is very similar to the bulb of *O. purpurea* and is therefore assigned to bulb-type 4. Like the sticky-bulb members of bulb-type 4, the sticky tunics of *O. luteola* display the globular balloons/secretory cells on their outer surfaces after soaking in benzene.

O. hirta var. *hirta* has spheroid bulbs, very thin membranous tunics, six brown fleshy leaves with wide membranous margins and a wide basal plate. All these characters are typical of bulb-type 2 and therefore *O. hirta* var. *hirta* is assigned to this bulb-type.

O. pocockiae is described under the project numbers MO 35, MO 32 and MO 37 (Gebregziabher, 2001). These specimens have oblong to fusiform bulbs, each with angular tunics that have two different widths per layer, a single fleshy leaf with narrow membranous margins and a narrow basal plate. The number of fleshy leaves, the angular tunics and the narrow basal plate of *O. pocockiae* correspond well with the bulbs of *O. lichenoides*. This bulb-type is therefore allocated to bulb-type 5.

4. 4. An evaluation of the current taxonomic classification, the palynology and the non-coding plastid *trnL-F* data with respect to bulb morphology

In this section, the available morphological, palynological and molecular data of the southern African *Oxalis* species is evaluated and compared to the classification based on bulb

Table 4.1. A classification of the bulb-types compared to Salter's (1944) classification, palynological results (Dreyer 1996) and the preliminary results of the *trnL-F*-based DNA sequence data (Oberlander 2003).

Bulb type	Sub-types	Member species	Salter's classification		Dreyer's Pollen type	Oberlander (2003) <i>trnL-F</i> phylogeny
			Sections	Subsections		
1	--	<i>O. monophylla</i>	<i>Unallocated</i>	--	C 10	Clade III
		<i>O. oculifera</i>	<i>Latifoliolatae</i>	--	C 10	Clade III
2	A	<i>O. cf. callosa</i>	<i>Latifoliolatae</i>	--	D 1	Not studied
		<i>O. hirta</i> var. <i>hirta</i>	<i>Angustatae</i>	<i>Sessilifoliatae</i>	D 1	Clade IV _B
		<i>O. hirta</i> var. <i>tubiflora</i>	<i>Angustatae</i>	<i>Sessilifoliatae</i>	D 4	Clade IV _B
		<i>O. linearis</i>	<i>Angustatae</i>	<i>Lineares</i>	D 3	Clade IV _B
		<i>O. cf. helicoides</i> var. <i>helicoides</i>	<i>Angustatae</i>	<i>Lineares</i>	D 1	Clade IV _B
	B	<i>O. engleriana</i>	<i>Angustatae</i>	<i>Multifoliolatae</i>	C 6	Clade IV _A
		<i>O. adspersa</i>	<i>Angustatae</i>	<i>Xanthotriche</i>	C 10	Clade III
		<i>O. truncatula</i>	<i>Oppositae</i>	<i>Subintegrae</i>	C 2	Clade IV _A
		<i>O. bifida</i>	<i>Oppositae</i>	<i>Bifurcatae</i>	C 2	Unresolved in Clade IV
	3	A	<i>O. eckloniana</i>	<i>Sagittatae</i>	--	A
<i>O. xantha</i>			<i>Angustatae</i>	<i>Lineares</i>	D 1	Clade IV _B
<i>O. oreophila</i>			<i>Angustatae</i>	<i>Lineares</i>	D 1	Clade IV _B
<i>O. tenella</i>			<i>Latifoliolatae</i>	--	D 1	Clade IV _B
<i>O. aridicola</i>			<i>Latifoliolatae</i>	--	D 1	Clade IV _B
B		<i>O. campylorrhiza</i>	<i>Latifoliolatae</i>	--	C 8	Clade III
4		<i>O. purpurea</i>	<i>Stictophyllae</i>	--	C 3	Clade III
		<i>O. luteola</i>	<i>Oppositae</i>	<i>Subintegrae</i>	C 2	Clade III
		<i>O. tenuifolia</i>	<i>Angustatae</i>	<i>Sessilifoliatae</i>	C 8	Clade IV _F
		<i>O. versicolor</i>	<i>Angustatae</i>	<i>Lineares</i>	C 8	Clade IV _F
		<i>O. stenopetala</i>	<i>Angustatae</i>	<i>Lineares</i>	C 7	Clade IV _F
		<i>O. ebracteata</i>	<i>Angustatae</i>	<i>Glandulosae</i>	C 8	Clade IV _F
5		<i>O. lichenoides</i>	<i>Foveolatae</i>	--	C 2	Clade III
		<i>O. pocockiae</i>	<i>Foveolatae</i>	--	C 2	Clade III
		<i>O. pulchella</i>	<i>Foveolatae</i>	--	C 3	Clade III
		<i>O. obtusa</i>	<i>Oppositae</i>	<i>Subintegrae</i>	C 3	Clade III
		<i>O. dregei</i>	<i>Campanulatae</i>	--	C 10	Clade III
		<i>O. urbaniana</i>	<i>Angustatae</i>	<i>Sessilifoliatae</i>	C 8	Clade IV _F
6		<i>O. salteri</i>	<i>Crassulae</i>	--	C 10	Clade III
7		<i>O. oligophylla</i>	<i>Angustatae</i>	<i>Lineares</i>	C 8	Clade IV _D
8	A	<i>O. pes-caprae</i>	<i>Cernuae</i>	<i>Eu-cernuae</i>	C 2	Clade II
		<i>O. dentata</i>	<i>Cernuae</i>	<i>Livida</i>	C 3	Clade II
		<i>O. caprina</i>	<i>Cernuae</i>	<i>Stellatae</i>	C 7	Clade III
	B	<i>O. commutata</i>	<i>Latifoliolatae</i>	--	C 10	Unresolved clade with Clade II, III & VI
9		<i>O. grammophylla</i>	<i>Angustatae</i>	<i>Pardales</i>	C 2	Clade IV _E
10		<i>O. viscosa</i>	<i>Angustatae</i>	<i>Sessilifoliatae</i>	C 2	Clade III

morphology. The three main datasets that will be discussed relative to the bulb morphology are the (1) Morphological classification by Salter (1944), (2) Palynological classification by Dreyer (1996) and (3) Preliminary *trnL-F* based molecular phylogeny by Oberlander (2003). These comparisons are summarized in Table 4.1.

4. 4. 1. Morphological classification (Salter, 1944)

Salter (1944) grouped the southern African *Oxalis* species into eleven sections. Two sections comprise introduced species and the remaining nine consist of species native to southern Africa. Of the nine native sections proposed by him, only four are regarded as natural sections, while the delimitation of the remaining five sections is regarded as doubtful. Section *Latifoliolatae* can be regarded as the most artificial of them all. Section *Angustatae* has only two subsections, subsection *Pardales* and subsection *Xanthotrichae*, which are regarded as natural units. The remaining four subsections are viewed as artificial. Subsections *Sessilifoliatae* and *Lineares* appear to consist of many diverse and unrelated species. In section *Oppositae*, subsection *Subintegrae* is thought to be artificial, while subsection *Bifurcatae* can probably be regarded as a natural unit (Salter, 1944).

When the classification based on bulb morphology is compared to Salter's (1944) morphological classification, one finds that section *Latifoliolatae* includes bulb-types 1, 2A, 3, and 8B (Table 4.1), section *Oppositae* subsection *Subintegrae* includes bulb-types 2B, 4 and 5, section *Angustatae* subsection *Lineares* includes bulb-types 2A, 3A, 4 and 7 and subsection *Sessilifoliatae* includes bulb-types 2A, 4, 5, and 10. This highlights the artificial delimitation of these sections and subsections. On the other hand, the three species studied of section *Foveolatae* have all the same bulb-type, supporting its delimitation as a natural taxon. Sections *Crassulae* and *Angustatae* subsection *Pardales* are both represented by a single species, so nothing can be deducted about bulb-type diversity in these taxa.

4. 4. 2. Palynology (Dreyer, 1996)

The palynological study of Dreyer (1996) identified four pollen types amongst southern African *Oxalis* species. Pollen type A has a rugulate-reticulate tectum with suprategical

spinules. This type is exclusive to section *Sagittatae*. A single species, *O. fibrosa* Bol. f., has pollen of the B type. This pollen type exhibits a micro-rugulate tectum with suprategal spines. The majority of *Oxalis* species have pollen of the type C, which has a micro-reticulate to reticulate tectum. Pollen type C is divided into 15 subtypes. Pollen type D displays a supra-areolate tectum. Species with this pollen type are dispersed through sections *Latifoliolatae* and *Angustatae* subsections *Sessilifoliolatae* and *Lineares*.

Palynology agrees with bulb type 1 delimitation as both species studied have pollen of the type C10. Palynology also supports the delimitation of bulb type 2A, as all the included taxa of this bulb type have supra-areolate pollen of the type D. Bulb type 2B appears to be unrelated to bulb type 2A based on pollen evidence, as bulb type 2B includes species with reticulate pollen of the type C. Bulb type 3A is palynologically almost homogenous, with all but one species, *O. eckloniana*, displaying supra-areolate pollen. Again, palynology questions the affinity between bulb types 3A and 3B, as the latter bulb type has unrelated reticulate pollen of the type C8. Bulb types 4, 5 and 8 appear to be palynologically rather homogenous, with all three bulb-types including species with reticulate pollen of the subtypes C2, C3, C7 and C8. Dreyer (*pers. com*) regards these latter subtypes to be very closely related. So by and large, palynology is congruent with the bulb type delimitation in these three bulb types. The only consistent exception applicable to all these three bulb types is that they each include one taxon with pollen of the subtype C10. This is problematic, as C10 pollen is quite dissimilar to the other four pollen types (C2, 3, 7 and 8). As bulb types 6, 7, 9 and 10 include a single taxon each, nothing can be said about the congruence between bulb types and palynology in these instances.

Species in bulb-type 3A have pollen of the type D1. Similarly, species in the bulb-type 2 group also represent pollen-type D. A possible bulb morphological character that links these two groups together is the modification of the tunic base, which can be either in the form of finger-like projections at the base of the tunics or tunic bases with longitudinal undulations. Although *O. oreophila* and *O. tenella* were allocated to bulb-type 3A, they both have characters intermediate between bulb types 2 and 3.

The species with pollen type C8 and C7, excluding *O. caprina* and *O. oligophylla*, share the presence of a membranous and a leathery tunic in a single bulb. Species with pollen subtypes

C2 and C3 are associated in bulb-type 2B, 4, 5, 8, 9 and 10, and there are no clear bulb characters that bind them together.

Palynology can be used to divide the bulb-types into two major groups. The first group consists of bulb-types 1 and 4–10, which include taxa with pollen type C. The second group consists of bulb-types 2 and 3, which predominantly include taxa with pollen type D, although a few members with pollen type A and C are also included here.

4. 4. 3. Molecular *trnL-F* data (Oberlander, 2003)

Oberlander (2003) completed a molecular study based on plastid non-coding *trnL-F* sequence data of 74 southern African *Oxalis* taxa, including four species from different genera in the family *Oxalidaceae* as outgroup taxa. Parsimony analysis was used to reconstruct a phylogenetic tree. The main focus of this study was to assess the monophyly of section *Angustatae* subsection *Lineares*. Therefore sampling was biased to address this question although each section and subsection, as proposed by Salter (1944), was represented. The naturalized weedy American species, the creeping *O. corniculata* L. and the bulbous *O. latifolia* H.B.K., were also included. Although not a perfect species-level phylogeny for southern African *Oxalis*, this work can to some extent be used for comparative purposes here.

Both the genus *Oxalis* and the southern African members of the genus were found to be monophyletic. This southern African *Oxalis* clade forms a basal polytomy with four weakly supported monophyletic branches. For convenience's sake, the author assigned roman numbers to the major clades, and alphabetical letters for the internal monophyletic sub-clades (Figure 4.11). Therefore, Clades IV_A, IV_B, IV_C, IV_D, IV_E and IV_F are monophyletic clades within the basal polytomy of Clade IV. Clades IV_B, IV_C and IV_D are sub-clades that all have more than 90% bootstrap support. These results suggested that section *Angustatae* subsections *Lineares* and *Sessilifoliolatae* represent artificial groupings. Additionally, the sub-groupings within subsection *Lineares* were found to be polyphyletic.

The choice of specimens used for the current study was based on specimens used in the molecular study. Hence, out of the 74 taxa included in the molecular study, 36 were chosen for detailed bulb morphological analyses, and thus used to define the bulb-types. In Figure

4.11, species included in the current study are indicated by bold print in the Oberlander (2003) phylogenetic reconstruction.

When bulb morphological characters are plotted onto this tree, it does not show exact congruence with any of the major monophyletic clades (I, II, III and IV). However, bulb morphology supports some of the sub-clades within the major clades. For example, species from Clade III appear in eight of the ten bulb-types. *O. adspersa* and *O. campylorrhiza* though, can not represent the bulb types, because they are just affiliated to the core group of bulb type 2 (sub-type A) and 3 (sub-type A) respectively, each with a single representative species (Table 4.2). Similarly, species from Clade IV occur in six of the bulb-types.

There are both congruent and non-congruent bulb associations for the internal nodes of the weakly supported Clade III. For example, *O. luteola*, *O. purpurea* and *O. melanosticta* Sond. form a monophyletic clade supported by 95% BS. This is supported by bulb morphology as both *O. luteola*, and *O. purpurea* belong to the bulb-type 4. In contrast, members of bulb-type 5 come out in an unresolved node with the monophyletic polytomy of *O. luteola*, *O. melanosticta* and *O. purpurea* clade. The other members of bulb-type 4 come out in Clade IV_F. A similar combination of Clade IV_F and III is also observed in bulb-type 5, where Clade IV_F is represented only by *O. urbaniana*. As explained when the bulb types were delimited, this species has an affinity to bulb-type 4 in possessing two different types of tunics in the same bulb. The presence of species from bulb-type 6 and 10 in this clade is interesting, as these suggest that they are probably related. The integrity of bulb-type 1 is supported by the inclusion of both species studied in clade III. Although they do not result in the same sub-clade, more sampling is likely to solve this problem.

The internal branches of Clade IV are mostly congruent with the bulb morphology. For example, bulb-types 7 and 9 are exclusive to Clade IV_D and IV_E, respectively. The majority of species belonging to the bulb-type 4 resolved in Clade IV_F. However, as discussed above, the rest of the members of this bulb-type resolved in Clade III (Table 4.2). Similarly *O. truncatula* and *O. engleriana* are affiliated to bulb-type 2 and congruently resolved in Clade IV_A. Conversely Clade IV_B includes members of two bulb-types, namely the core members of bulb-types 2 and 3B. Both of these bulb-types share the presence of modified tunic bases and a spotted tunic surface.

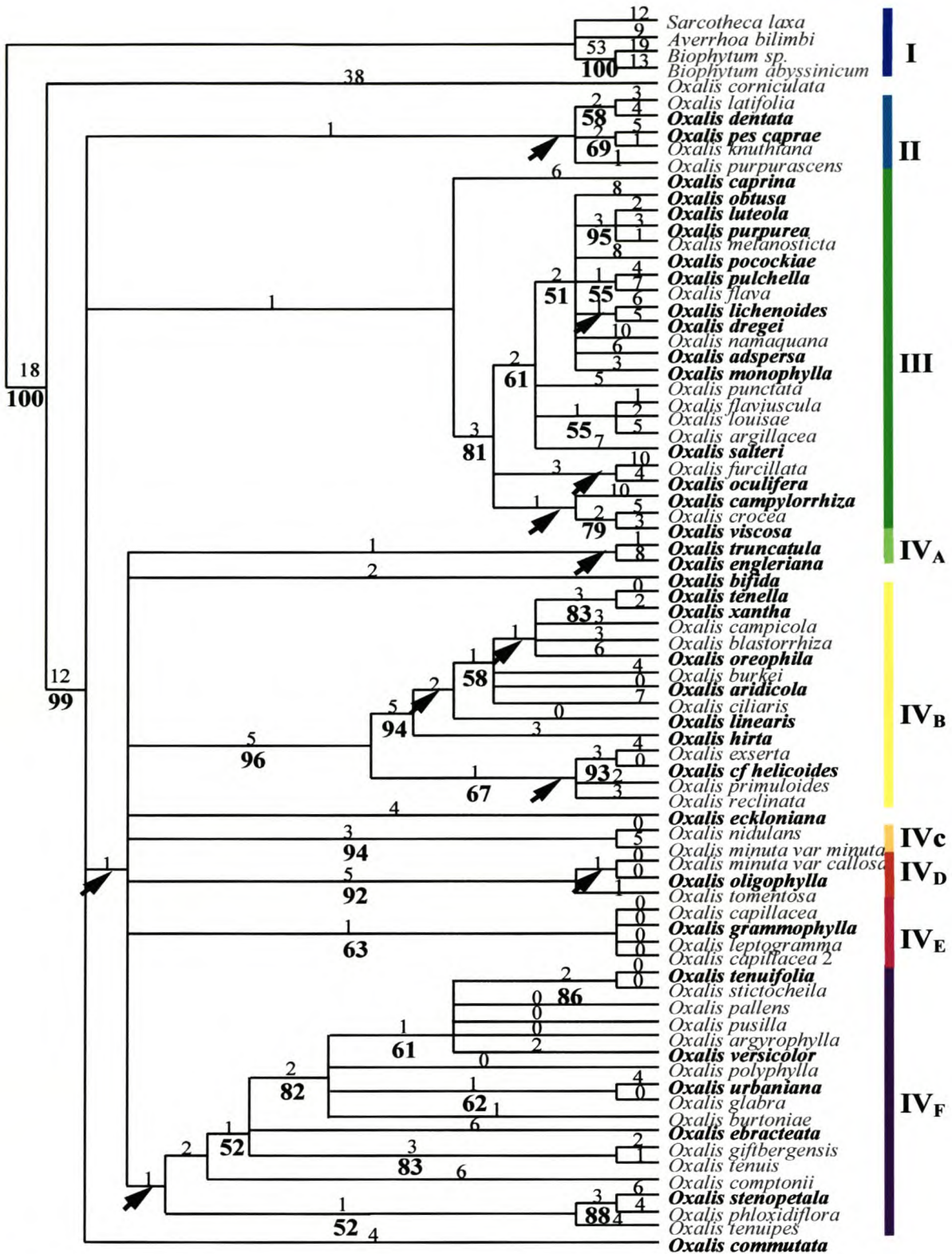


Figure 4.11 One of 9890 equally most parsimonious trees based on non-coding plastid *trnL-trnF* data. Figures above the branches indicate branch lengths, whilst figures in bold beneath the branches refer to bootstrap percentages. Arrows indicate nodes that collapse in the strict consensus of 9890 trees. (Figure taken from Oberlander (2003)). Bold prints indicate species included in the current study.)

O. dentata and *O. pes-caprae* resolved in Clade II and both of them belong to bulb-type 8. The other members of bulb-type 8 resolve together in Clade III and in unresolved positions within the Clades II, III and IV. Members of this bulb type thus seem to be unrelated.

In summary, the bulb morphological classification is thus largely congruent with the monophyletic sub-clades in Clade IV. In contrast, the internal clades of Clade III show little congruence with bulb morphology. Since the main focus of the molecular study was on section *Angustatae* subsection *Lineares* and not on all the southern African *Oxalis* species, most of the studied species resolved in Clade III, the clade that binds most of the poorly represented taxonomic groups together. Until a more comprehensive, inclusive species-level phylogeny is available, affinities of taxa within this clade thus remain unclear, and no final deductions should be made now.

4. 4. 4. Summary and comparison of the congruence between bulb morphological, morphological, palynological and molecular datasets

In this section, the ten different bulb types are individually discussed and compared in terms of the morphological, palynological and molecular datasets.

Bulb-type 1 includes two species, one from section *Latifoliolatae* and the other one unplaced by Salter (1944). They share the same pollen type (C10) (Dreyer 1996), and both resolve in Clade III in the *trnL-F* based molecular phylogeny of Oberlander (2003). This bulb-type is thus strongly congruent with most other datasets.

Bulb-type 2 has been divided into two sub-groups, 2A and 2B. Sub-group 2A includes the core members of this bulb-type, and includes four taxa from section *Angustatae* and one taxon from section *Latifoliolatae*. Of the four taxa from section *Angustatae*, two reside in subsection *Lineares*, while the other two belong to subsection *Sessilifoliolatae*. All of the taxa in type 2A have pollen type D, and all resolve together in Clade IV_B (Oberlander, unpublished data and Oberlander, 2003). Although the delimitation of this bulb-type conflicts with the morphological classification, it is congruent with the palynological and molecular datasets.

Bulb-type 2B includes species of which the bulb morphology appears to be affiliated with species in bulb-type 2A, but for which this match is not perfect in terms of all characters (see

section 4.2.4 above). This bulb-type includes four taxa, two from section *Angustatae* and the other two from section *Oppositae*. Of the two taxa in section *Angustatae* one is from subsection *Multifoliolatae* and the other one from *Xanthotriche*. Similarly, of the two species from section *Oppositae*, one belongs to subsection *Subintegrae* and the other to subsection *Bifurcatae*. The two species from section *Oppositae* have pollen of the type C2 and those from section *Angustatae* have pollen types C6 and C10 respectively. With the exception of the species from subsection *Xanthotriche*, all the other species resolved in Clade IV. Within this clade, two species are placed together in sub-clade IV_A, while *O. bifida* is excluded. This bulb sub-type is thus reasonably supported by molecular data, but conflicts with morphological and palynological data.

Bulb-type 3 is also divided into two sub-groups, 3A and 3B. Sub-group 3A includes the core members of bulb-type 3, which include two species from section *Angustatae* subsection *Lineares*, two species from section *Latifoliolatae* and one species from section *Sagittatae*. With the exception of *O. eckloniana*, all species have pollen type D1 and resolved in Clade IV_B. The core group of bulb type 3 therefore is largely congruent with both the palynological and molecular datasets, but conflicts with the morphological dataset. Bulb-type 3B is affiliated to the core group of bulb type 3A and consists of only one species from section *Latifoliolatae*. This species has pollen type C8 and resolved in Clade III, which is incongruent to the core group.

Bulb-type 4 includes four species from section *Angustatae*, one species from section *Oppositae* subsection *Subintegrae* and another species from section *Stictophyllae*. Of the species included from section *Angustatae*, two reside in subsection *Lineares*, while the other two belong to subsections *Sessilifoliatae* and *Glandulosae* respectively. Three of the species from section *Angustatae* have pollen type C8 and *O. stenopetala* has pollen type C7. These four species resolved in Clade IV_F. On the other hand, the two species from section *Oppositae* and section *Stictophyllae* have pollen types C2 and C3 respectively, and both of them resolved in Clade III. Therefore bulb type 4 reveals a low degree of congruency with the morphological, molecular and palynological data.

Bulb-type 5 includes three species from section *Foveolatae*, one species from section *Oppositae* subsection *Subintegrae*, another species from section *Campanulatae* and another species from section *Angustatae* subsection *Sessilifoliatae*. With the exception of *O.*

urbaniana, all resolved in Clade III. All species have pollen of the type C, but the subtypes vary between C2, C3, C10 and C8. With the exception of pollen type C10, all of the other pollen subtypes are thought to be related. So this bulb-type agrees both with the molecular phylogeny and palynology, but shows little congruence with the morphological classification.

Bulb-type 8 includes three species from section *Cernuae* and one species from section *Latifoliolatae*. Section *Cernuae* is represented by a single species each from subsections *Eucernuae*, *Lividae* and *Stellatae*. All of the included species have pollen type C, but each of them with a different subtype. Pollen subtypes C2, C3 and C8 are thought to be closely related, but dissimilar to pollen subtype C10. Two species of the section *Cernuae* resolved in Clade II, one of them in Clade III and the species from section *Latifoliolatae* is unresolved. Thus, this bulb-type is not very congruent with the molecular phylogeny or palynology datasets.

The remaining four bulb types are unique, but it must be kept in mind that each type is represented by a single species. Bulb types 7 and 9 resolved in Clade IV_D and IV_E respectively. They are also the only representatives of these clades in the current study. Both the remaining two bulb-types, bulb-type 6 and 10, resolved in Clade III.

CONCLUSION

Although the detailed bulb morphology of only a relatively small sample of species was examined here, significant bulb morphological variation was detected. The number of fleshy leaves per bulb, nature of the tunics, basal plate morphology and to some extent rhizome characters proved to be very variable between species, and formed the basis for the delimitation of the ten bulb-types. The inclusion of more species is likely to increase the number of bulb types recognized in the genus, but may also help to clarify some of the more diverse bulb types (e.g. bulb type 5). Such further studies may also help to clarify the association and affinities between the sub-types of bulb types 2 and 3.

Although many potentially informative characters were listed along with clear character states, the ratio between character number and species number was not sufficient to reconstruct a significant morphological phylogeny. It is, however, strongly suggested that these characters (with their defined states) be included in future morphological cladistic analyses of the southern African member of *Oxalis*. It is highly likely that more informative characters (and/or states) may be added to this list once the bulb morphology of more species are analyzed. I am also convinced that an anatomical assessment of bulb characters will contribute significantly to the systematics of this genus. In this regard, I suggest that bulbs of different ages be evaluated and compared.

The bulb morphological variation found in the present study compares surprisingly well with both pollen and molecular datasets. Previous studies have already revealed a strong affinity between palynological and DNA based results (Oberlander *et al.*, 2003), and based on the preliminary results presented here, bulb morphology appears to corroborate this. Tunic base modification and the presence of clusters of inflated cells on the outer tunics surfaces were found to be a potential morphological synapomorphy for the well-supported monophyletic clade that includes all taxa with D-type pollen. Similarly, the presence of tunics with more than one texture type per bulb may prove to be synapomorphic for the core-*O. glabra* clade.

Palynology, preliminary *cp*-DNA-based phylogenetic reconstruction and now also bulb morphology, seriously question the validity of the current morphological taxonomy of the

southern African members of *Oxalis*. Although all three of these data sources do agree with at least some of the Salter (1944) sections, they all conflict with other parts of this classification. Bulb morphology principally support the delimitation of sections *Cernua* (but not of the subsections included within) and *Foveolatae* (to some extent). The most serious conflicts in terms of all three the more recent datasets (including bulb morphology) revolve around the delimitations of sections *Latifoliolatae* and *Angustatae*.

Based on the bulb morphological results obtained in the present study, it is strongly recommended that bulb morphology be seriously considered in future taxonomic classifications of this large and interesting Cape genus.

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