DREYER, LéANNE LAURETTE

A PALYNOLOGICAL REVIEW OF OXALIS (OXALIDACEAE) IN SOUTHERN AFRICA

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A palynological review of *Oxalis* (Oxalidaceae) in southern Africa

by

LÉANNE LAURETTE DREYER

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CHAPTER 1
INTRODUCTION

The Oxalidaceae is predominantly confined to the tropical and subtropical regions of Asia, Africa and Central and South America, with relatively few representatives in the more temperate regions of the world.

Most modern systems of classification include the Oxalidaceae as one of the primitive families in the Geraniales. Other families included in this order are Geraniaceae, Limnanthaceae, Tropaeolaceae and Balsaminaceae (Cronquist 1981); Geraniaceae, Lepidobotryaceae, Hypseocharitaceae and Biebersteiniaceae (Takhtajan 1980); Geraniaceae, Zygophyllaceae, Erythroxylaceae, Balanitaceae, Humiriaceae, Linaceae and Lepidobotryaceae (Dahlgren 1983) and Geraniaceae, Balsaminaceae, Tropaeolaceae and Limnanthaceae (Thorne 1983). There is general agreement that the Oxalidaceae, Geraniaceae and Balsaminaceae are related, with the affinity between the Oxalidaceae and the Geraniaceae being the strongest (Robertson 1975).

Controversy prevails as to which genera should be included in the Oxalidaceae. Traditional oxalidaceous genera include *Biophytum* DC. (70 species), *Oxalis* L. (*ca*. 800 species), *Averrhoa* L. (2 species), *Sarcotheca* Blume (11 species), *Dapania* Korth. (3 species), *Lepidobotrys* Engl. (1 species) and *Hypsocharis* Remy (9 species) (Boesewinkel 1985). Knuth (1930) includes these seven genera along with *Eichleria* (2 species). Hutchinson (1959) places *Averrhoa* in the Averrhoaceae with the Rutales, while *Dapania* and *Sarcotheca* are referred to the Lepidobotryaceae in the Malpigiales. Chant (1978, 1993) restricts the genera in the Oxalidaceae to *Oxalis*, *Biophytum* and *Eichleria* and includes *Sarcotheca* and *Averrhoa* in the Averrhoaceae. *Hypsocharis* and *Lepidobotrys* are poorly known and their affinities uncertain. Some authors place them in the monotypic families Hypsocharitaceae and Lepidobotryceae. The genus *Hypsocharis* has been suggested as the link between the Oxalidaceae and the Geraniaceae (Veldkamp 1971).

This uncertainty concerning the taxonomic status and true affinities of oxalidaceous genera and families can only be resolved once more detailed information is available for all of the genera concerned. For the present most authors seem content to define the Oxalidaceae to include the genera *Oxalis* (type genus), *Biophytum*, *Dapania*, *Sarcotheca*, *Averrhoa*, *Hypsocharis* and *Lepidobotrys* (Veldkamp 1971; Robertson 1975; Lourteig 1979; Cronquist 1981; Boesewinkel 1985).

Oxalis is by far the largest and the most widespread genus in the family. It displays two centres of diversity, one in southern Africa and another in South America. Only a few weedy species, including *O. acetocella* L., *O. latifolia* H.B.K. and *O. corniculata* L., are cosmopolitan, extending into Europe, Asia and Australia (Marks 1956).

Oxalis is particularly well represented in southern Africa, with 210 species (270 taxa) recorded from South Africa (Dreyer 1993). Bayer (1992) gives a detailed account of the distribution of the group within this region. The genus extends from Namibia in the north (eight species) (Schreiber 1967), progressively increasing in numbers southwards into the winter rainfall region of the southwestern Cape. Here it proliferates, forming a distinct centre of diversity with more than 170 species. There is a slight eastern extension of range into the summer rainfall area, with 12 species recorded from the Eastern Cape region. Only 16 species have a wider southern African distribution.

Despite the large size of the genus, very few taxa are being utilised by man. The stems and leaves of some species (e.g. *O. pes-caprae* L.) are eaten (Chant 1993), while others such as *O. corniculata*, *O. latifolia* and *O. caprina* L. are well-known weeds. The weedy nature of *O. corniculata* has been especially well-studied and documented. It is renowned in Europe as an aggressive garden, lawn and greenhouse pest, control of which is complicated by various unique features. It is an extremely variable species complex with numerous ecotypes (Eiten 1963; Lourteig 1979). Additionally it has a highly efficient reproductive system, retaining the ability to outcross while normally reproducing vegetatively (Holt 1987). Although largely unexploited, the genus has considerable horticultural potential. Plants are easily propagated, mainly winter flowering and display a wide range of attractive flower colours. The limited commercial use is probably largely due to our poor taxonomic understanding of the group. A historic overview of the taxonomy of the genus, with special reference to the southern African species, is provided in Chapter 2.

Salter (1944) published the most comprehensive revision of the southern African species to date. Unfortunately his work was essentially alpha-taxonomical, containing very little or no information on aspects such as karyology, anatomy, chemotaxonomy, embryology or palynology. An updated revision of *Oxalis* in southern Africa is therefore urgently needed. Due to the size of the genus, however, a comprehensive multidisciplinary approach would be very expensive and time consuming. It seems more practical to study one particular discipline at a time, results of which could be used for integration with future data. In this way evidence from many congruent studies could be superimposed, hopefully resulting in the incremental emergence of a clearer picture.

In recent years palynological data have proved successful in resolving taxonomic problems at various taxonomic levels (Steussey 1990). The developmental history and applications of palynology are discussed in Chapter 3, along with a summary of the palynological information available for the genus *Oxalis*. The most detailed palynological study undertaken in the genus thus far has been that of Huynh (1969a & 1969b). The results of this work clearly emphasised the potential taxonomic value of palynological characters in both the intra- and infrageneric classification of *Oxalis*.

1.1 Objectives

The main objective of the present study was to assess the taxonomic significance of palynological characters in the southern African members of the genus *Oxalis*. To this end light microscope (LM), scanning electron microscope (SEM) and transmission electron microscope (TEM) techniques were employed. Preliminary atomic force microscopy (AFM) analyses were also undertaken to evaluate the significance of this new study method. The following sub-objectives were identified:

- to identify pollen types within the genus.
- to compile keys to the pollen types.
- to provide a descriptive analysis of *Oxalis* pollen.
- to establish the possible effect of tristyly on pollen morphology.
- to investigate aberrant grain formation.
- to compare results of the present study with the palynological findings of previous researchers.
- to compare the palynological groupings with the existing classification of the genus.
- to hypothesise on possible evolutionary trends in the pollen morphology of the genus.
- to compare *Oxalis* pollen with that of other genera in the family Oxalidaceae and with other families in the Geraniales.

1.2 Outline of this study

This investigation starts with a brief taxonomic review of the genus *Oxalis* in southern Africa (Chapter 2). A summary of the main taxonomic contributions to date is followed by discussions on current problems with the classification of *Oxalis* in southern Africa. Chapter 3 (Palynological review) provides a review of the palynological work done in the genus to date. Chapter 4 (Material and Methods) summarises the sources of material, explains how material was prepared for analysis and how the different analyses were conducted. Material used in the LM and SEM studies are summarised in Table 4.1, while Table 4.2 summarises the material used for TEM and AFM studies. Chapter 5 (Character analysis) can be considered the core of the present study. Here the palynological features of the genus are discussed, evaluated and interpreted under separate headings. The chapter includes the important Table 5.3, which compares palynological results with the current taxonomic classification of *Oxalis*. Although this table is also referred to in Chapters 6 and 7, it was included in Chapter 5 for easy reference. Chapter 6 provides keys to the pollen types and subtypes identified in Chapter 5. This is followed by formal descriptions of the 21 pollen types found in the genus. Palynological results are discussed under five different headings in Chapter 7, starting with an introduction in which the structure of the discussion is clearly outlined. The conclusions that could be drawn from the present study are summarised under separate headings in Chapter 8. This is followed by a summary in both English (Chapter 9) and Afrikaans (Chapter 10), a reference list (Chapter 11), acknowledgements (Chapter 12) and a short Curriculum Vitae (Chapter 13). Preliminary AFM results are provided as an Appendix at the end of the study.

CHAPTER 2
TAXONOMIC REVIEW

2.1 Historical contributions

The genus name *Oxalis*, derived from the Greek words for "acid" and "salt", was first used by Linnaeus. He described an initial eight species (Linnaeus 1753), with an additional five added by his son (Linnaeus f. 1781).

Jacquin (1795) gave the first comprehensive account of the genus, publishing a total of 78 detailed specific descriptions with accompanying colour plates. An unfortunate shortcoming of his work is the failure to recognise heterostyly, resulting in stylar morphs of the same species being described as separate species. His work was also largely based on cultivated material.

Savigny (1797) added three new species in his dissertations on the genus, followed by a new species described by De Candolle (1824).

Sonder (1860) upheld 108 species (47 newly described) in his rather comprehensive account of the southern African members of the genus. Many of his names have subsequently been reduced to synonymy.

The work of Knuth (1930) is significant mainly because it is a comprehensive generic treatment, including taxa from all over the world. Taxonomically it is not held in very high regard. Salter (1944) referred to it as "merely a compilation made from *Oxalis* literature amplified by citation, often erroneously, of specimens in the Berlin herbarium". Salter (1944) claimed that this infrageneric classification fails to reflect the natural affinities of species, often resulting in different varieties of the same species being placed in completely different sections.

In 1944 Salter published the most comprehensive revision of the southern African taxa to date. This publication was the culmination of more than 20 years of extensive field work and is based mainly on a detailed study of living material. He described 65 new taxa and acknowledged 208 existing species, including numerous subspecies, varieties and forma. These he arranged into 11 sections and 13 subsections, as far as possible reflecting natural affinities.

Ornduff (1973) made the next contribution to the taxonomy of the genus, raising subspecies *O. disticha* Jacq. var. *alba* Salter to specific level as *O. dines* Ornduff.

Bayer (1992) discussed Salter's revision, supplementing it with brief accounts of his own plant collecting activities, including notes on the distribution and variability of certain species. He reduced the 11 species included in the section *Pardalis* to the single species *O. pardalis* Sond. Similarly *O. dentata* Jacq. and *O. laterifolia* Jacq. were reduced to synonyms of *O. livida* Jacq., while *O. urbaniana* Schltr. and *O. callimarginata* Weintroub were synonymized under *O. goniorrhiza* Eckl. & Zeyh.

Oliver (1993) described *O. oculifera* H.E.G. Oliver as a new species and referred it to the section *Latifoliolatae*.

The American members of the genus have been studied in detail by Dr A. Lourteig, resulting in a series of publications (Lourteig 1975; 1979; 1981; 1984; 1988).

2.2 Problems with the classification of *Oxalis* in southern Africa.

Oxalis rates as one of the larger genera in southern Africa and is taxonomically regarded as one of the most problematic groups. Salter (1944) contributed greatly to a better understanding of the genus, but realised the shortcomings of his own work. He regarded his efforts as an incomplete taxonomic revision which should merely be seen as a first step towards a better understanding of this complicated group. Many of the problems concerning Salter's work were highlighted in the review by Bayer (1992). These include:

- Poor geographical coverage of Salter's field collections.
- Inconsistency in taxonomic delimitations, on the one hand recognising broadly defined and highly variable aggregate species ('group-species'), while splitting other species down to subspecies, varieties and forma.
- Limited herbarium material for some taxa. Salter described 13 species which were known to him only from the type material and another 21 species known only from two collections.
- Salter stressed the importance of bulb characters and frequently included these in his keys. This complicates current herbarium identifications, as a large percentage of specimens received for identification lack bulbs.

Numerous additional features obscure our understanding of the taxonomy of *Oxalis*. These include:

- Size of the genus
- Geographical variation
- Aggregate species complexes
- Tristyly
- Complex breeding systems
- Successful vegetative reproduction
- Mimicry
- Limited published research

CHAPTER 3

PALYNOLOGICAL REVIEW

Although the existence of pollen grains has been known since the seventeenth century, palynology as a discipline is fairly young, the term only having been coined by G. Erdtman in 1945. It was boosted by two marked events during it's development; firstly by the invention of the acetolysis method by Erdtman (1952); secondly by the development of the scanning electron microscope some 25 years later. Both of these developments helped establishing palynology as a taxonomically significant study field, the value of which has become so obvious that it is now routinely incorporated in most systematic and evolutionary studies.

Palynological data have proved to be useful at all levels of the taxonomic hierarchy. Results from SEM (revealing external features) tend to be more useful at lower taxonomic levels, whereas those from TEM (revealing internal features) are often more significant at higher levels (Stuessy 1990). Examples of palynology resolving taxonomic problems abound in the literature. Only a few examples, reflecting the value of pollen data on family, tribal and subtribal levels, are mentioned here.

Palynological evidence strongly support the separation of the Bombacaceae and Malvaceae as two distinct families (Humphries 1993). Vezy *et al.* (1988) use pollen data to evaluate the variation within and among the tribes traditionally included in the Rhizophoraceae, resulting in the delimitation of the separate family Anisophylleaceae. Donoghue (1985) recognises two distinct lineages in the palynology of the family Caprifoliaceae *s.l.* and uses this, in combination with morphological features, to question the assumed monophyletic status of the family.

Ferguson & Skvarla (1991) propose, on the grounds of palynological evidence, that the current generic classification in the tribe *Swartzieae* (Papilionoideae: Leguminoseae) and the position of this tribe within the family, should be re-evaluated. Chesselet & Linder (1993) uses pollen data to resolve taxa at the subtribal level in the tribe *Diseae* (Orchidaceae). Johansson (1987) uses pollen morphology to facilitate generic delimitations in the tribe *Morindeae* of the Rubiaceae. In his study of the genus *Psychotria* L. Johansson (1992) applied pollen characters to indicate that the current delimitation of the genus constitutes an artificial arrangement. Although 22 pollen types could be identified within the genus, he is reluctant to propose a new classification using only palynology. He concludes that pollen data can be successfully used to identify related groups of species and should form an integral part of any future taxonomic delimitations of this genus.

Despite the obvious taxonomic value of pollen data, certain cautions must be kept in mind in any palynological study. Muller (1979) views exine structure ultimately to be a compromise between the protective, harmomegathic and reservoir functions it fulfils. The basic structure of the exine is therefore the net product of various selective pressures. This must inevitably have led to widespread parallelism and convergence in grain features.

Previous palynological work on the genus *Oxalis* has largely been restricted to smaller studies on a few taxa, often as part of a Flora treatment for a particular region (Gagnepain 1903; Van Zinderen Bakker & Coetzee 1959; Huang 1966; Raj 1966; Arachi 1968; Banerjee & Barghoorn 1970; Heusser 1971; Oltman 1971; Huang 1972; Oltman 1972; Rao & Tian 1974; Serbanescu-Jitariu *et al.* 1974; Oltman 1975; Kuprionova & Alyoshina 1978; Markgraf & D'Antoni 1978; Pargney 1978; Bir & Sidhu 1981; Mandal & Charda 1981; Weller 1981; Andrew 1984; Lobreau-Callan *et al.* 1984; Ghosh & Verma 1985; Gupta & Sharma 1986; Luque & Candau 1987; Iwanami *et al.* 1988; Durdana & Nair 1989). In 1969, however, Huynh published the results of a very comprehensive palynological study on the Oxalidaceae and some related families (Huynh, 1969a & 1969b). Her study concentrated on *Oxalis*, including 424 species from both the American and African centres of diversity of the genus. For the American taxa, the classification proposed by Knuth (1930) was used, with some determinations and verifications done by Dr A. Lourteig at the Paris Herbarium. Representative species from almost all the American sections were included. For South African taxa, the work by Salter (1944) was used as a basis, including species from all nine his endemic sections.

Huynh (1969a) recognised the marked palynological diversity displayed by *Oxalis* and described four pollen types and 13 subtypes. The main delimiting characters included features such as the presence or absence of a tectum and the number of apertures. Her work clearly emphasised the potential taxonomic value of palynological characters in *Oxalis*, both on specific and supraspecific levels. Unfortunately Huynh restricted her investigations to light microscopy, leaving a wealth of structural features unexplored.

CHAPTER 4
MATERIALS AND METHODS

A total of 570 specimens, representing 270 southern African *Oxalis* taxa were studied palynologically (Table 4.1). Most of the pollen material was collected from specimens at the National Herbarium, Pretoria (PRE), supplemented by material from the Bolus (BOL) and Compton (NBG) Herbaria in Cape Town. A few specimens were also obtained from the Royal Botanic Gardens, Kew (K) and the South African Museum (SAM).

In selecting specimens, the work of Salter (1944) was used as a basis. His meticulous revision of the southern African members of *Oxalis* is the most comprehensive study available and includes a great number of subspecies, varieties and forma. Although the work of Ornduff (1973) and Bayer (1992) is acknowledged, names and taxonomic states proposed by Salter (1944) are retained in the present study. This made it possible to evaluate Salter's (1944) classification and to include the widest possible range of variation. In addition a number of manuscript species identified by Bayer, a newly described species *O. oculifera* E.G.H. Oliver and a few morphologically unique, unidentified specimens from PRE and NBG were included. At least two specimens of each taxon were studied. Due to the large number of misidentified specimens in South African herbaria, selection of material was restricted to either type material or specimens collected or seen by Salter. Where the pollen seemed unique or unusual, an additional two to four specimens were studied for that specific taxon. Additional material from Salter's aggregate species was also included. Anthers were dissected from mature flowers and care was taken to include anthers from both stylar whorls. This ensured that palynological differences associated with tristyly would be detected.

All the taxa included in the present study were awarded taxon numbers which were used throughout the investigation. Where these numbers are referred to in the text, they are supplied in square brackets. Due to the inclusion of subspecies and varieties, this numbering system deviates form the one used by Salter (1944). The reader is therefore cautioned to refer back to Table 4.1 of the present study to avoid confusion. No suitable specimens or pollen material could be found for the following taxa: [20]; [37]; [38]; [44]; [125]; [128]; [129]; [144]; [155]; [157]; [161]; [177]; [184]; [185]; [191]; [248]; [258]; [272]; [273]; [274]; [275]; [276]; [277]; [278].

A pilot SEM study of 12 taxa from eight different sections was conducted. Both acetolysed and unacetolysed material was studied and the results were compared. For acetolysis the standard method proposed by Erdtman (1960) was followed. Due to the large number of specimens, the negligible differences between acetolysed and unacetolysed material and the predominantly introspective nature of the present study, most of the pollen investigated was not acetolysed. Acetolysed material of a few taxa was used only for verification of the different pollen types identified within the genus.

LM

The specimens listed in Table 4.1 were studied by light microscopy. Pollen grains were mounted in glycerine jelly under cover slips sealed with paraffin wax and studied within three days after mounting. At least 20 grains of each taxon were measured with the aid of a Kontron image analyser. Where grain sizes differed between the different stylar whorls, separate measurements were taken.

SEM

The SEM study formed the core of this investigation and included all the specimens listed in Table 4.1. Unacetolysed, dry pollen samples were mounted onto custom made aluminium discs (12 mm diameter, 1 mm thick), using Gold Size oil-modified polymerising resin as glue. The discs were mounted onto brass stubs using Leit-C 1-Conductive Carbon cement. Acetolysed material was dehydrated in 99% ethanol and transferred to aluminium discs mounted on brass stubs, using the method described above. Both acetolysed and unacetolysed material was sputter-coated with a gold-palladium layer. Scanning electron micrographs were taken using a Joel JSM 25S11 scanning electron microscope and Ilford FP4 film. Fixed magnifications were chosen for the micrographs to enable comparisons between different taxa.

TEM

A total of 32 specimens, representing the 21 pollen types identified through SEM results, were selected for the TEM study (Table 4.2). The methods for TEM analysis proposed by Skvarla (1966) were followed, using both acetolysed and unacetolysed material. The material was fixed in a 2.5% glutar aldehyde solution in a 0.075M phosphate buffer (pH 7.4—7.6) for two days. It was then fixed in a watery 0.25% OsO_4 solution for 3 hours, dehydrated in a graded acetone series and embedded in Quetol 652 epoxy resin (Van der Merwe & Coetzee 1992). Ultra-thin sections of the pollen grains were cut using a diamond knife on a Reichert Jung Ultracut E ultra-microtome. The sections were stained with uranyl acetate, lead citrate and toluidin blue and photographed using a Phillips 301A transmission electron microscope.

AFM

The recent introduction of the Atomic Force Microscope (AFM) has extended the range of techniques available to study the morphology of surfaces. As far as known, non-contact mode AFM techniques have only twice before been employed in the study of pollen grains, and proved to be a valuable complementary technique (Rowley *et al.* 1995; Demanet *et al.* 1996). For comparative reasons, the selection of specimens for AFM analysis was restricted to those specimens of which LM, SEM and TEM studies were also undertaken. These specimens are listed in Table 4.2. Pollen grains were acetolysed and mounted onto fine sand paper sections. These sections were attached to steel discs using double-sided tape. The grains were scanned using a Autoprobe CP Atomic Force Microscope. Because of the provisional nature of the AFM scans, these results are not reported in the main part of the thesis, but are included as an Appendix.

The terminology of Punt *et al.* (1994) was followed in the description of pollen characters.

Table 4.1 Summary of the specimens from which pollen material was collected for the present study. Taxon names and taxonomic positions, taxon numbers, collectors and collectors' numbers, herbaria of origin and type status (where applicable) are given. See end of table for an explanation of symbols.

TAXON	**TAXON No.**	**COLLECTOR**	**COLL. No.**	**HERB.**	**TP**
SECTION *CORNICULATAE*					
O. corniculata L.	1.1	Galpin	6302	PRE	—
O. corniculata L.	1.2	Galpin	1970	PRE	—
SECTION *IONOXALIS*					
O. latifolia Humbolt	2.1	Gilmore	1718	PRE	—
O. latifolia Humbolt	2.2	Salter	2677	PRE	—
SECTION *CERNUAE* SUBSECTION *EU-CERNUAE*					
O. compressa L.f. var. *compressa*	3.1	Bolus	12634	PRE	—
O. compressa L.f. var. *compressa*	3.2	Bolus	BH 3811	BOL	—
O. compressa L.f. var. *purpurascens* Salter	4.1	Salter	2503	BOL	X
O. compressa L.f. var. *purpurascens* Salter	4.2	Pillans	7293	BOL	—
O. pes-caprae L. var. *pes-caprae*	5.1	Bolus	7244	PRE	—
O. pes-caprae L. var. *pes-caprae*	5.2	Duthie	1223	BOL	—
O. pes-caprae L. var. *sericea* Salter	6.1	Bolus	3954	PRE	—
O. pes-caprae L. var. *sericea* Salter	6.2	Salter	6602	BOL	—
O. haedulipes Salter	7.1	Esterhuysen	764	BOL	X
O. haedulipes Salter	7.2	Salter	5781	BOL	—
O. copiosa Bol. f.	8.1	Bolus	6653	BOL	X
O. copiosa Bol. f.	8.2	—	BH 19200	BOL	—
O. luederitzii Schinz.	9.1	Schenk	87	PRE	—
O. luederitzii Schinz.	9.2	Dinter	6361	BOL	—
O. knuthiana Salter	10.1	Salter	2569	BOL	X
O. knuthiana Salter	10.2	Bolus	6655	BOL	—
O. schaeferi Knuth	11.1	Dinter	3567	BOL	—
O. schaeferi Knuth	11.2	Dinter	6082	PRE	—
O. dentata Jacq.	12.1	Prior	PRE 56405	PRE	—
O. dentata Jacq.	12.2	Salter	7186	BOL	—
O. lateriflora Jacq.	13.1	Salter	7187	BOL	—
O. lateriflora Jacq.	13.2	Bolus	BH 14566	BOL	—
O. laterifolia Jacq.	13.3	Salter	6593	PRE	—
O. livida Jacq. var. *livida*	14.1	Salter	8377	BOL	—
O. livida Jacq. var. *livida*	14.2	Bolus	BH 20434	BOL	—
O. livida Jacq. var. *altior* Salter	15.1	Schltr.	7964	BOL	—
O. livida Jacq. var. *altior* Salter	15.2	Edwards	106	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. livida Jacq. var. *altior* Salter	15.3	Salter	7350	BOL	X
SUBSECTION *PURPURATAE*					
O. purpurata Jacq.	16.1	Salter	702	PRE	—
O. bowiei Lindl.	17.1	Galpin	9967	PRE	—
O. bowiei Lindl.	17.2	Bolus	BH 19786	BOL	—
O. semiloba Sond.	18.1	Flanagan	1281	PRE	X
O. semiloba Sond.	18.2	Burke	9132	PRE	—
SUBSECTION *COSTATAE*					
O. purpurascens Salter	19.2	Pearson	9600	BOL	X
O. pseudo-cernua Knuth	20.1	Dinter	6231	PRE	—
O. pseudo-cernua Knuth	20.2	Dinter	3568	BOL	—
SUBSECTION *GOETZEA*					
O. davyana Knuth	21.1	Galpin	1010b	PRE	X
SUBSECTION *STELLATAE*					
O. stenorrhyncha Salter	22.1	Salter	2290	BOL	X
O. stenorrhyncha Salter	22.1	Wood	3243	PRE	—
O. stellata Eckl. & Zeyh. var. *stellata*	23.1	Eckl. & Zeyh.	661	PRE	X
O. stellata Eckl. & Zeyh. var. *stellata*	23.2	Marloth	12004	PRE	—
O. stellata Eckl. & Zeyh. var. *glandulosa* Salter	24.1	Salter	8078	BOL	X
O. stellata Eckl. & Zeyh. var. *glandulosa* Salter	24.2	Salter	2397	BOL	—
O. stellata Eckl. & Zeyh. var. *montaguensis* Salter	25.1	Salter	2315	BOL	X
O. stellata Eckl. & Zeyh. var. *gracilior* Salter	26.1	Salter	3175	BOL	X
O. lindaviana Schltr.	27.1	Schltr.	7940	PRE	X
O. dichotoma Salter	28.1	Salter	6720	PRE	X
O. caprina L.	29.1	Salter	3131	PRE	—
O. caprina L.	29.2	Bolus	BH 20112	BOL	—
O. tragopoda Salter	30.1	Salter	6010	BOL	X
O. tragopoda Salter	30.2	Duthie	1219	BOL	—
O. anomale Salter	31.1	Salter	2334	BOL	X
O. anomale Salter	31.2	Salter	2332	PRE	—
SECTION *OPPOSITAE* SUBSECTION *SUBINTEGRAE*					
O. psilopoda Turcz.	32.1	Esterhuysen	18421	PRE	—
O. psilopoda Turcz.	32.2	Leipoldt	BH 21326	BOL	—
O. imbricata Eckl. & Zeyh. var. *imbricata*	33.1	Galpin	6404	PRE	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. imbricata Eckl. & Zeyh. var. *imbricata*	33.2	Paterson	541	BOL	—
O. imbricata Eckl. & Zeyh. var. *violacea* Knuth	34.1	Galpin	10803	PRE	—
O. imbricata Eckl. & Zeyh. var. *violacea* Knuth	34.2	Salter	2338	BOL	—
O. imbricata Eckl. & Zeyh. var. *cuneifolia* Salter	35.1	Pillans	6654	BOL	X
O. imbricata Eckl. & Zeyh. var. *cuneifolia* Salter	35.2	Salter	2387	BOL	—
O. ioeides Salter	36.1	Salter	2342	BOL	—
O. ioeides Salter	36.2	Esterhuysen	4729	BOL	—
O. calvinensis Knuth	37	—	—	—	—
O. incerta Knuth	38	—	—	—	—
O. orbicularis Salter	39.1	Salter	2323	PRE	X
O. orbicularis Salter	39.2	Bolus	20109	NBG	—
O. marlothii Schltr. ex Knuth	40.1	Marloth	9909	PRE	X
O. obtusa Jacq. var. *obtusa*	41.1	Muir	3653	PRE	—
O. obtusa Jacq. var. *obtusa*	41.2	Salter	893	PRE	—
O. obtusa Jacq. var. *obtusa*	41.3	Marloth	6786	PRE	—
O. obtusa Jacq. var. *obtusa*	41.4	Salter	2825	BOL	—
O. obtusa Jacq. var. *atrata* (Weintroub) Salter	42.1	Pillans	BH 19227	BOL	X
O. obtusa Jacq. var. *atrata* (Weintroub) Salter	42.2	Salter	2584	BOL	—
O. lanata L.f. var. *lanata*	43.1	Marloth	5578	PRE	—
O. lanata L.f. var. *lanata*	43.2	Salter	4871	PRE	—
O. lanata L.f. var. *rosea* Salter	44.1	Schltr.	4802	PRE	—
O. lanata L.f. var. *rosea* Salter	44.2	Bolus	BH 22159	BOL	X
O. truncatula Jacq.	45.1	Bolus	6463	PRE	—
O. truncatula Jacq.	45.2	Salter	4390	BOL	—
O. lasiorrhiza Salter	46.1	Salter	4555	BOL	X
O. strigosa Salter	47.1	Salter	557	BOL	X
O. strigosa Salter	47.2	Salter	522	BOL	—
O. zeekoevleyensis Knuth	48.1	Salter	6699	PRE	—
O. zeekoevleyensis Knuth	48.2	Schltr.	10548	BOL	X
O. virginea Jacq.	49.1	Salter	1572	BOL	—
O. virginea Jacq.	49.2	Salter	6653	PRE	—
O. ambigua Jacq. var. *ambigua*	50.1	Salter	6662	PRE	—
O. ambigua Jacq. var. *ambigua*	50.2	Salter	2529	BOL	—
O. ambigua Jacq. var. *fuscata* (Jacq.) Salter (Jacq.) Salter	51.1	Salter	PRE 16351	PRE	—
O. rhomboidea Salter	52.1	Salter	930	PRE	X
O. crispula Sond. var. *crispula*	53.1	Salter	932A	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. crispula Sond. var. *glandulosa* Salter	54.1	Salter	932B	BOL	X
O. luteola Jacq. var. *luteola*	55.1	Marloth	575	PRE	—
O. luteola Jacq. var. *luteola*	55.2	Edwards	232	BOL	—
O. luteola Jacq. var. *minor* Salter	56.1	Salter	7235	BOL	X
O. luteola Jacq. var. *minor* Salter	56.2	Schltr.	7931	BOL	—
O. adenodes Sond. (Form C)	57.1	Schltr.	73	BOL	—
O. adenodes Sond. (Form D)	57.2	Salter	5512	BOL	—
O. adenodes Sond. (Form A)	57.3	Salter	892	BOL	—
O. incarnata L.	58.1	Thode	A763	PRE	—
O. incarnata L.	58.2	Wolley-Dod	1058	BOL	—
O. duriuscula Schltr.	59.1	Schltr.	7599	PRE	X
O. duriuscula Schltr.	59.2	Bolus	BH 20435	BOL	—
O. pendulifolia Salter	60.1	Thode	A2303	PRE	—
O. pendulifolia Salter	60.2	Schltr.	2294	BOL	X
SUBSECTION *BIFURCATAE*					
O. heterophylla DC.	61.1	Marloth	9208	PRE	—
O. heterophylla DC.	61.2	Muir	2713	PRE	X
O. extensa Salter	62.1	Leipoldt	BH 21730	BOL	—
O. bifurca Lodd. var. *bifurca*	63.1	Pegler	695	PRE	—
O. bifurca Lodd. var. *bifurca*	63.2	MacOwan	892	PRE	—
O. bifurca Lodd. var. *angustiloba* Sond.	64.1	Flanagan	2326	BOL	—
O. bifurca Lodd. var. *angustiloba* Sond.	64.2	Bolus	BH 22234	BOL	—
O. tysoni Phillips	65.1	Tyson	1334	BOL	X
O. tysoni Phillips	65.2	Pegler	695	BOL	—
O. orthopoda Salter	66.1	Salter	6794	BOL	—
O. comosa E. Mey. ex Sond.	67.1	Marloth	6746	PRE	—
O. comosa E. Mey. ex Sond.	67.2	Esterhuysen	5447	BOL	—
O. bifida Thunb.	68.1	Bolus	BH 14502	PRE	—
O. bifida Thunb.	68.2	Pillans	2468	BOL	—
O. smithiana Eckl. & Zeyh.	69.1	Edwards	BH 21189	BOL	—
O. smithiana Eckl. & Zeyh.	69.2	Galpin	BH 2225	BOL	—
O. smithiana Eckl. & Zeyh.	69.3	Eckl. & Zeyh.	740	NBG	X
SECTION *STICTOPHYLLAE*					
O. purpurea L. (Form C)	70.1	Salter	8184	PRE	—
O. purpurea L. (Form E)	70.2	Salter	676	PRE	—
O. purpurea L. (Form A)	70.3	Marloth	75	PRE	—
O. purpurea L. (Form D)	70.4	Salter	2489	BOL	—
O. purpurea L. (Form F)	70.5	Duthie	806A	BOL	—
O. purpurea L. (Form J)	70.6	Salter	6827	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. melanosticta Sond. var. *melanosticta*	71.1	Bolus	BH 21357	BOL	—
O. melanosticta Sond. var. *melanosticta*	71.2	Marloth	3909	PRE	—
O. melanosticta Sond. var. *latifolia* Salter	72.1	Salter	5361	PRE	X
O. rubro-punctata Salter	73.1	Salter	5371	BOL	X
SECTION *FOVEOLATAE*					
O. convexula Jacq.	74.1	Salter	1049	BOL	—
O. convexula Jacq.	74.2	Page	BH 15622	BOL	—
O. attaquana Salter	75.1	Salter	2341	BOL	X
O. foveolata Turcz.	76.1	Leipoldt	BH 21728	BOL	—
O. foveolata Turcz.	76.2	Zeyher	238	PRE	—
O. pulchella Jacq. var. *pulchella*	77.1	Salter	3707	BOL	—
O. pulchella Jacq. var. *tomentosa* Sond.	78.1	Leipoldt	BH 19704	BOL	—
O. pulchella Jacq. var. *tomentosa* Sond.	78.2	Salter	3328	PRE	—
O. pulchella Jacq. var. *glauca* Salter	79.1	Salter	850	PRE	—
O. pulchella Jacq. var. *glauca* Salter	79.2	Bolus	BH 19888	BOL	X
O. pulchella Jacq. var. *leucotricha* (Turcz.) Salter	80.1	Salter	6651	PRE	—
O. pulchella Jacq. var. *leucotricha* (Turcz.) Salter	80.2	Zeyher	228	PRE	—
O. pulchella Jacq. var. *beneprotecta* (Knuth) Salter	81.1	Dinter	5182	PRE	X
O. pulchella Jacq. var. *beneprotecta* (Knuth) Salter	81.2	Dinter	15004	PRE	—
O. depressa Eckl.& Zeyh.	82.1	Schoenfelder	871	PRE	—
O. depressa Eckl.& Zeyh.	82.2	Salter	2197	BOL	—
O. obliquifolia Steud. ex Rich.	83.1	Bryant	A10	PRE	—
O. obliquifolia Steud. ex Rich.	83.2	Rogers	18181	BOL	—
O. setosa E. Mey. ex Sond.	84.1	Acocks	226	PRE	—
O. setosa E. Mey. ex Sond.	84.2	Salter	4404	NBG	—
O. reflexa Salter	85.1	Salter	5318	BOL	X
O. reflexa Salter	85.2	Salter	5327	BOL	—
O. dilatata L. Bol.	86.1	Leipoldt	BH 19125	BOL	X
O. dilatata L. Bol.	86.2	Leipoldt	BH 22596	BOL	—
O. pocokiae L. Bol.	87.1	Pocock	S90	PRE	X
O. pocokiae L. Bol.	87.2	Salter	1653	BOL	—
O. oreithala Salter	88.1	Leipoldt	BH 22672	BOL	X
O. punctata L.f. (Form C)	89.1	Salter	3177	PRE	—
O. punctata L.f. (Form B)	89.2	Duthie	1226	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. lichenoides Salter	90.1	Salter	928	BOL	X
O. inaequalis Weintraub.	91.1	Leipoldt	1457/30	BOL	X
O. inaequalis Weintraub.	91.2	Compton	2679	BOL	—
O. bullutata Salter	92.1	Salter	5552	BOL	X
O. bullutata Salter	92.2	Salter	2513	BOL	—
O. fergusoniae Salter	93.1	Ferguson	BH 20176	BOL	X
O. fergusoniae Salter	93.2	Fourcade	5037	BOL	—
O. grammopetala Sond.	94.1	Zeyher	266	BOL	X
O. grammopetala Sond.	94.2	Salter	2572	BOL	—
O. algoensis Eckl. & Zeyh.	95.1	Archibald	5185	BOL	—
O. algoensis Eckl. & Zeyh.	95.2	Kensit	1	BOL	—
O. fourcadei Salter	96.1	Fourcade	5063	BOL	X
O. fourcadei Salter	96.2	Fourcade	5223	PRE	—
O. lawsonii Bol. f.	97.1	Lawson	BH 13378	BOL	X
O. lawsonii Bol. f.	97.2	Pole-Evans	BH 11597	PRE	—
O. nortieri Salter	98.1	Nortier	BH 21532	BOL	X
O. nortieri Salter	98.2	Taylor	450	BOL	—
O. annae Bol. f.	99.1	Salter	6654	PRE	X
O. annae Bol. f.	99.2	Tugwell	BH 13380	BOL	—
O. senecta Salter	100.1	Salter	5490	BOL	X
O. senecta Salter	100.2	Salter	2510	PRE	—
O. densa N.E. Br.	101.1	Salter	4456	BOL	—
O. densa N.E. Br.	101.2	Marloth	10211	PRE	—
O. densa N.E. Br.	101.3	Johanssen	9	SAM	X
O. furcillata Salter var. *furcillata*	102.1	Salter	2576	BOL	X
O. furcillata Salter var. *furcillata*	102.2	Salter	2593	BOL	—
O. furcillata Salter var. *caulescens* Salter	103.1	Salter	854	PRE	X
O. furcillata Salter var. *caulescens* Salter	103.2	Salter	4607	BOL	—
SECTION *SAGITTATAE*					
O. fibrosa Bol. f.	104.1	Bolus	BH 13379	BOL	X
O. fibrosa Bol. f.	104.2	Salter	6048	PRE	—
O. microdonta Salter	105.1	Salter	1047	BOL	X
O. microdonta Salter	105.2				—
O. nidulans Eckl.& Zeyh. var. *nidulans*	106.1	Bolus	14623	PRE	—
O. nidulans Eckl.& Zeyh. var. *nidulans*	106.2	Salter	2651	BOL	—
O. nidulans Eckl.& Zeyh. var. *denticulata* (Wolley-Dod) Salter	107.1	Schltr.	7761	PRE	—
O. nidulans Eckl.& Zeyh. var. *denticulata* (Wolley-Dod) Salter	107.2	Salter	5417	BOL	—

TAXON	**TAXON No.**	**COLLECTOR**	**COLL. No.**	**HERB.**	**TP**
O. minuta Thunb. var. *minuta*	108.1	Salter	8363	PRE	—
O. minuta Thunb. var. *minuta*	108.2	Salter	3580	BOL	—
O. minuta Thunb. var. *callosa* Salter	109.1	Bolus	BH 9400	BOL	X
O. minuta Thunb. var. *callosa* Salter	109.2	Leipoldt	30372	SAM	—
O. eckloniana Presl. var. *eckloniana*	110.1	MacOwan	1814	PRE	—
O. eckloniana Presl. var. *eckloniana*	110.2	Salter	3355	PRE	—
O. eckloniana Presl. var. *montigena* (Schltr.) Knuth	111.1	Schltr.	7565	PRE	X
O. eckloniana Presl. var. *montigena* (Schltr.) Knuth	111.2	Martin	714/37	BOL	—
O. eckloniana Presl. var. *hopefieldiana* Knuth	112.1	Marloth	642	PRE	—
O. eckloniana Presl. var. *hopefieldiana* Knuth	112.2	Bolus	TM 15407	BOL	—
O. eckloniana Presl. var. *robusta* Salter	113.1	Salter	6617	BOL	X
O. eckloniana Presl. var. *robusta* Salter	113.2	Bolus	BH 14614	BOL	—
O. eckloniana Presl. var. *sonderi* Salter	114.1	Marloth	60	PRE	—
O. eckloniana Presl. var. *sonderi* Salter	114.2	Salter	6615	BOL	—
SECTION *CAMPANULATAE*					
O. dregei Sond.	115.1	Lavis	BH 19901	BOL	—
O. dregei Sond.	115.2	Leighton	1150	BOL	—
O. simplex Salter	116.1	Salter	2464	BOL	X
O. simplex Salter	116.2	Salter	3513	BOL	—
O. disticha Jacq. var. *disticha*	117.1	Salter	2608	BOL	—
O. disticha Jacq. var. *disticha*	117.2	Schltr.	4911	PRE	—
O. disticha Jacq. var. *alba* Salter	118.1	Salter	2602	PRE	—
O. disticha Jacq. var. *alba* Salter	118.2	Schlechter	10874	K	X
O. natans L. f.	119.1	Bolus	4544	BOL	—
O. natans L. F.	119.2	Salter	1712	PRE	—
O. uliginosa Schltr.	120.1	Schltr.	8015	PRE	X
O. uliginosa Schltr.	120.2	Schltr.	5085	PRE	—
SECTION *LATIFOLIOLATAE*					
O. stenoptera Turcz. var. *stenoptera*	121.1	Zeyher	239	PRE	X
O. stenoptera Turcz. var. *stenoptera*	121.2	Salter	6638	BOL	—
O. stenoptera Turcz. var. *alba* Salter	122.1	Salter	950	PRE	X
O. stenoptera Turcz. var. *alba* Salter	122.2	Salter	6637	K	—
O. stenoptera Turcz. var. *undulata* Salter	123.1	Salter	5339	BOL	X

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. stenoptera Turcz. var. *undulata* Salter	123.2	Salter	5342	BOL	—
O. aurea Schltr.	124.1	Schltr.	7967	PRE	X
O. aurea Schltr.	124.2	Leipoldt	4294	PRE	—
O. suavis Knuth	125.1	Salter	4520	K	—
O. suavis Knuth	125.2	Salter	4519	NBG	—
O. viscidula Schltr.	126.1	Schltr.	7832	BOL	X
O. campylorrhiza Salter	127.1	Salter	5553	BOL	X
O. campylorrhiza Salter	127.2	Salter	860	BOL	—
O. amblyosepala Schltr. var. *amblyosepala*	128.1	Schltr.	8671	BOL	X
O. amblyosepala Schltr. var. *amblyosepala*	128.2	Schltr.	10829	PRE	—
O. amblyosepala Schltr. var. *minor* Salter	129.1	Leipoldt	4293	NBG	—
O. amblyosepala Schltr. var. *minor* Salter	129.2	Leipoldt	22671	NBG	X
O. ausensis Knuth	130.1	Dinter	6256	BOL	—
O. sonderiana (Kuntze) Salter var. *sonderiana*	131.1	Zeyher	237	PRE	X
O. sonderiana (Kuntze) Salter var. *sonderiana*	131.2	Salter	1546A	PRE	—
O. sonderiana (Kuntze) Salter var. *alba* Salter	132.1	Salter	5309	BOL	X
O. sonderiana (Kuntze) Salter var. *alba* Salter	132.2	Salter	7244	BOL	—
O. inconspicua Salter	133.1	Salter	817	PRE	X
O. inconspicua Salter	133.2	Salter	2590	BOL	—
O. petraea Salter	134.1	Salter	5354	BOL	X
O. petraea Salter	134.2	Salter	5487	BOL	—
O. commutata Sond. var. *commutata*	135.1	Salter	3307	PRE	—
O. commutata Sond. var. *commutata*	135.2	Bolus	BH 14561	BOL	—
O. commutata Sond. var. *concolor* Salter	136.1	Pillans	2480	PRE	—
O. commutata Sond. var. *concolor* Salter	136.2	Salter	8407	BOL	X
O. commutata Sond. var. *montana* Salter	137.1	Leipoldt	BH 19757	BOL	X
O. commutata Sond. var. *montana* Salter	137.2	Edwards	230	BOL	—
O. tenella Jacq.	138.1	Leipoldt	4269	PRE	—
O. tenella Jacq.	138.2	Salter	672	BOL	—
O. aridicola Salter	139.1	Salter	2467	PRE	X
O. aridicola Salter	139.2	Salter	4547	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. stokoei Weintraub	140.1	Salter	6079	PRE	—
O. stokoei Weintraub	140.2	Stokoe	BH 19226	BOL	X
O. petiolulata Bol. f.	141.1	Bolus	BH 8952	BOL	X
O. petiolulata Bol. f.	141.2	Adamson	20492	NBG	—
O. callosa Knuth var. *callosa*	142.1	Salter	5363	BOL	X
O. callosa Knuth var. *callosa*	142.2	Salter	4472	BOL	—
O. callosa Knuth var. *minor* Salter	143.1	Salter	2482	PRE	—
O. callosa Knuth var. *minor* Salter	143.2	Salter	5372	BOL	X
O. hirsuta Sond	144.1	De Jager	BH 21533	K	—
O. hirsuta Sond.	144.2	Salter	4413	NBG	—
SECTION *CRASSULAE*					
O. fabaefolia Jacq. (Form Bii)	145.1	Salter	5323	BOL	—
O. fabaefolia Jacq. (Form A)	145.2	Salter	5311	BOL	—
O. cathara Salter	146.1	Salter	6669	PRE	—
O. cathara Salter	146.2	Salter	2526	BOL	X
O. pulvinata Salter	147.1	Salter	7340	BOL	X
O. flava L. (Form A)	148.1	Schltr.	10486	PRE	—
O. flava L.	148.2	Salter	8637	PRE	—
O. flava L. (Form H)	148.3	Salter	703A	PRE	—
O. flava L. (Form B)	148.4	Salter	5344A	BOL	—
O. flava L.	148.5	Pillans	2488	PRE	—
O. flava L. (Form A)	148.6	Dummer	1296	PRE	—
O. flaviuscula Salter var. *flaviuscula*	149.1	Salter	5524	BOL	X
O. flaviuscula Salter var. *flaviuscula*	149.2	Salter	896	BOL	—
O. flaviuscula Salter var. *longifolia* Salter	150.1	Schltr.	72	PRE	—
O. flaviuscula Salter var. *longifolia* Salter	150.2	Salter	2563	BOL	X
O. namaquana Sond.	151.1	Drege	PRE 12604	PRE	X
O. namaquana Sond.	151.2	Salter	819	BOL	—
O. louisae Salter	152.1	Salter	818	BOL	X
O. louisae Salter	152.2	Salter	2557	PRE	—
O. salteri Bolus	153.1	Salter	5303A	PRE	X
O. salteri Bolus	153.2	Salter & Pillans	BH 18937	BOL	—
SECTION *ANGUSTATAE* SUBSECTION *PARDALES*					
O. capillacea E. Mey. ex Sond. var. *capillacea*	154.1	Galpin	9954	PRE	—
O. capillacea E. Mey. ex Sond. var. *capillacea* (Form C)	154.2	Salter	2112	PRE	—
O. capillacea E. Mey. ex Sond. var. *capillacea*	154.3	Salter	2274	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. capillacea E. Mey. ex Sond. var. *capillacea*	154.4	Leipoldt	BH 19743	BOL	—
O. capillacea E. Mey. ex Sond. var. *ternata* Salter	155.1	Salter	6697	BOL	X
O. leptogramma Salter var. *leptogramma*	156.1	Salter	2178	PRE	X
O. leptogramma Salter var. *leptogramma*	156.2	Salter	6045	BOL	—
O. leptogramma Salter var. *brevifolia* Salter	157.1	Salter	2208	BOL	X
O. leptogramma Salter var. *brevifolia* Salter	157.2	Salter	2203	K	—
O. leptogramma Salter var. *lutea* Salter	158.1	Salter	2316	PRE	X
O. leptogramma Salter var. *lutea* Salter	158.2	Salter	2321	K	—
O. lineolata Salter	159.1	Salter	5382	BOL	X
O .lineolata Salter	159.2	Salter	4442	BOL	—
O. massoniana Salter var. *massoniana*	160.1	Salter	705	PRE	X
O. massoniana Salter var. *massoniana*	160.2	Leipoldt	4297	PRE	—
O. massoniana Salter var. *flavescens* Salter	161.1	Salter	4474	BOL	X
O. massoniana Salter var. *flavescens* Salter	161.2	Salter	4566	K	—
O. melanograpta Salter	162.1	Salter	714	PRE	X
O. melanograpta Salter	162.2	Salter	5322	BOL	—
O. camelopardalis Salter	163.1	Salter	2308	PRE	X
O. camelopardalis Salter	163.2	Salter	6039	PRE	—
O. confertifolia (Kuntze) Knuth var. *petiolata* Salter	164.1	Salter	2380	BOL	X
O. confertifolia (Kuntze) Knuth var. *lutea* Salter	165.1	Leipoldt	BH 22594	BOL	X
O. confertifolia (Kuntze) Knuth var. *confertifolia*	166.1	Drege	7426	PRE	X
O. confertifolia (Kuntze) Knuth var. *confertifolia*	166.2	Salter	2388	PRE	—
O. heidelbergensis Salter	167.1	Salter	2385	PRE	X
O. heidelbergensis Salter	167.2	Salter	5414	NBG	—
O. pardalis Sond.	168.1	Salter	6042	PRE	—
O. pardalis Sond.	168.2	Zeyher	253	K	X
O. grammophylla Salter	169.1	Salter	4469	BOL	X
O. grammophylla Salter	169.2	Salter	2478	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. robinsonii Salter & Exell.	170.1	Salter	2357	BOL	—
O. robinsonii Salter & Exell.	170.2	Salter	3278	PRE	—
SUBSECTION *SESSILIFOLIATAE*					
O. hirta L. var. *hirta* (FORM F)	171.1	Bolus	14567	PRE	—
O. hirta L. var. *hirta* (FORM E)	171.2	Salter	3341	PRE	—
O. hirta L. var. *hirta* (FORM D)	171.3	Salter	4512	BOL	—
O. hirta L. var. *hirta* (FORM B)	171.4	Wolley-Dod	1177	PRE	—
O. hirta L. var. *canescens* Knuth	172.1	Salter	506	PRE	—
O. hirta L. var. *canescens* Knuth	172.2	Schltr.	7793	PRE	—
O. hirta L. var. *tenuicaulis* Knuth	173.1	Salter	8635	PRE	—
O. hirta L. var. *tenuicaulis* Knuth	173.2	Salter	4521	PRE	—
O. hirta L. var. *intermedia* Salter	174.1	Edwards	60	PRE	—
O. hirta L. var. *intermedia* Salter	174.2	Schltr.	7845	PRE	—
O. hirta L. var. *polioeides* Salter	175.1	Leipoldt	BH 21479	BOL	—
O. hirta L. var. *polioeides* Salter	175.2	Eckl. & Zeyh.	674	BOL	—
O. hirta L. var. *tubiflora* (Jacq.) Salter	176.1	Edwards	222	PRE	—
O. hirta L. var. *tubiflora* (Jacq.) Salter	176.2	Schltr.	8301	PRE	—
O. hirta L. var. *secunda* (Jacq.) Salter	177.1				—
O. pseudo-hirta Salter	178.1	Galpin	9937	PRE	—
O. pseudo-hirta Salter	178.2	Salter	2310	BOL	X
O. subsessilis L. Bol.	179.1	Leipoldt	BH 18702	BOL	X
O. subsessilis L. Bol.	179.2	Loustein	NBG 905/35	NBG	—
O. crocea Salter	180.1	Salter	5550	BOL	X
O. meisneri Sond.	181.1	Salter	2096	PRE	—
O. meisneri Sond.	181.2	Leipoldt	BH 19732	K	—
O. viscosa E. Mey. ex Sond.	182.1	Leipoldt	4281	PRE	—
O. viscosa E. Mey. ex Sond.	182.2	Drege	BH 56682	BOL	X
O. porphyriosiphon Salter	183.1	Salter	5399	PRE	—
O. porphyriosiphon Salter	183.2	Salter	2454	BOL	X
O. leipoldtii Schltr.	184	—	—	—	—
O. giftbergensis Salter	185.1	Salter	7263	PRE	X
O. giftbergensis Salter	185.2	Salter	8128	PRE	—
O. macra Salter	186.1	Schltr.	7928	BOL	X
O. macra Salter	186.2	Salter	5431	BOL	—
O. tenuifolia Jacq.	187.1	Smith	4197	PRE	—
O. tenuifolia Jacq.	187.2	Salter	2656	BOL	—
O. multicaulis Eckl. & Zeyh. var. *multicaulis*	188.1	Salter	6210	PRE	—

TAXON	**TAXON No.**	**COLLECTOR**	**COLL. No.**	**HERB.**	**TP**
O. multicaulis Eckl. & Zeyh. var. *multicaulis*	188.2	Ecklon & Zeyh.	681	PRE	X
O. multicaulis Eckl. & Zeyh. var. *stolonifera* Salter	189.1	Salter	3444	BOL	X
O. multicaulis Eckl. & Zeyh. var. *stolonifera* Salter	189.2	Salter	4636	BOL	—
O. urbaniana Schltr. var. *urbaniana*	190.1	Schltr.	7859	PRE	X
O. urbaniana Schltr. var. *urbaniana*	190.2	Salter	4636	BOL	—
O. urbaniana Schltr. var. *leipoldtii* Salter	191	—	—	—	—
O. callimarginata Weintroub.	192.1	Leipoldt	BH 18619	BOL	X
O. callimarginata Weintroub.	192.2	Salter	2613	PRE	—
O. recticaulis Sond.	193.1	Salter	3383	PRE	—
O. tecticaulis Sond.	193.2	Leipoldt	BH 19920	BOL	—
SUBSECTION *XANTHOTRICHAE*					
O. pillansiana Salter & Exell.	194.1	Salter	679	PRE	—
O. pillansiana Salter & Exell.	194.2	Salter	382/27	BOL	X
O. argillacea Bol. f.	195.1	Leipoldt	700	PRE	X
O. argillacea Bol. f.	195.2	Salter	4562	BOL	—
O. adspersa Eckl. & Zeyh.	196.1	Salter	3322	PRE	—
O. adspersa Eckl. & Zeyh.	196.2	Salter	738	PRE	—
O. adspersa Eckl. & Zeyh.	196.3	Salter	7238	BOL	—
SUBSECTION *LINEARIS*					
O. primuloides Knuth	197.1	Salter	4455	BOL	—
O. primuloides Knuth	197.2	Salter	4468	BOL	—
O. linearis Jacq.	198.1	Salter	2518	PRE	—
O. linearis Jacq.	198.2	Zeyher	229	PRE	—
O. quinata Savign.	199	—	—	—	—
O. exserta Salter	200.1	Salter	4589	PRE	X
O. exserta Salter	200.2	Salter	1251	BOL	—
O. gracilis Jacq. var. *gracilis*	201.1	Salter	674	PRE	—
O. gracilis Jacq. var. *gracilis*	201.2	Salter	2554	BOL	—
O. gracilis Jacq. var. *purpurea* Salter	202.1	Salter	6652	PRE	—
O. gracilis Jacq. var. *purpurea* Salter	202.2	Salter	3406	PRE	X
O. gracilis Jacq. var. *lilacea* Salter	203.1	Salter	5501	PRE	X
O. gracilis Jacq. var. *lilacea* Salter	203.1	Salter	5346	K	—
O. helicoides Salter var. *helicoides*	204.1	Salter	851	PRE	X
O. helicoides Salter var. *helicoides*	204.2	Salter	1405A	PRE	—
O. helicoides Salter var. *alba* Salter	205.1	Salter	857	PRE	X
O. campicola Salter	206.1	Salter	716	PRE	—
O. campicola Salter	206.2	Salter	4445	BOL	X
O. stenopetala Salter	207.1	Salter	2469	PRE	X
O. stenopetala Salter	207.2	Salter	7325	PRE	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. xantha Salter	208.1	Salter	2470	PRE	—
O. xantha Salter	208.2	Salter	2472	PRE	X
O. tenuipes Salter var. *tenuipes*	209.1	Salter	7267	PRE	X
O. tenuipes Salter var. *biapiculata* Salter	210.1	Bolus	BH 14605	PRE	X
O. tenuipes Salter var. *biapiculata* Salter	210.2	Edwards	231	PRE	—
O. phloxidiflora Schltr.	211.1	Leipoldt	4295	PRE	—
O. phloxidiflora Schltr.	211.2	Leipoldt	4270	PRE	—
O. involuta Salter	112.1	Salter	3381	PRE	X
O. involuta Salter	112.2	Leipoldt	BH 19747	K	—
O. goniorrhiza Eckl. & Zeyh.	213.1	Salter	3440	PRE	—
O. goniorrhiza Eckl. & Zeyh.	213.2	Salter	3450	PRE	—
O. fragilis Salter var. *fragilis*	214.1	Salter	660	PRE	X
O. fragilis Salter var. *fragilis*	214.2	Salter	2418	K	—
O. fragilis Salter var. *pellucida* Salter	215.1	Salter	3427	PRE	—
O. fragilis Salter var. *pellucida* Salter	215.2	Salter	5426	K	X
O. pallens Eckl. & Zeyh.	216.1	Salter	748	PRE	—
O. pallens Eckl. & Zeyh.	216.2	Salter	739	PRE	—
O. glabra Thunb.	217.1	Salter	3443	PRE	—
O. glabra Thunb.	217.2	Marloth	5352	PRE	—
O. pusilla Jacq.	218.1	Salter	8665	PRE	—
O. pusilla Jacq.	218.2	Kensit	BH 14520	BOL	—
O. leptocalyx Sond.	219.1	Edwards	63	PRE	—
O. leptocalyx Sond.	219.2	Salter	4545	BOL	—
O. versicolor L. var. *versicolor*	220.1	Salter	3303	PRE	—
O. versicolor L. var. *versicolor*	220.2	Salter	6804	PRE	—
O. versicolor L. var. *flaviflora* Sond.	221.1	Salter	2276	PRE	—
O. versicolor L. var. *flaviflora* Sond.	221.2	Salter	5411	BOL	—
O. versicolor L. var. *latifolia* Wolley-Dod	222.1	Salter	6834	PRE	—
O. versicolor L. var. *latifolia* Wolley-Dod	222.2	Salter	1187	K	—
O. polyphylla Jacq. var. *polyphylla*	223.1	Pillans	2473	PRE	—
O. polyphylla Jacq. var. *pentaphylla* (Sims) Salter	224.1	Salter	3309	PRE	—
O. polyphylla Jacq. var. *pentaphylla* (Sims) Salter	224.2	Bolus	BH 14525	PRE	—
O. polyphylla Jacq. var. *heptaphylla* Salter	225.1	Schltr.	7805	PRE	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. polyphylla Jacq. var. *heptaphylla* Salter	225.2	Galpin	12670	NBG	X
O. polyphylla Jacq. var. *pubescens* Sond.	226.1	Salter	8123	PRE	—
O. polyphylla Jacq. var. *pubescens* Sond.	226.2	Bolus	BH 14607	PRE	—
O. polyphylla Jacq. var. *alba* Salter	227.1	Salter	5251	PRE	—
O. polyphylla Jacq. var. *alba* Salter	227.2	Salter	5271	K	—
O. polyphylla Jacq. var. *minor* Salter	228.1	Salter	8117	PRE	X
O. burtoniae Salter	229.1	Burton & Leipoldt	BH 22615	BOL	X
O. gracilipes Schltr.	230.1	Salter	8151	PRE	—
O. gracilipes Schltr.	230.2	Salter	7236	BOL	—
O. falcatula Salter	231.1	Salter	6605	PRE	—
O. falcatula Salter	231.2	Salter	6577	BOL	—
O. argyrophylla Salter	232.1	Marloth	452	PRE	—
O. argyrophylla Salter	232.2	Bolus	BH 14539	BOL	—
O. perineson Salter & Exell	233.1	Salter	5427	PRE	—
O. perineson Salter & Exell	233.2	Salter	2438	NBG	—
O. stictocheila Salter	234.1	Marloth	9363	PRE	—
O. stictocheila Salter	234.2	Salter	6147	PRE	X
O. levis Salter	235.1	Salter	3358	PRE	X
O. ciliaris Jacq. var. *ciliaris*	236.1	Fourcade	4998	BOL	—
O. ciliaris Jacq. var. *ciliaris*	236.2	Salter	2317	BOL	—
O. ciliaris Jacq. var. *pageae* (L. Bol.) Salter	237.1	Page	BH 17473	PRE	—
O. ciliaris Jacq. var. *pageae* (L. Bol.) Salter	237.2	Muir	2590	PRE	—
O. burkei Sond.	238.1	Salter	2194	BOL	—
O. burkei Sond.	238.2	Salter	2186	BOL	—
O. cuneata Jacq.	239.1	Salter	6634	BOL	—
O. oreophila Salter	240.1	Salter	5397	BOL	X
O. oreophila Salter	240.2	Leipoldt	BH 19691	BOL	—
O. blastorrhiza Salter	241.1	Salter	5607	BOL	X
O. creaseyi Salter	242.1	Salter	6680	BOL	X
O. comptonii Salter	243.1	Salter	7286	BOL	X
O. comptonii Salter	243.2	Salter	7292	BOL	—
O. reclinata Jacq. var. *reclinata*	144.1	Salter	5345	BOL	—
O. reclinata Jacq. var. *micromera* (Sond.) Salter	245.1	Salter	6661	BOL	—
O. reclinata Jacq. var. *micromera* (Sond.) Salter	245.2	Zeyher	204	PRE	—
O. reclinata Jacq. var. *quinata* Salter	246.1	Salter	6646	PRE	X

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. reclinata Jacq. var. *gracillima* Salter	247.1	Salter	801	PRE	X
O. reclinata Jacq. var. *gracillima* Salter	247.2	Salter	4574	K	—
O. linoides Knuth	248	—	—	—	—
O. albiuscula Salter	249.1	Salter	4608	PRE	X
O. albiuscula Salter	249.2	Salter	5572	BOL	—
O. kamiesbergensis Salter	250.1	Salter	5513	BOL	X
O. kamiesbergensis Salter	250.2	Salter	6677	BOL	—
O. oligophylla Salter	251.1	Salter	7266	BOL	X
SUBSECTION *GLANDULOSA*					
O. clavifolia Sond.	252.1	Salter	6645	PRE	—
O. clavifolia Sond.	252.2	Salter	2531	BOL	—
O. deserticola Salter	253.1	Salter	711	BOL	X
O. deserticola Salter	253.2	Salter	2493	BOL	—
O. droseroides E. Mey. ex Sond.	254.1	Drege	3212	PRE	X
O. droseroides E. Mey. ex Sond.	254.2	Salter	2169	BOL	—
O. suteroides Salter var. *suteroides*	255.1	Salter	700	PRE	X
O. suteroides Salter var. *suteroides*	255.2	Salter	2500	NBG	—
O. suteroides Salter var. *latituba* Salter	256.1	Salter	4475	BOL	X
O. suteroides Salter var. *latituba* Salter	256.2	Salter	7326	BOL	—
O. ebracteata Savign.	257.1	Edwards	218	PRE	—
O. ebracteata Savign.	257.2	Leipoldt	4285	BOL	—
O. *neglecta* Knuth	258				—
O. tenius Salter	259.1	Salter	7260	BOL	X
O. tenuis Salter	259.2	Leipoldt	22670	NBG	—
SUBSECTION *MULTIFOLIOLATAE*					
O. engleriana Schltr.	260.1	Salter	3314	PRE	—
O. engleriana Schltr.	260.2	Schltr.	7755	BOL	X
O. henrici Bol. f.	261.1	Bolus	BH 13079	BOL	X
O. henrici Bol. f.	261.2	Esterhuyzen	10170	NBG	—
O. zeyheri Sond.	262.1	Zeyher	248	BOL	X
O. zeyheri Sond.	262.2	Salter	2191	BOL	—
O. amblyodonta Salter (Form B)	263.1	Salter	2612	PRE	—
O. amblyodonta Salter	263.2	Salter	2279	BOL	X
O. variifolia Steud. var. *variifolia*	264.1	Schltr.	7973	PRE	—
O. variifolia Steud. var. *variifolia*	264.2	Salter	665	NBG	—
O. variifolia Steud. var. *ternata* Salter	265.1	Salter	5620	K	X
O. palmifrons Salter	266.1	Salter	6063	PRE	—
O. tomentosa L.	267.1	Pillans	2502	PRE	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. tomentosa L.	267.2	Schltr.	7852	PRE	—
TAXA NOT ALLOCATED TO A SPECIFIC SECTION					
O. monophylla L. var. *monophylla*	268.1	Pillans	2491	PRE	—
O. monophylla L. var. *monophylla*	268.2	Galpin	BH 3388	PRE	—
O. monophylla L. var. *stenophylla* (Meisn.) Sond.	269.1	Schltr.	7893	PRE	—
O. monophylla L. var. *stenophylla* (Meisn.) Sond.	269.2	Edwards	62	PRE	—
O. monophylla L. var. *rotundifolia* Salter	270.1	Salter	3332	PRE	X
O. monophylla L. var. *rotundifolia* Salter	270.2	Salter	673	NBG	—
O. monophylla L. var. *minor* Salter	271.1	Salter	5392	PRE	—
O. monophylla L. var. *minor* Salter	271.2	Salter	2463	PRE	X
O. ligulata E. Mey. ex Sond.	272	—	—	—	—
O. gustavi Knuth	273	—	—	—	—
O. laxicaulis Knuth	274	—	—	—	—
O. ononifolia Willd. ex Knuth	275	—	—	—	—
O. laxiuscula Knuth	276	—	—	—	—
O. albella Knuth	277	—	—	—	—
O. austro-occidentalis Knuth	278	—	—	—	—
POSSIBLE UNDESCRIBED SPECIES					
O. sp.	279	Mauve	1054	PRE	—
O. sp.	280	Jurgens	26594	PRE	—
O. sp.	281	Spilhaus	8084	PRE	—
O. sp.	282	Tyson	505	PRE	—
O. sp.	283	Jurgens	22483	PRE	—
O. sp.	284	Oliver, Venter & Tolken	306	PRE	—
O. sp.	285	Reid	139	PRE	—
O. sp.	286	Acocks	19368	PRE	—
O. sp.	287	Olivier	262	PRE	—
O. sp.	288	Giess	12847	PRE	—
O. sp. nov. (sensu Bayer)	289	Bayer	1919	NBG	—
O. sp. nov. (sensu Bayer)	290	Bayer	1792	NBG	—
O. sp.	291	Acocks	22236	PRE	—
O. sp. nov. (sensu Bayer)	292	Bayer	5304	NBG	—
O. magnifolia MS (sensu Bayer)	293	Bayer	1496	NBG	—
O. canaliculata MS (sensu Bayer)	294	Bayer	1022	NBG	—
O. glauca MS (sensu Bayer)	295	Bayer	1023	NBG	X
O. sp.	296	Bayer	847A	PRE	—
O. sp.	297	Leipoldt	4299	BOL	—

TAXON	TAXON No.	COLLECTOR	COLL. No.	HERB.	TP
O. klaasvoogdensis MS (sensu Bayer)	298	Bayer	1259	NBG	X
O. heptaphylla MS (sensu Bayer)	299	Bayer	851	NBG	—
O. fragrans MS (sensu Bayer)	300	Bayer	644	NBG	X
O. bombycina MS (sensu Bayer)	301	Bayer	1346	NBG	—
O. oculifera E.G.H. Oliver	302	Oliver	9558	PRE	X

TAXON No. = Taxon number; COLL. No. = Collector's number; HERB. = Herbarium from which specimen was obtained; TP = Type material; MS = Manuscript name

Table 4.2 Summary of the specimens used for TEM and AFM analysis.

TAXON	**TAXON No.**	**PT**	**TEM**	**AFM**
O. microdonta	105.1	A	X	
O. nidulans var. *denticulata*	107.1	A	X	
O. eckloniana var. *sonderi*	114.1	A	X	X
O. fibrosa	104.1; 104.2	B	X	X
O. psilopoda	32.1	C1	X	
O. davyana	25.1	C1	X	X
O. stellata var. *montaguensis*	21.1	C2	X	X
O. obtusa var. *obtusa*	41.1	C3	X	X
O. purpurea	70.1	C3	X	
O. inaequalis	91.1	C4	X	X
O. levis	235.1	C5	X	X
O. engleriana	260.1	C5	X	
O. henrici	261.1	C6	X	X
O. caprina	29.1	C7	X	
O. suteroides var. *latituba*	256.1	C7	X	X
O. campylorrhiza	127.1	C8	X	X
O. stictocheila	234.1	C8	X	
O. deserticola	253.1	C9	X	X
O. fabaefolia	145.1	C10	X	X
O. pillansiana	194.1	C10	X	
O. adspersa	196.1	C10	X	
O. flaviuscula var. *flaviuscula*	149.1	C10	X	
O. sonderiana var. *alba*	132.1	C11	X	X
O. polyphylla var. *pubescens*	226.1	C11	X	
O. monophylla var. minor	271.1	C11	X	
O. tenuipes var. *tenuipes*	209.1	C12	X	X
O. droseroides	254.1	C13	X	X
O. phloxidiflora	211.1	C14	X	X
O. giftbergensis	185.1	C15	X	X
O. tenella	138.1	D1	X	X
O. hirta var. *hirta*	171.1	D1	X	
O. xantha	208.1	D1	X	
O. albiuscula	249.1	D1	X	
O. hirta var. *polioeides*	175.1	D1	X	
O. petiolulata	141.1	D2	X	X
O. linearis	198.1	D3	X	X
O. hirta var. *intermedia*	174.1	D4	X	X
O. hirta var. *tubiflora*	176.1	D4	X	

TAXON No. = Taxon number; PT = Pollen type; TEM = Transmission electron microscopy; AFM = Atomic force microscopy

CHAPTER 5

CHARACTER ANALYSIS

5.1 Introduction

Palynology provides a multitude of characters with taxonomic significance. Traditionally grain size and shape, apertures and exine structure are considered important. The degree of detail in which each of these features is investigated, is mostly determined by the characteristics of the group under study.

In this chapter the significance of grain size, grain shape, apertures and exine structure are considered under separate headings (5.2—5.5). Each discussion starts with a general assessment of the character and the problems that could be encountered when studying it. This is supplemented by an overview of the known state of the character within *Oxalis.* Finally the value of each character, as determined in the present study, is discussed in some detail. Due to the frequent grain aberrations observed in the genus, aberrant grain formation is discussed in detail in section 5.6. Since polyploidy is known to influence both grain size and abnormal grain formation, it is referred to under a separate heading in section 5.7.

Numerous figures are included in the text. These comprise LM micrographs of various pollen types (Figures 5.1—5.2), a schematic summary of exine stratification (Figure 5.3), a cluster diagram (Figure 5.4) and schematic presentations of the subtypes of pollen type C (Figures 5.5.1—5.5.15) and SEM micrographs of aberrant pollen grains (Figures 5.6—5.7). Tables summarising average grain diameters (Table 5.1), lumina size classes (Table 5.2), the distribution of pollen types within the genus (Table 5.3), average thickness of the pollen wall layers (Table 5.4) and chromosome numbers, ploidy levels and grain aberrations (Table 5.5) are supplied at the end of the chapter.

5.2 Grain size

Although palynological classifications are seldomly based on grain size, this character is often used as an additional feature when describing a specific pollen type. Erdtman (1971) proposed a number of pollen size classes which can be used as reference when documenting pollen characters.

In her comprehensive LM pollen study of the Oxalidaceae, Huynh (1969a) found a progression in grain size from the allegedly most primitive genera (*Averrhoa* and *Sarcotheca*) to the most advanced genus *Oxalis*. She also noted a difference in grain size from the anthers of the different stylar whorls of the tristylic *Oxalis* flower. Grains from anthers of the upper stylar whorl proved to be the largest, while grains from anthers of the other two whorls were found to be much smaller. In her descriptions she referred to the diameters of the larger grains only. Ornduff 1970 notes that the stylar configurations may vary considerably between plants of the same species in a given population. This obviously complicates the use of grain size in palynological descriptions.

It has been widely observed that grain size is directly proportional to the level of ploidy, with a polyploid plant producing larger pollen grains than a diploid plant of the same species (Muller 1979). Unfortunately karyological information on *Oxalis* is very limited. When working from herbarium material, as in this study, it is almost impossible to tell the ploidy level of a given specimen. The influence of polyploidy on palynological features is discussed in more detail under a separate heading (section 5.7).

A third problem often encountered when documenting pollen diameter is that the preparation of LM slides causes the grains to swell, resulting in pollen dimorphisms. This can be reduced to a minimum if glycerine embedded material is studied within three days after mounting.

In view of the above mentioned problems, pollen size was used cautiously in the present study. As far as possible grains from both stylar whorls were examined. Polar and equatorial measurements were taken for both small and large grains (Table 5.1). In *Oxalis* the larger grains have an average diameter of 30—50 X 35—55 μm, with the polar diameter normally slightly lower than the equatorial diameter. The apolar pollen grains (type D4) found in *O. hirta* var. *intermedia* are the largest with an average diameter of 81.99 μm. The smallest grains were found in *O. camelopardalis*, with an average diameter of 25.26 X 26.08 μm. Grains of pollen types A, B and C are proportionally smaller than those of pollen type D[1]. This holds true for grains from both stylar whorls. Size characters, therefore, to some extent support the pollen types delimited through sexine structure.

5.3 Grain shape

Most palynological discussions mention pollen grain shape. Descriptions are based on the polar view outline (the so called amb) and/or the equatorial view outline. Erdtman (1971) suggested a widely used range of shape classes based on the P/E ratio of grains, where the P/E ratio is the ratio of the polar axis (P) to the equatorial diameter (E). Grain shape may hold taxonomic value, as in the case of the Lauraceae (Van der Merwe *et al.* 1990). The African members of this family are distinguished from their counterparts in other parts of the world on the basis of pollen grain shape. Mostly, however, shape is used with caution since it

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[1] See Chapter 6 for a formal description of the different pollen types identified in the present study.

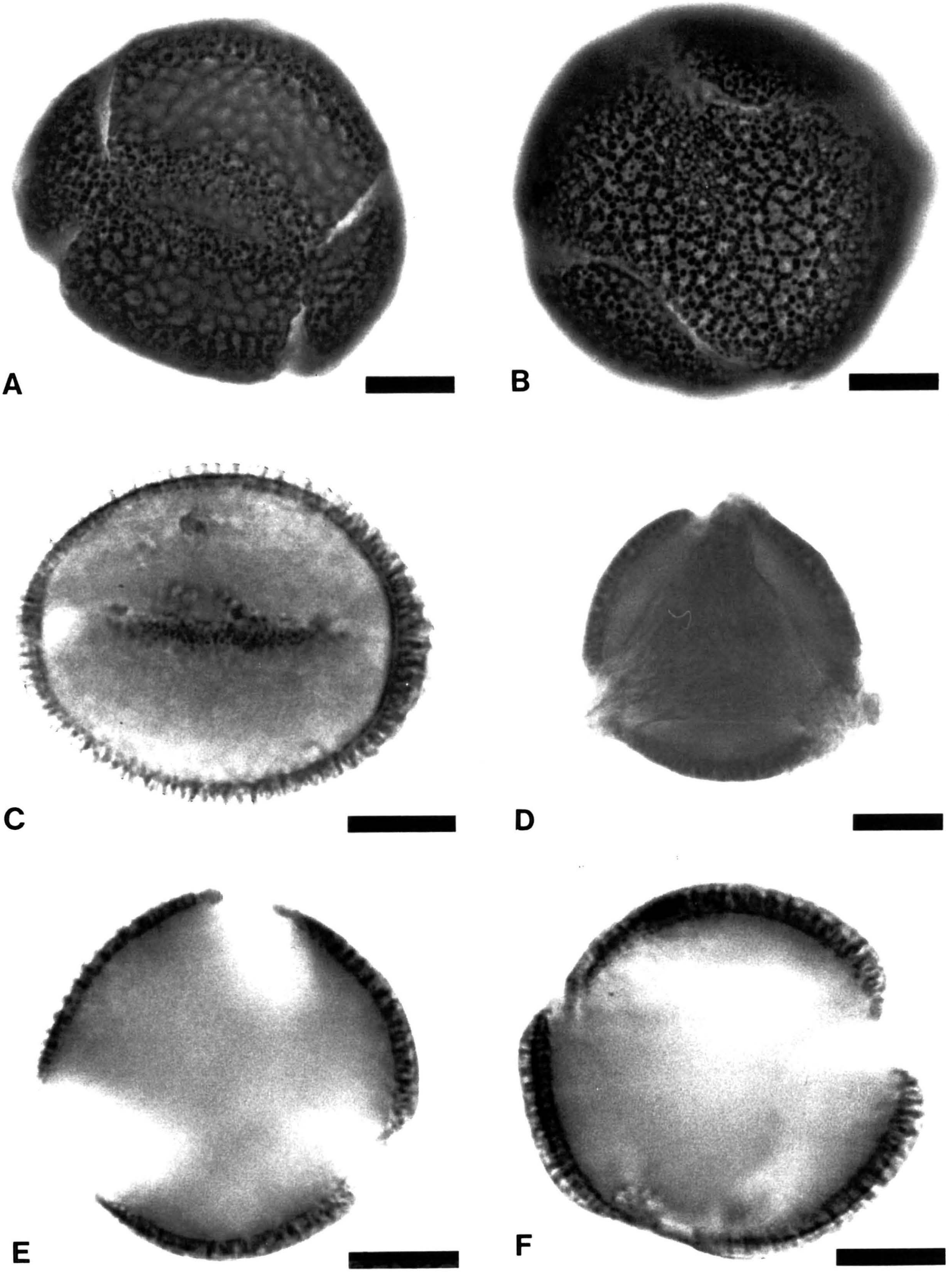


Figure 5.1 A—F. LM micrographs of *Oxalis* pollen. A, B: Pollen type A. (A) *O. microdonta* [105.1], showing sculptural detail and colpi. (B) *O. eckloniana* var. *sonderi* [114.1], showing sculptural detail and colpi. C—D: Pollen subtype C2. (C) *O. stellata* var. *montaguense* [21.1], optical section in equatorial view. (D) *O. attaquana* [75.1], optical section in polar view. E, F: Pollen subtype C3. (E) *O. obtusa* var. *obtusa* [41.1], optical section in polar view. (F) *O. purpurea* [70.1], optical section in polar view. Scale bar = 10 μm

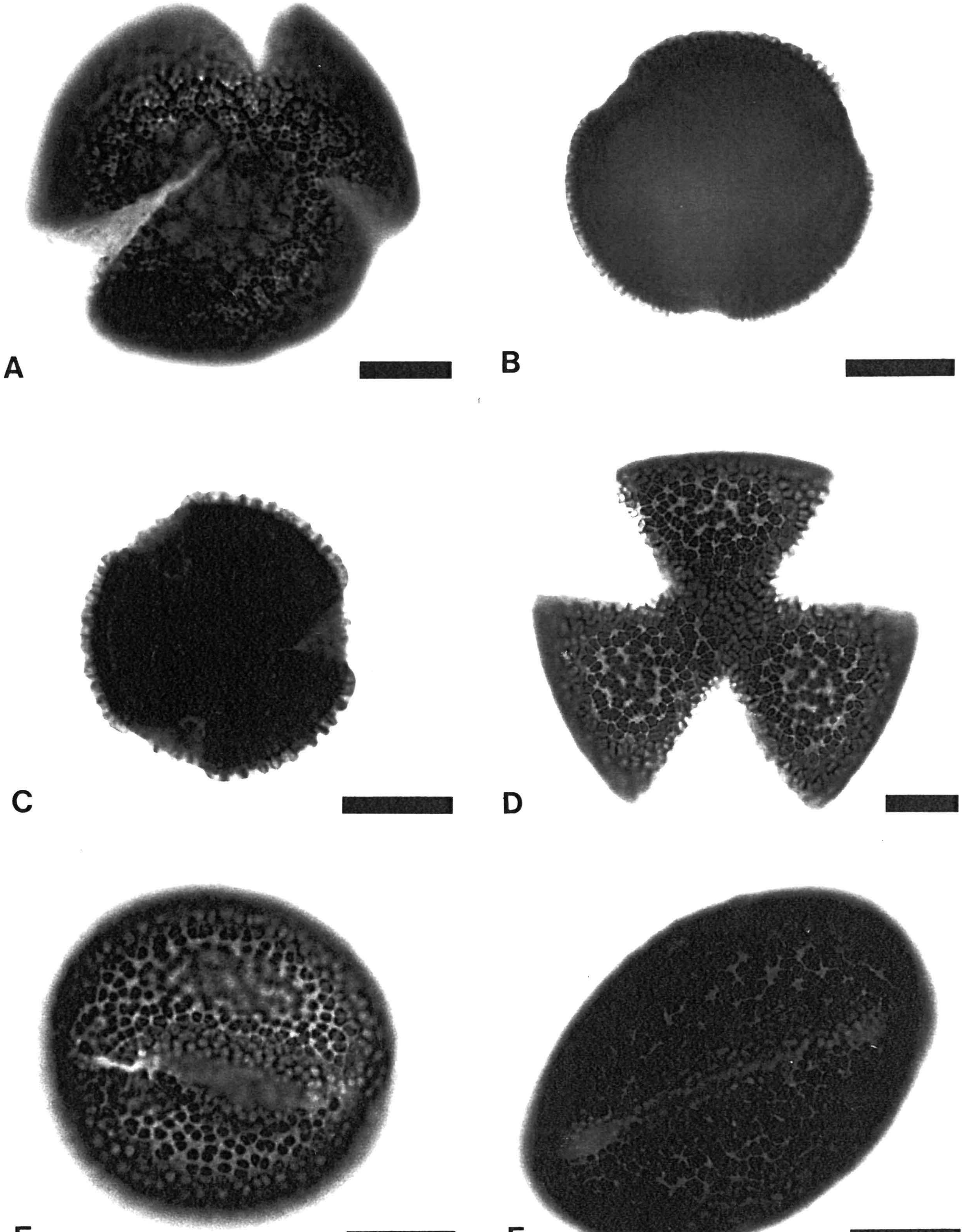


Figure 5.2 A—F. LM micrographs of *Oxalis* pollen. (A) Pollen subtype C6, *O. henrici* [261.1], polar view showing sculptural detail. (B) Pollen subtype C9, *O. deserticola* [253.1], optical section in polar view. (C) Pollen subtype C11, *O. sonderiana* var. *alba* [132.1], optical section in polar view. D—F: Pollen subtype D1. (D) *O. tenella* [138.1], polar view showing sculptural detail. (E) *O. xantha* [208.1], equatorial view showing sculptural detail. (F) *O. hirta* var. *polioeides* [175.1], equatorial view showing sculptural detail. Scale bar = 10 μm.

can vary considerably within one grain type or even within a particular species (Moore & Webb 1987). Variation in grain shape can also be caused by the preparatory treatment of the pollen, the choice of embedding medium and the time lapse between specimen preparation and study.

Very little is known about the shape of pollen grains in the Oxalidaceae. Huynh (1969a) generally refers to *Oxalis* pollen as being prolate. Erdtman (1952) described oxalidaceous pollen as subprolate, spherical or oblate. The only *Oxalis* species he mentions is the South American *O. acetocella* L., with subprolate pollen grains.

Grain shapes were investigated in the LM analysis of this study (Figures 5.1—5.2). It was found to be of minor importance, with most grains being triangularly rounded in polar view and spherical to oblate (seldomly prolate) in equatorial view. The apolar grains of pollen types A and D are mostly isodiametical, while some of the polar grains of pollen type D seem almost square in polar view.

5.4 Apertures

Traditionally aperture shape, number and arrangement are considered important taxonomic characters. Erdtman (1971) developed the NPC-system (N = number; P = position; C = character) which is commonly used to classify pollen grains by means of their apertures. This classification method is basically simple and consistent.

Huynh (1969a) stressed the taxonomic importance of apertures in the pollen of the Oxalidaceae. She found only colporate grains in the genera *Averrhoa, Sarcotheca, Eichleria, Dapania, Hypsocharis* and *Biophytum,* all of which are considered more primitive than *Oxalis.* Within *Oxalis* colporate grains dominate in the four most primitive South American sections, while the more advanced South American sections mostly have colpate grains. Porate pollen was recorded from in a single species. Only colpate grains were found among the South African species. These are mostly tricolpate or pantocolpate, with only a few taxa having tetracolpate or aberrant pollen grains. Within the colpate group, Huynh (1969a) used sculptural features to define pollen types, and found that the division between tricolpate and pantocolpate grains was mostly congruent with divisions based on sexine structure.

Due to these findings and the fact that Huynh (1969 a & b) used only LM analysis, detailed SEM and TEM studies of the pollen wall sculpture and structure were emphasised in this investigation. They were primarily used to define 21 different pollen types/subtypes, while aperture number and arrangement were considered of secondary importance.

All the southern African species were found to have tricolpate, tetracolpate or pantocolpate grains. Within pollen type A apolar, pantocolpate grains dominate with only two taxa having tricolpate or tetracolpate grains. Tricolpate grains were found to be the norm in both pollen types B and C, with some apertural aberrations recorded within pollen type C. Pollen type D is predominantly pantocolpate, although tricolpate and tetracolpate grains were found in a few taxa. This pollen type is renowned for a high occurrence of apertural aberrations (see section 5.6).

Due to the variations in grain size between the different stylar whorls, detailed measurements of apocolpial diameters and exact colpus lengths were not undertaken. These dimensions are directly proportional to the actual grain diameter, which, as was discussed earlier, is a rather variable character within *Oxalis*. For the purpose of this discussion it is sufficient to note that most polar grains have well-defined but reduced apocolpial areas, with colpi reaching well into the polar regions. The colpi of pantocolpate grains are much shorter than those of tri- and tetracolpate grains. Although the colpus membrane of all the pollen types appear moderately to coarsely granular, this feature is the most pronounced in pollen types A and D. Here distinct sexine islands interrupt the actual colpus membrane.

5.5 Exine structure

The exine is defined as the outer layer of the pollen grain wall which is highly resistant to strong acids and bases and which is comprised primarily of sporopollinin. Two conventions exist to describe the different exine layers. They are both referred to in the present study, and are therefore summarised in Figure 5.3 to avoid confusion.

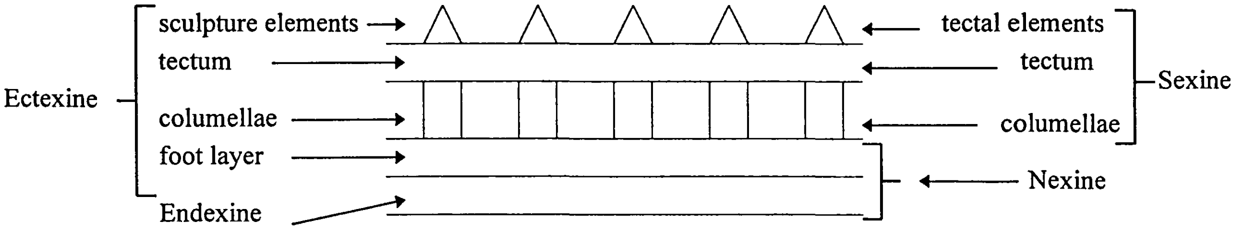


Figure 5.3 Diagrammatic presentation of the different exine layers recognised in a pollen grain wall (after Punt *et al.* 1994).

Modern SEM and TEM techniques have facilitated detailed exine studies, which have resulted in the identification of numerous taxonomically significant characters (Hong &

Hedberg 1990; Luegmayer 1993). Amongst others, these include features such as exine thickness, ratio between sexine and nexine diameters, occurrence and type of tectum, occurrence and type of supratectal structures, structure of the infra-reticulum, presence or absence of a footlayer and footlayer diameter.

In *Oxalis* exine characters proved to be most useful in classifying the grains, and formed the basis of the primary delimitation of various pollen types. Four main exine types were identified and used to subdivide the genus palynologically into the following four groups:

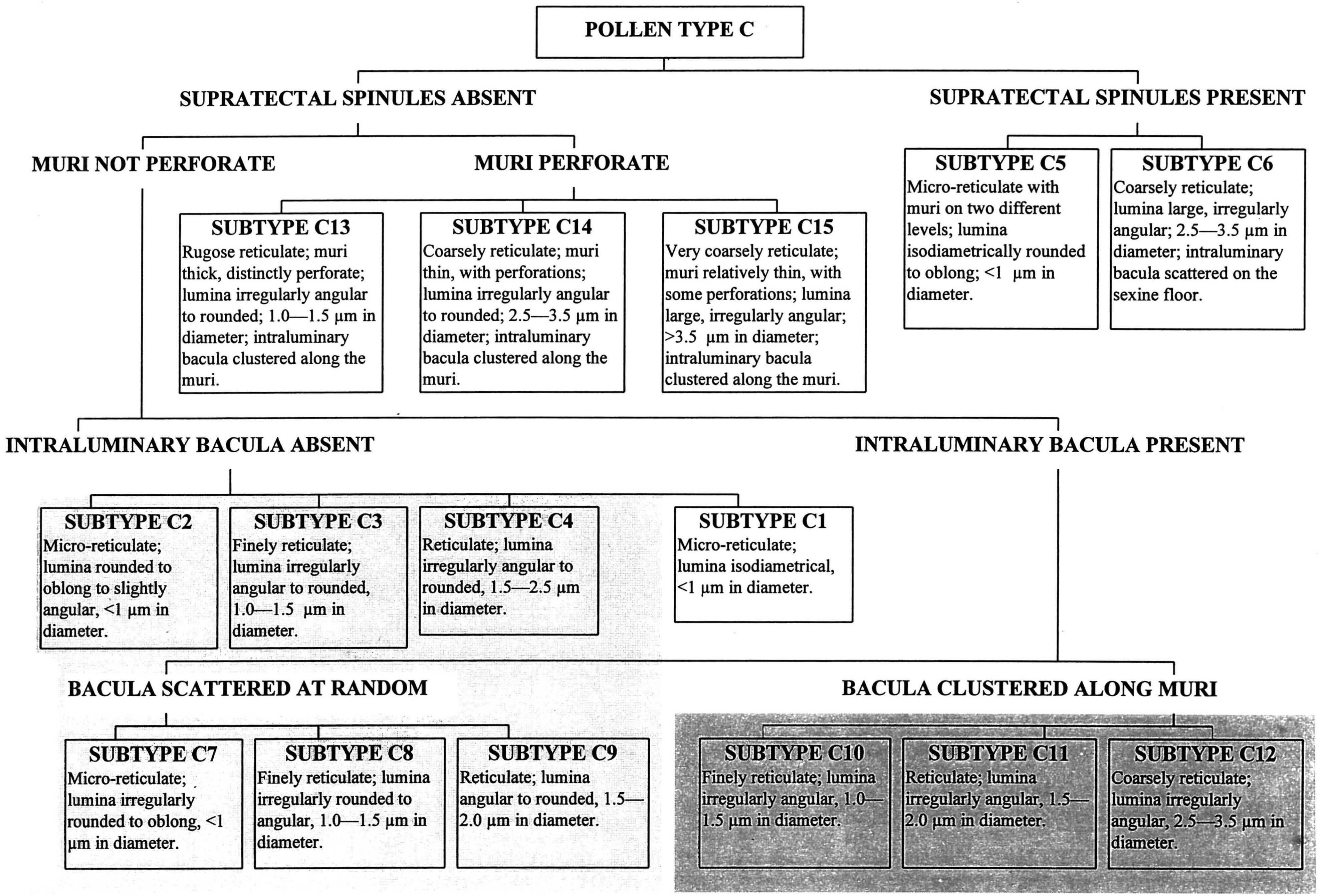
- Rugulate-reticulate group (Pollen type A)
- Micro-rugulate-spinate group (Pollen type B)
- Reticulate group (Pollen type C)
- Supra-areolate group (Pollen type D)

Pollen type A is characterised by a unique, stable rugulate-reticulate tectum with small, sharp supratectal spinules. It displays very little tectal variation, and grains are pantocolpate or less often tricolpate/tetracolpate.

Pollen type B has a very distinct micro-rugulate tectum with large supratectal spines and was only observed in one species. The grains are always tricolpate.

Pollen type C is semitectate with a reticulate wall structure and is by far the most frequent among the taxa examined. In *Oxalis* this pollen type is predominantly tricolpate, with only a few tetracolpate or aberrant grains having been observed. It is, however, characterised by considerable structural variation. Detailed exine characters were therefore used to subdivide pollen type C into 15 subtypes (Figure 5.4). These included:

- presence or absence of intraluminary processes in the mesocolpium
- distribution of the intraluminary processes (scattered randomly throughout the lumina or predominantly clustered along the muri)
- presence or absence of supratectal processes
- presence or absence of muri perforations
- lumina shape
- predominant lumina diameter



POLLEN TYPE C

SUPRATECTAL SPINULES ABSENT

MURI NOT PERFORATE

MURI PERFORATE

SUBTYPE C13
Rugose reticulate; muri thick, distinctly perforate; lumina irregularly angular to rounded; 1.0—1.5 µm in diameter; intraluminary bacula clustered along the muri.

SUBTYPE C14
Coarsely reticulate; muri thin, with perforations; lumina irregularly angular to rounded; 2.5—3.5 µm in diameter; intraluminary bacula clustered along the muri.

SUBTYPE C15
Very coarsely reticulate; muri relatively thin, with some perforations; lumina large, irregularly angular; >3.5 µm in diameter; intraluminary bacula clustered along the muri.

SUPRATECTAL SPINULES PRESENT

SUBTYPE C5
Micro-reticulate with muri on two different levels; lumina isodiametrically rounded to oblong; <1 µm in diameter.

SUBTYPE C6
Coarsely reticulate; lumina large, irregularly angular; 2.5—3.5 µm in diameter; intraluminary bacula scattered on the sexine floor.

INTRALUMINARY BACULA ABSENT

SUBTYPE C2
Micro-reticulate; lumina rounded to oblong to slightly angular, <1 µm in diameter.

SUBTYPE C3
Finely reticulate; lumina irregularly angular to rounded, 1.0—1.5 µm in diameter.

SUBTYPE C4
Reticulate; lumina irregularly angular to rounded, 1.5—2.5 µm in diameter.

SUBTYPE C1
Micro-reticulate; lumina isodiametrical, <1 µm in diameter.

INTRALUMINARY BACULA PRESENT

BACULA SCATTERED AT RANDOM

SUBTYPE C7
Micro-reticulate; lumina irregularly rounded to oblong, <1 µm in diameter.

SUBTYPE C8
Finely reticulate; lumina irregularly rounded to angular, 1.0—1.5 µm in diameter.

SUBTYPE C9
Reticulate; lumina angular to rounded, 1.5—2.0 µm in diameter.

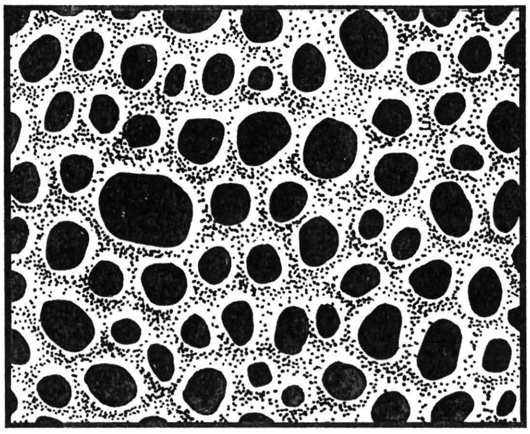
BACULA CLUSTERED ALONG MURI

SUBTYPE C10
Finely reticulate; lumina irregularly angular, 1.0—1.5 µm in diameter.

SUBTYPE C11
Reticulate; lumina irregularly angular, 1.5—2.0 µm in diameter.

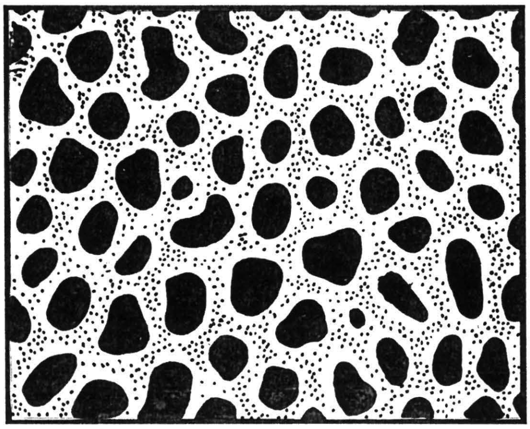
SUBTYPE C12
Coarsely reticulate; lumina irregularly angular, 2.5—3.5 µm in diameter.

Figure 5.4 Cluster diagram of the subtypes of pollen type C



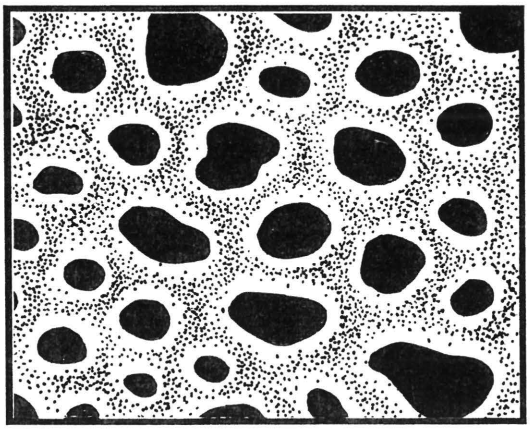
Tectum micro-reticulate; lumina isodiametrically rounded; mesocolpial intraluminary bacula absent.

Figure 5.5.1 Schematic presentation of pollen subtype C1



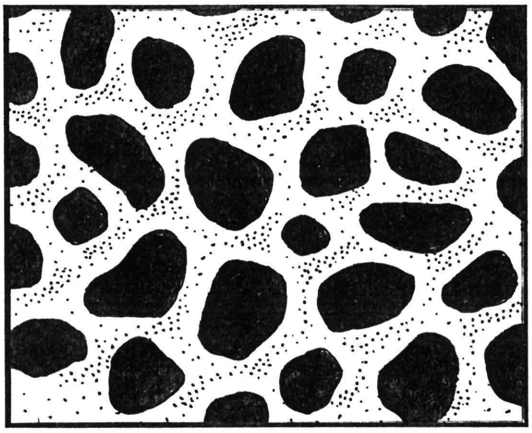
Tectum micro-reticulate; lumina rounded to oblong to slightly angular; mesocolpial intra-luminary bacula absent.

Figure 5.5.2 Schematic presentation of pollen subtype C2



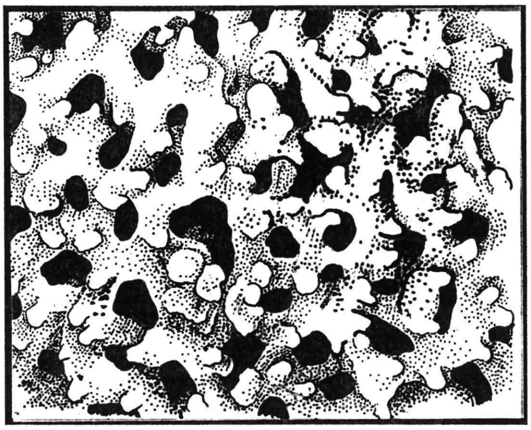
Tectum finely reticulate; lumina irregularly angular to rounded; mesocolpial intraluminary bacula absent.

Figure 5.5.3 Schematic presentation of pollen subtype C3



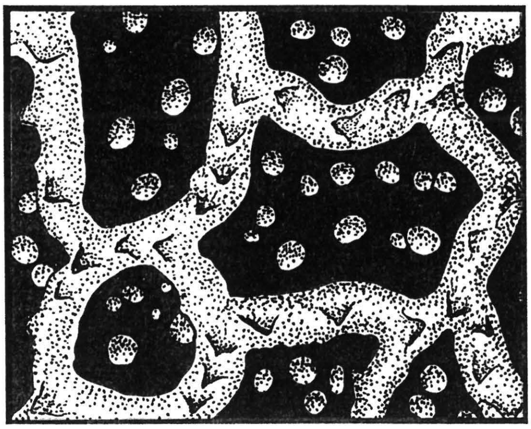
Tectum reticulate; lumina large, irregularly angular to rounded; mesocolpial intraluminary bacula absent.

Figure 5.5.4 Schematic presentation of pollen subtype C4



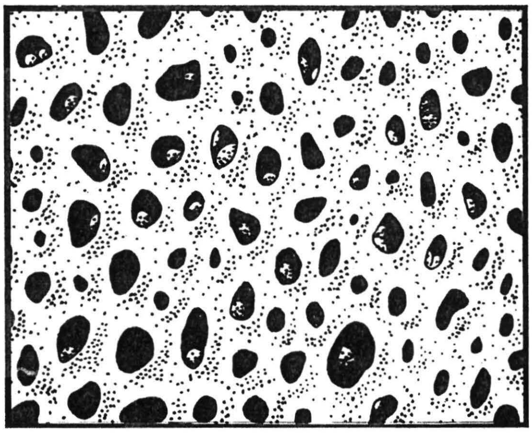
Tectum complex, micro-reticulate with muri on two different levels; blunt supra-tectal spinules present.

Figure 5.5.5 Schematic presentation of pollen subtype C5



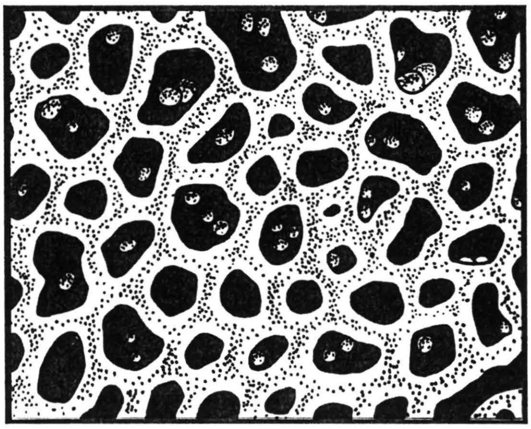
Tectum a coarse open reticulum; lumina irregularly angular; supratectal spinules present; intra-luminary bacula scattered on the nexine floor.

Figure 5.5.6 Schematic presentation of pollen subtype C6



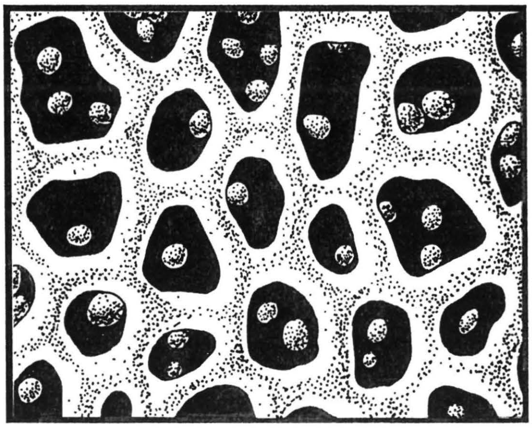
Tectum micro-reticulate; lumina irregularly rounded to oblong; intraluminary bacula scattered on the nexine floor.

Figure 5.5.7 Schematic presentation of pollen subtype C7



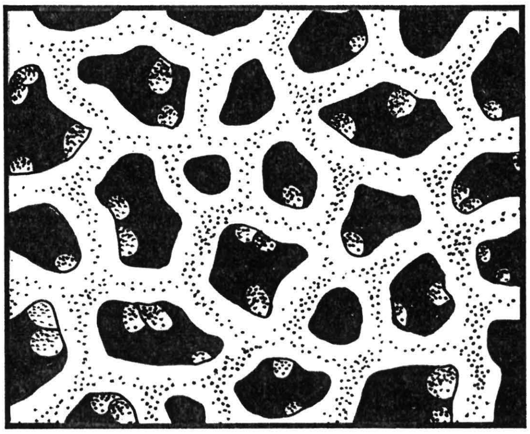
Tectum finely reticulate; lumina irregularly rounded to angular; intra-luminary bacula scattered on the nexine floor.

Figure 5.5.8 Schematic presentation of pollen subtype C8



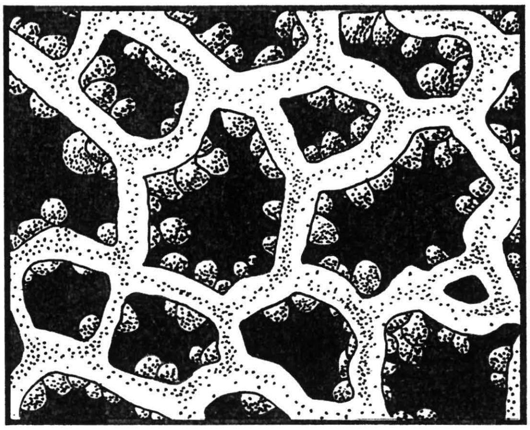
Tectum reticulate; lumina angular to rounded; intra-luminary bacula scattered on the nexine floor.

Figure 5.5.9 Schematic presentation of pollen subtype C9



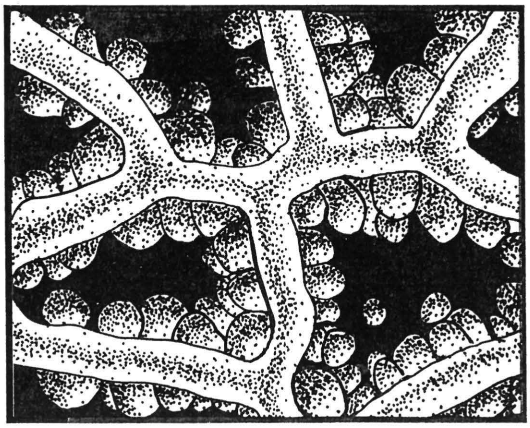
Tectum finely reticulate; lumina irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.10 Schematic presentation of pollen subtype C10



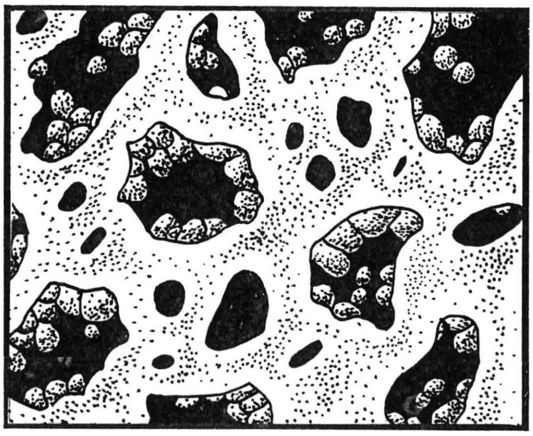
Tectum reticulate; lumina irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.11 Schematic presentation of pollen subtype C11



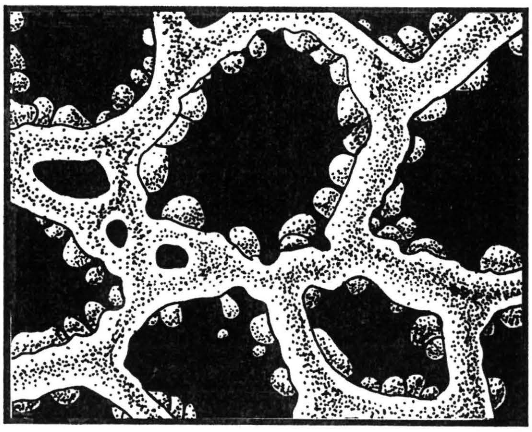
Tectum coarsely reticulate; lumina irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.12 Schematic presentation of pollen subtype C12



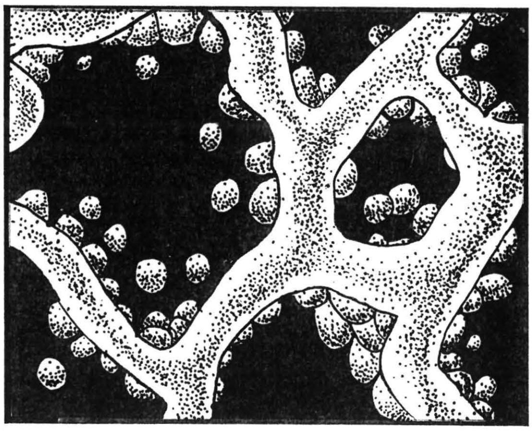
Tectum rugose reticulate; muri thick, distinctly perforated; lumina irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.13 Schematic presentation of pollen subtype C13



Tectum coarsely reticulate; muri thin, sometimes perforated; lumina irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.14 Schematic presentation of pollen subtype C14



Tectum very coarsely reticulate; muri relatively thin, sometimes perforated; lumina large, irregularly angular; intraluminary bacula clustered along the muri.

Figure 5.5.15 Schematic presentation of pollen subtype C15

The arbitrary size classes identified and used in the delimitation are summarised in Table 5.2. Schematic presentations of the 15 subtypes are provided in Figures 5.5.1—5.5.15. The subdivisioning was complicated by the uninterrupted continuum displayed by most of the above-mentioned taxonomically viable characters. Demarcating the subtypes was therefore difficult and done somewhat arbitrarily. While some taxa agreed with a specified subtype with little or no uncertainty, others were more difficult to group. This subgrouping within pollen type C may thus be a fairly artificial arrangement. However, as noted by Stace (1984), the only way to understand a group of organisms is to subdivide them into recognisable categories and then sorting out and understanding the array that exists. The different subgroups help to display the range of variation that exists and might even contribute to a better understanding of the taxonomy of the genus as a whole. A statistical analysis of unweighted, numerical data obtained in the preliminary AFM study correlates remarkably well with the groupings proposed here (see Appendix).

Pollen type D has a unique, supra-areolate wall structure. It is characterised by high, free-standing supratectal areaolae on an uneven, sometimes verrucate to baculate tectum traversed by micro-channels. The areolae are irregular, triangular, rounded or club-shaped, each terminating in a central spinule. They are separated by grooves which form a negative reticulum. The infratectum consists of a weakly developed columellar layer subtend by an uneven footlayer interrupted by micro-channels. An identical wall structure was recorded from the grass species *Pariana stenolemma* Tutin (Salgado-Labouriau *et al.* 1992). Areolar pollen is also known from the genera *Apama* Lam. (Aristilogiaceae) and *Phyllanthus* L. (Euphorbiaceae), but in both of these cases the areolae constitute tectal rather than supratectal structures (Punt *et al.* 1994). This wall structure is also reminiscent of the crotonoid type (Punt *et al.* 1994) found in families such as the Thymelaeaceae and Euphorbiaceae, but lacks the characteristic underlying ring structure. Pollen type D has tri-, tetra- or pantocolpate grains and apertural characters were initially considered for the delimitation of subtypes. Due to the high percentage of apertural grain aberrations, this character was, however, considered too unstable. Alternatively variations in the shape, size and arrangement of the areolae were used to demarcate four subtypes. Pollen subtype D1 (Figures 6.18 & 6.19) represents the most typical form, while the other subtypes (D2, D3 & D4) (Figures 6.20—6.22) are merely constant variations on the same basic theme.

Table 5.3 summarises the distribution of the different pollen types within the genus. It also indicates how the pollen groupings correspond to the taxonomic groupings proposed by Salter (1944). The average thickness of the individual wall layers of the different pollen types are provided in Table 5.4.

5.6 Aberrant grains

The occurrence of aberrant or abnormal pollen is a well-documented phenomenon found in various angiosperm families. Some examples include the Boraginaceae (Johnston 1953), Clusiaceae (Clarke 1975), Iridaceae (Mulcahy 1965), Fabaceae (Ferguson 1980), Linaceae (Saad 1961), Saxifragaceae (Ornduff 1970), Sterculiaceae (Köhler 1973) and the Rubiaceae (Bremekamp 1963; Baker 1956).

Species displaying pollen aberrations normally have a distinct, regular pollen type, which can be distinguished by such features as the P/E ratio, exine structure or aperture number and/or shape. Additional to these normal grains, they produce a variable proportion of irregular grains. The term irregular could refer to distinct differences in grain size, a phenomenon often observed in *Oxalis* and many other tristylic flowers (Johansson 1992). In the majority of studied cases, however, it refers to asymmetric grains with a haphazard structural appearance and considerable variation in aperture number and shape. In *Oxalis* these aberrations affect the arrangement of the colpi and never the exine structure. The aberrant grains are highly variable to the extent that two grains rarely look identical. Generalised categories, based on aperture number and arrangement, could, however, be identified:

- 2-zonocolpate (Figure 5.6 A). Isopolar grains with two equatorial colpi. The colpi are close to each other, leaving the impression that a third one is lacking.
- 4-zonocolpate (Figures 5.6 B—C). Isopolar grains with four equatorial colpi. (Similar to tetracolpate, but viewed as aberrant when it is the exception rather than the rule)
- 6-pantocolpate (Figure 5.6 D). Anisopolar grains with three longitudinal colpi meeting or approaching one another at one pole, but extending only about two-thirds of the way down the grain where they are linked together by three subsidiary transverse colpi.
- 2-pantocolpate (Figure 5.6 E). Anisopolar grains with the surface of the grain divided into six more or less square areas delimited by 12 colpi which fuse.
- 4-aperturate (Figures 5.7 A). Isopolar grains with two pairs of colpi, each pair joined to form a ring running longitudinally around the grain, avoiding the poles.
- Spiralaperturate (Figures 5.7 B—D). Anisopolar grains with a single aperture running around the grain in a spiral fashion without running over the poles.
- 3-zonocyclicolpate (Figure 5.7 E). Isopolar grains with three circular colpi evenly arranged on the equatorial plane.

Individual grains can be roughly referred to one of these categories, even though the members of a single category are far more variable than the members of a normal pollen type. Categorising abnormal pollen grains in this way does not exhaust the possibilities of forms one could find, but at least it indicates the range of variation that exists. In general grains with higher aperture numbers were found to be slightly bigger than normal, while grains with a lower number of apertures showed a slight reduction in size.

Aberrant grains were detected in a number of *Oxalis* taxa (Table 5.5), especially amongst those with pollen type D (supra-areolate). In this group 78% of all the included taxa, belonging either to the subsections *Sessilifoliatae* or *Linearis* of the section *Angustatae*, display pollen abnormalities. There is a very high frequency of aberrant grains per anther, so that normal tricolpate grains are reduced to a vast minority. Aberrant forms 12-pantocolpate, 4-aperturate and spiralaperturate are most frequently found.

Table 5.5 also reflects the occurrence of abnormal pollen in a small number of taxa (5 %) included in the reticulate pollen subtypes C1, C4, C7 and C8. In total twelve taxa from three different sections and two different subsections display aberrant grains. In this group, aberrant grains are limited in numbers and only form a very small percentage of the total number of grains per anther. The most frequent aberrations include 4-zonocolpate and 6-pantocolpate grains.

No abnormal grains were found in pollen types A or B. Although the exine structure of pollen types C and D differs markedly, it is curious to note that in both of these groups grains from Salter's section *Angustatae* subsection *Sessilifoliatae* and subsection *Linearis* display pollen aberrations. Ferguson (1980) mentions that the abnormalities seen phenotypically probably result from abnormalities during meioses, which results in variation in spatial relations of the grains in the tetrad. Such grains are produced almost at random, rather than being the result of selection. This implies that the abnormalities can be attributed to physical rather than genetic deviation from the standard condition. Ultimately this means that the distribution of the phenomenon in a genus would not necessarily coincide with the taxonomic relationships. Susceptibility towards the tendency to produce abnormal grains may, however, have a genetic basis. The evolutionary significance of grain aberrations is discussed in more detail in section 7.5.6.1.

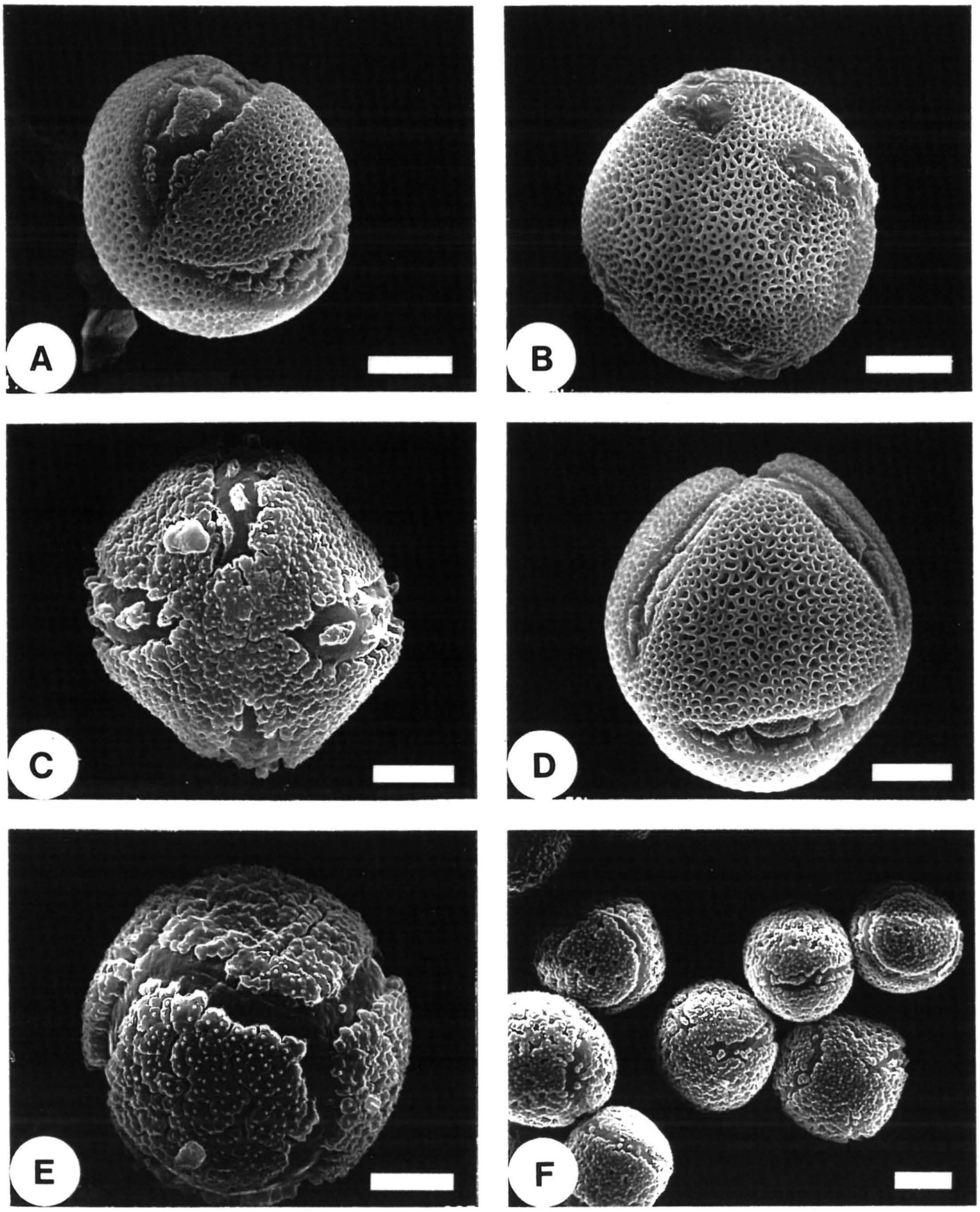


Figure 5.6 A—F. Aberrant pollen grains of *Oxalis* species. (A) 2-zonocolpate grain of *O. purpurascens* [19.1]. (B, C) 4-zonocolpate grains of *O. polyphylla* var. *alba* [227.1] and *O. reclinata* var. *quinata* [246.1]. (D) 6-pantocolpate grain of *O. polyphylla* var. *hirta* [225.1]. (E) 12-pantocolpate grains of *O. cuneata* [239.1]. (F) aberrant grains of *O. burkei* [238.1]. Scale bar = 10 μm.

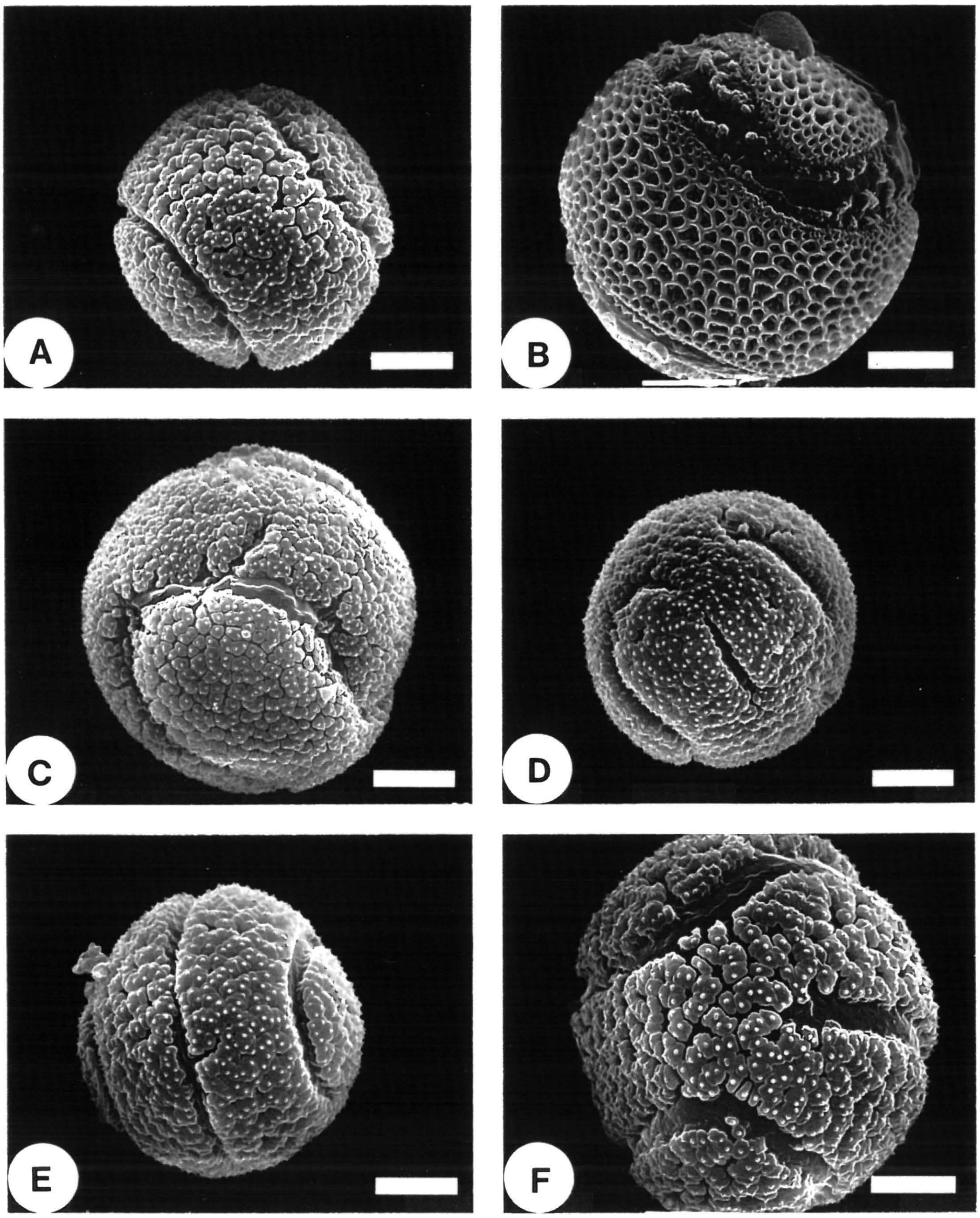


Figure 5.7 A—F. Aberrant pollen grains of *Oxalis* species. (A) 4-aperturate grains of *O. cuneata* [239.1]. (B—D) spiralaperturate grains of *O. flaviuscula* var. *longifolia* [150.1], *O. oreophila* [240.1] and *O. sp.* [297]. (E) 3-zonocyclicolpate grain of *O.* sp. [297]. (F, G) aberrant grains of *O. sp.* [297]. Scale bar = 10 µm.

5.7 Polyploidy

Various previous studies indicated that higher ploidy levels often concur with an increase in grain size, an increase in the number of apertures per grain and an increase in the percentage of abnormal grains (Bronckers 1963; Punt *et al.* 1974; Clarke 1975; Chaturvedi *et al.* 1990). Clark (1975), however, warns against the generalised assumption that polyploidy promotes irregular meiotic behaviour, resulting in aberrant pollen.

Very limited cytogenetic work has been done in *Oxalis*, the most comprehensive being that of Marks (1956). He followed the classification system of Salter (1944) and used plants donated to him by Salter for his chromosome counts. His results, summarised in Table 5.5, indicate a very high degree of polyploidy for the genus as a whole. Of the 27 taxa studied, 18 display polyploid levels from tetraploids up to octaploids. Marks (1956) gives chromosome numbers for three taxa with aberrant pollen grains: *O. hirta* var. *hirta*, *O. ciliaris* var. *ciliaris* and *O. cuneata*. Of these, only two are polyploid. This, together with the fact that so many other polyploid taxa seem to have normal pollen grains, casts further doubt on the assumption that polyploidy is directly correlated with an increase in pollen abnormalities.

Table 5.1 Summary of polar axis and equatorial diameters of *Oxalis* pollen from different stylar whorls, as determined by LM analysis. PT = Pollen type

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (μm)	Equatorial diameter (μm)	Polar axis (μm)	Equatorial diameter (μm)	
3.1	46.24	48.72	28.04	28.95	C2
4.1	31.23	32.23	27.32	28.17	C2
5.1	39.69	43.05	26.99	28.68	C2
6.1	37.04	37.56	27.40	28.22	C2
7.1	39.84	40.58	30.91	28.65	C2
8.1	41.10	45.03	35.82	37.44	C2
9.2	49.84	50.06	29.88	29.00	C2
10.2	39.10	43.30	27.71	30.58	C3
11.2	41.52	44.00	30.48	28.09	C2
12.2	52.50	54.64	46.25	47.40	C3
13.1	50.85	51.71	37.05	38.53	C3
14.1	50.47	51.99	35.08	36.60	C3
15.2	50.18	55.40	39.37	45.04	C3
16.1	40.12	44.84	31.17	32.86	C7
17.2	52.45	55.58	34.14	36.30	C1
18.1	45.96	47.73	32.13	36.30	C1
19.2	37.72	38.25	33.00	33.89	C8
22.1	38.55	38.14	32.64	32.39	C7
23.2	45.80	50.76	33.89	30.47	C9
24.2	38.69	40.12	29.65	30.55	C8
26.1	40.77	41.71	28.80	30.87	C7
27.1	38.95	40.48	27.39	33.06	C9
28.1	30.34	33.37	29.18	29.66	C9
29.1	31.26	33.20	25.72	26.78	C7
30.2	42.44	44.04	37.77	36.53	C1
31.2	39.92	41.80	36.92	37.71	C3
32.2	34.05	34.61	28.15	28.38	C1
33.1	41.55	43.54	35.15	36.62	C3
34.1	39.57	41.86	35.93	34.35	C2
35.1	41.94	43.14	32.67	33.01	C2
36.2	34.68	37.37	—	—	C2

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (µm)	Equatorial diameter (µm)	Polar axis (µm)	Equatorial diameter (µm)	
39.1	47.32	48.20	38.15	39.97	C8
40.1	44.14	48.79	26.88	28.06	C2
41.1	39.60	41.64	—	—	C3
42.1	43.29	45.52	32.01	34.10	C2
43.1	49.15	50.01	36.70	37.06	C9
45.2	42.16	47.20	29.15	34.46	C2
46.1	42.78	46.54	28.00	31.84	C2
47.1	56.33	60.44	42.61	46.16	C8
48.1	42.93	46.81	34.04	36.34	C8
49.1	33.47	35.85	27.06	29.12	C2
50.1	42.57	46.14	26.71	29.73	C3
51.1	39.82	39.98	29.84	27.52	C4
52.1	39.74	40.98	33.83	34.61	C3
53.1	47.53	48.24	37.79	38.15	C2
55.2	53.07	58.70	45.23	51.46	C3
56.1	53.07	54.46	35.06	37.62	C2
57.1	50.63	51.40	42.56	43.89	C8
58.2	44.16	47.69	35.39	36.08	C8
59.2	40.99	43.86	31.23	32.31	C2
61.1	42.27	43.58	34.74	35.85	C4
62.1	44.70	47.37	25.37	29.35	C2
63.1	43.27	43.58	35.83	36.82	C2
64.1	40.88	42.54	30.31	32.91	C2
65.2	53.80	54.63	34.72	36.82	C2
66.1	47.40	48.49	34.90	35.83	C2
67.2	57.92	58.72	47.00	48.09	C8
69.2	49.44	51.48	40.55	43.07	C2
70.3	41.72	43.26	35.47	36.03	C3
71.1	41.17	41.66	49.29	50.25	C2
73.1	37.88	38.63	26.10	27.91	C3
74.1	68.21	68.48	51.23	52.43	C4
75.1	52.36	53.66	45.29	45.91	C2

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (µm)	Equatorial diameter (µm)	Polar axis (µm)	Equatorial diameter (µm)	
77.1	47.68	49.07	35.49	37.45	C3
78.2	49.01	51.07	34.89	36.43	C2
79.2	52.06	55.24	33.11	35.47	C2
80.2	44.01	44.49	33.55	34.99	C2
81.2	47.11	47.80	36.38	37.32	C10
82.2	48.01	51.68	32.84	35.49	C2
83.1	48.94	49.24	35.31	38.09	C2
84.2	39.38	40.36	30.95	31.27	C2
85.2	39.45	41.64	34.42	36.33	C2
86.2	37.08	40.10	30.01	31.75	C2
87.2	53.34	56.15	42.70	44.93	C2
88.1	48.34	51.60	35.09	37.38	C2
89.1	45.37	45.73	35.61	35.96	C2
90.2	54.16	56.98	—	—	C2
91.1	54.88	56.19	—	—	C4
92.1	50.01	51.87	40.95	41.77	C2
93.1	48.83	49.59	40.72	41.73	C2
94.1	39.00	39.11	31.86	32.27	C2
95.1	52.82	55.21	40.08	42.09	C4
96.1	54.94	59.43	42.51	45.17	C3
97.2	37.68	39.28	29.39	30.48	C3
98.2	46.83	47.47	—	—	C3
99.1	46.15	46.84	26.55	27.70	C2
100.1	46.50	46.99	—	—	C3
101.1	—	—	31.16	31.93	C4
102.1	45.69	46.24	34.55	34.89	C2
103.1	46.69	46.82	28.65	28.78	C10
104.1	42.14	47.89	33.32	34.28	B
106.1	—	44.32	—	35.79	A
107.1	—	38.27	—	32.68	A
108.2	—	39.06	—	31.55	A
109.1	41.43	41.89	32.80	33.97	C7

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (µm)	Equatorial diameter (µm)	Polar axis (µm)	Equatorial diameter (µm)	
110.2	—	42.14	—	32.25	A
111.1	37.33	37.76	33.74	34.90	A
112.1	—	48.04	—	37.03	A
113.2	—	40.05	—	35.01	A
114.2	—	41.08	—	33.41	A
115.2	35.72	37.20	29.46	30.56	C10
116.2	41.05	42.64	32.06	34.39	C10
117.1	42.19	43.67	48.95	51.01	C10
118.1	48.49	50.50	30.85	31.86	C10
119.2	37.58	38.29	29.40	30.67	C10
120.2	44.67	45.87	32.62	33.33	C10
122.1	38.17	38.55	33.52	34.22	C10
123.2	35.76	49.41	30.97	32.75	C10
126.1	43.54	45.97	—	34.03	C2
127.2	41.75	42.15	33.57	34.12	C8
130.1	41.75	43.73	33.16	34.91	C2
131.2	35.70	37.48	29.80	31.49	C10
132.2	38.04	39.24	27.15	29.61	C11
133.2	33.39	34.02	29.37	29.96	C10
134.1	—	—	27.11	27.13	C11
135.2	45.50	46.53	27.19	27.47	C10
136.2	33.51	33.84	26.03	26.41	C10
137.1	40.63	41.22	26.13	26.33	C11
138.2	39.16	39.18	32.12	33.10	D1
139.2	43.33	44.25	32.79	33.12	D1
140.2	62.04	62.34	39.65	39.70	D1
142.2	52.59	53.54	36.43	38.38	D1
143.2	45.63	46.57	33.85	35.40	D1
145.2	46.72	47.67	33.62	34.84	C10
146.2	50.03	52.69	37.57	40.36	C7
149.2	50.28	50.89	32.01	32.30	C10
150.2	44.70	46.39	34.50	36.94	C10

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (µm)	Equatorial diameter (µm)	Polar axis (µm)	Equatorial diameter (µm)	
151.1	42.20	44.70	31.22	33.01	C2
152.1	44.24	45.24	32.58	33.57	C10
153.2	47.98	49.59	34.75	36.41	C10
154.2	38.51	40.45	31.64	32.17	C2
156.2	43.96	45.09	30.21	31.71	C2
160.1	43.96	45.19	31.61	33.02	C3
162.1	43.38	44.44	35.64	36.23	C9
163.1	33.43	34.01	25.26	26.08	C2
164.1	36.53	37.12	29.01	30.23	C2
165.1	37.85	37.90	28.30	30.20	C2
166.2	43.92	45.20	31.74	32.53	C3
169.1	32.52	33.12	26.09	26.27	C2
170.2	38.04	39.61	29.05	29.64	C2
171.2	52.49	53.90	38.20	39.95	D1
172.2	52.67	53.98	38.71	39.45	D1
174.3	—	81.99	—	58.34	D4
175.2	—	61.23	—	42.75	D1
176.2	—	75.21	—	44.15	D4
178.2	39.58	41.67	32.01	33.97	D1
179.1	49.30	51.43	37.78	39.75	D1
180.1	51.15	52.55	41.94	42.05	C7
181.1	49.58	51.50	45.01	45.56	C9
182.2	46.83	47.35	36.60	36.82	C2
185.2	38.84	40.60	33.81	35.14	C15
186.1	38.83	39.78	33.83	34.69	D1
187.1	45.82	46.17	36.69	37.14	C8
188.1	34.05	35.28	30.40	30.70	C8
189.1	46.06	47.76	38.68	39.43	C8
190.1	44.85	45.72	26.64	28.79	C8
192.1	42.37	43.45	37.22	38.04	C9
193.1	48.26	50.98	38.57	39.25	C2
194.2	46.44	50.11	31.92	34.14	C10

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (µm)	Equatorial diameter (µm)	Polar axis (µm)	Equatorial diameter (µm)	
195.1	39.18	40.33	28.27	29.62	C10
196.1	34.08	36.03	25.67	27.14	C10
197.2	54.54	55.31	35.06	36.47	D1
198.2	—	40.52	—	30.65	D3
201.2	50.00	50.42	37.57	37.64	D1
202.2	46.14	46.42	33.40	34.15	D1
203.1	44.77	45.70	33.80	32.87	D1
204.2	42.65	43.18	33.57	34.50	D1
205.1	—	53.54	—	37.31	D1
206.1	—	52.15	—	42.13	D1
207.2	38.51	39.64	30.85	32.53	C7
208.2	—	37.65	—	31.46	D1
209.1	42.16	44.65	31.51	33.77	C12
210.2	40.84	42.15	27.94	30.80	C11
211.2	34.66	35.08	27.96	28.20	C14
213.2	37.31	38.37	30.91	31.82	C8
216.1	—	—	32.34	33.44	C2
217.2	49.25	50.97	42.34	43.90	C8
219.2	49.70	50.11	37.93	38.58	C8
220.3	39.27	42.71	34.84	36.91	C8
221.2	52.58	53.00	41.72	42.12	C8
222.1	40.63	41.25	32.91	34.51	C8
224.2	46.08	48.31	39.52	40.41	C8
225.1	45.70	46.44	35.76	37.49	C8
226.2	50.60	51.68	37.47	38.25	C8
229.1	42.27	42.37	35.17	35.52	C9
230.2	48.19	48.59	37.22	38.04	C2
231.2	36.50	37.75	30.27	31.27	C7
232.2	39.29	42.10	29.93	31.55	C8
233.1	42.38	43.85	27.69	28.63	C8
234.2	42.13	44.57	33.99	36.14	C8
235.1	42.24	43.78	33.43	35.71	C5

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (μm)	Equatorial diameter (μm)	Polar axis (μm)	Equatorial diameter (μm)	
237.1	42.97	43.69	34.53	35.52	D1
238.1	—	34.13	—	29.16	D1
239.1	—	57.37	—	44.95	D1
240.1	—	58.40	—	44.36	D1
241.1	—	46.00	—	32.06	D1
242.1	—	54.63	—	39.03	D1
243.2	42.55	43.70	34.12	35.40	C8
244.1	53.68	53.52	39.36	39.71	D1
246.1	—	62.79	—	45.13	D1
247.1	—	42.00	—	34.23	D1
249.2	45.29	46.13	29.19	30.47	D1
250.2	—	54.24	—	38.89	D1
251.1	46.93	47.29	39.90	40.24	C8
252.1	38.25	43.15	31.66	34.00	C2
253.2	44.29	44.78	34.83	34.90	C9
254.2	44.40	44.78	35.05	35.88	C13
255.1	37.42	37.81	29.67	30.29	C9
256.1	38.49	39.66	28.79	30.19	C7
257.1	46.66	47.42	35.53	36.76	C8
259.1	44.30	45.81	34.96	36.91	C9
260.2	44.05	45.00	33.46	33.12	C6
262.1	40.23	40.80	29.23	29.72	C8
263.1	46.29	48.70	34.62	30.09	C8
264.1	53.57	56.23	37.01	38.29	C9
266.1	43.11	44.26	31.51	32.79	C11
267.1	43.62	44.57	31.78	34.83	C8
268.1	44.06	45.84	37.58	38.93	C10
269.1	39.77	40.56	28.36	29.35	C8
270.1	36.17	36.66	27.73	27.54	C11
271.1	39.38	40.69	27.14	27.90	C11
272.1	—	—	—	—	—
273.1	—	—	—	—	—

TAXON No.	LARGE GRAINS		SMALL GRAINS		PT
	Polar axis (μm)	Equatorial diameter (μm)	Polar axis (μm)	Equatorial diameter (μm)	
274.1	—	—	—	—	—
275.1	—	—	—	—	—
276.1	—	—	—	—	—
277.1	—	—	—	—	—
278.1	—	—	—	—	—
279	48.10	48.79	32.43	33.59	C2
280	—	—	—	—	—
281	—	45.55	—	33.92	A
282	46.01	46.71	26.51	27.47	C2
283	53.15	54.92	30.32	31.27	C2
284	45.43	46.25	33.8s	35.41	C2
285	39.04	43.23	26.87	28.99	C2
286	38.50	38.56	32.16	32.31	C7
287	52.89	55.01	45.58	46.09	C4
289	44.37	45.71	26.62	28.79	C8
290	47.13	47.77	36.27	37.44	C10
291	—	81.27	—	59.15	D1
292	34.18	35.61	28.38	31.14	C10
293	51.00	52.60	41.94	42.88	C2
294	40.39	41.82	28.34	30.05	C7
295	39.44	44.16	29.21	30.62	C10
296	—	53.21	—	42.03	D1
297	54.61	55.98	35.25	36.79	D1
298	48.37	49.10	38.32	39.19	C2
299	38.04	41.31	35.65	36.96	C2
300	50.36	53.22	45.13	47.72	C7
301	38.49	39.67	29.73	30.66	C7

Table 5.2. Terminology used in describing the sexine structure and lumina diameters of the reticulate pollen grains of pollen type C (based on Johansson 1992).

Reticulum type	**Lumina**	**Predominant lumen diameter**
micro-reticulate	very small	< 1 μm
finely reticulate	small	1—1.5 μm
reticulate	relatively large	> 1.5—2.5 μm
coarsely reticulate	large	> 2.5—3.5 μm
very coarsely reticulate	very large	> 3.5 μm

Table 5.3 Summary of the distribution of pollen types in *Oxalis*, with reference to the taxonomic position of each taxon (according to Salter (1944)), the pollen types (PT) recognised in the present study and the pollen types proposed by Huynh (1969a). See end of table for an explanation of symbols.

SECTION	**SUBSECTION**	**TAXON**	**TAXON No.**	**PT**	**HUYNH PT**
Corniculatae		*O. corniculata*	1.1	C2	—
Ionoxalis		*O. latifolia*	2.1	C7	—
Cernuae	*Eu-cernuae*	*O. compressa* var. *compressa*	3.1	C2	A1
Cernuae	*Eu-cernuae*	*O. compressa* var. *purpurascens*	4.1	C2	A1
Cernuae	*Eu-cernuae*	*O. pes-caprae* var. *pes-caprae*	5.1	C2	A1
Cernuae	*Eu-cernuae*	*O. pes-caprae* var. *sericea*	6.1	C2	A1
Cernuae	*Eu-cernuae*	*O. haedulipes*	7.1	C2	—
Cernuae	*Eu-cernuae*	*O. copiosa*	8.1	C2	A1
Cernuae	*Eu-cernuae*	*O. luederitzii*	9.1; 9.2	C2	A1
Cernuae	*Eu-cernuae*	*O. knuthiana*	10.1	C3	—
Cernuae	*Eu-cernuae*	*O. schaeferi*	11.1	C2	A1
Cernuae	*Eu-cernuae*	*O. dentata*	12.1	C3	A1
Cernuae	*Eu-cernuae*	*O. laterifolia*	13.1	C3	A1
Cernuae	*Eu-cernuae*	*O. livida* var. *livida*	14.1	C3	A1
Cernuae	*Eu-cernuae*	*O. livida* var. *altior*	15.1	C3	A1
Cernuae	*Purpuratae*	*O. purpurata*	16.1	C7	A1
Cernuae	*Purpuratae*	*O. bowiei*	17.1; 17.2	C7	A1
Cernuae	*Purpuratae*	*O. semiloba*	18.1	C1	A1
Cernuae	*Costatae*	*O. purpurascens*	19.1	C8	A1
Cernuae	*Costatae*	*O. pseudo-cernua*	20.1	—	A1
Cernuae	*Goetzea*	*O. davyana*	21.1; 21.2	C2	—

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Cernuae	*Stellatae*	*O. stenorrhyncha*	22.1	C7	—
Cernuae	*Stellatae*	*O. stellata* var. *stellata*	23.1	C9	A1
Cernuae	*Stellatae*	*O. stellata* var. *glandulosa*	24.1	C8	—
Cernuae	*Stellatae*	*O. stellata* var. *montaguensis*	25.1	C1	—
Cernuae	*Stellatae*	*O. stellata* var. *gracilior*	26.1	C7	—
Cernuae	*Stellatae*	*O. lindaviana*	27.1	C9	A1
Cernuae	*Stellatae*	*O. dichotoma*	28.1	C9	—
Cernuae	*Stellatae*	*O. caprina*	29.1	C7	A1
Cernuae	*Stellatae*	*O. tragopoda*	30.1	C1	A1
Cernuae	*Stellatae*	*O. anomale*	31.1	C3	—
Oppositae	*Subintegrae*	*O. psilopoda*	32.1	C1	A1
Oppositae	*Subintegrae*	*O. imbricata* var. *imbricata*	33.1	C3	A1
Oppositae	*Subintegrae*	*O. imbricata* var. *violacea*	34.1	C2	A1
Oppositae	*Subintegrae*	*O. imbricata* var. *cuneifolia*	35.1	C2	A1
Oppositae	*Subintegrae*	*O. ioeides*	36.1	C2	—
Oppositae	*Subintegrae*	*O. calvinensis*	37.1	—	—
Oppositae	*Subintegrae*	*O. incerta*	38.1	—	—
Oppositae	*Subintegrae*	*O. orbicularis*	39.1	C8	—
Oppositae	*Subintegrae*	*O. marlothii*	40.1	C2	—
Oppositae	*Subintegrae*	*O. obtusa* var. *obtusa*	41.1	C3	—
Oppositae	*Subintegrae*	*O. obtusa* var. *atrata*	42.1	C2	—
Oppositae	*Subintegrae*	*O. lanata* var. *lanata*	43.1	C9	A1
Oppositae	*Subintegrae*	*O. lanata* var. *rosea*	44.1	—	—
Oppositae	*Subintegrae*	*O. truncatula*	45.1	C2	A1
Oppositae	*Subintegrae*	*O. lasiorrhiza*	46.1	C2	—
Oppositae	*Subintegrae*	*O. strigosa*	47.1	C8	—
Oppositae	*Subintegrae*	*O. zeekoevleyensis*	48.1	C8	A1
Oppositae	*Subintegrae*	*O. virginea*	49.1	C2	—
Oppositae	*Subintegrae*	*O. ambigua* var. *ambigua*	50.1	C3	A1

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Oppositae	*Subintegrae*	*O. ambigua* var. *fuscata*	51.1	C4	A1
Oppositae	*Subintegrae*	*O. rhomboidea*	52.1	C3	—
Oppositae	*Subintegrae*	*O. crispula* var. *crispula*	53.1	C2	A1
Oppositae	*Subintegrae*	*O. crispula* var. *glandulosa*	54.1	C2	—
Oppositae	*Subintegrae*	*O. luteola* var. *luteola*	55.1	C3	A1
Oppositae	*Subintegrae*	*O. luteola* var. *minor*	56.1	C2	—
Oppositae	*Subintegrae*	*O. adenodes*	57.1	C8	A1
Oppositae	*Subintegrae*	*O. incarnata*	58.1	C8	A1
Oppositae	*Subintegrae*	*O. duriuscula*	59.1	C2	A1
Oppositae	*Subintegrae*	*O. pendulifolia*	60.1	C2	—
Oppositae	*Bifurcatae*	*O. heterophylla*	61.1	C4	A1
Oppositae	*Bifurcatae*	*O. extensa*	62.1	C2	A1
Oppositae	*Bifurcatae*	*O. bifurca* var. *bifurca*	63.1	C2	A1
Oppositae	*Bifurcatae*	*O. bifurca* var. *angustiloba*	64.1	C2	—
Oppositae	*Bifurcatae*	*O. tysoni*	65.1	C2	—
Oppositae	*Bifurcatae*	*O. orthopoda*	66.1	C2	—
Oppositae	*Bifurcatae*	*O. comosa*	67.1	C8	A1
Oppositae	*Bifurcatae*	*O. bifida*	68.1	C2	A1
Oppositae	*Bifurcatae*	*O. smithiana*	69.1	C2	A1
Stictophyllae		*O. purpurea*	70.1	C3	A1
Stictophyllae		*O. melanosticta* var. *melanosticta*	71.1	C2	A1
Stictophyllae		*O. melanosticta* var. *latifolia*	72.1	C4	—
Stictophyllae		*O. rubro-punctata*	73.1	C3	—
Foveolatae		*O. convexula*	74.1	C4	A1
Foveolatae		*O. attaquana*	75.1	C2	—
Foveolatae		*O. foveolata*	76.1	C8	A3

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Foveolatae		*O. pulchella* var. *pulchella*	77.1	C3	A1
Foveolatae		*O. pulchella* var. *tomentosa*	78.1	C2	—
Foveolatae		*O. pulchella* var. *glauca*	79.1	C2	—
Foveolatae		*O. pulchella* var. *leucotricha*	80.1	C2	—
Foveolatae		*O. pulchella* var. *beneprotecta*	81.1	C10	—
Foveolatae		*O. depressa*	82.1	C2	A1
Foveolatae		*O. obliquifolia*	83.1	C2	A1
Foveolatae		*O. setosa*	84.1	C2	A1
Foveolatae		*O. reflexa*	85.1	C2	A1
Foveolatae		*O. dilatata*	86.1	C2	—
Foveolatae		*O. pocockiae*	87.1	C2	—
Foveolatae		*O. oreithala*	88.1	C2	—
Foveolatae		*O. punctata*	89.1	C2	A1
Foveolatae		*O. lichenoides*	90.1	C2	—
Foveolatae		*O. inaequalis*	91.1	C4	—
Foveolatae		*O. bullutata*	92.1	C2	A1
Foveolatae		*O. fergusoniae*	93.1	C2	A1
Foveolatae		*O. grammopetala*	94.1	C2	A1
Foveolatae		*O. algoensis*	95.1	C4	A1
Foveolatae		*O. fourcadei*	96.1	C3	—
Foveolatae		*O. lawsonii*	97.1	C3	A1
Foveolatae		*O. nortieri*	98.1	C3	—
Foveolatae		*O. annae*	99.1	C2	A1
Foveolatae		*O. senecta*	100.1	C3	—
Foveolatae		*O. densa*	101.1	C4	—
Foveolatae		*O. furcillata* var. *furcillata*	102.1	C2	A1
Foveolatae		*O. furcillata* var. *caulescens*	103.1	C10	—
Sagittatae		*O. fibrosa*	104.1; 104.2	B	C5

SECTION	**SUBSECTION**	**TAXON**	**TAXON No.**	**PT**	**HUYNH PT**
Sagittatae		*O. microdonta*	105.1	A	C2
Sagittatae		*O. nidulans* var. *nidulans*	106.1	A	C1
Sagittatae		*O. nidulans* var. *denticulata*	107.1	A	C3
Sagittatae		*O. minuta* var. *minuta*	108.1	A	C3
Sagittatae		*O. minuta* var. *callosa*	109.1	C7	—
Sagittatae		*O. eckloniana* var. *eckloniana*	110.1	A	C3
Sagittatae		*O. eckloniana* var. *montigena*	111.1	A	C1
Sagittatae		*O. eckloniana* var. *hopefieldiana*	112.1	A	—
Sagittatae		*O. eckloniana* var. *robusta*	113.1	A	—
Sagittatae		*O. eckloniana* var. *sonderi*	114.1	A	C3
Campanulatae		*O. dregei*	115.1	C10	A1
Campanulatae		*O. simplex*	116.1	C11	—
Campanulatae		*O. disticha* var. *disticha*	117.1	C10	A1
Campanulatae		*O. disticha* var. *alba*	118.1	C10	—
Campanulatae		*O. natans*	119.1	C10	A1
Campanulatae		*O. uliginosa*	120.1	C10	A1
Latifoliolatae		*O. stenoptera* var. *stenoptera*	121.1	C10	A1
Latifoliolatae		*O. stenoptera* var. *alba*	122.1	C10	—
Latifoliolatae		*O. stenoptera* var. *undulata*	123.1	C10	—
Latifoliolatae		*O. aurea*	124.1	C10	A1
Latifoliolatae		*O. suavis*	125.1	C2	A1
Latifoliolatae		*O. viscidula*	126.1	C2	—
Latifoliolatae		*O. campylorrhiza*	127.1	C8	A1
Latifoliolatae		*O. amblyosepala* var. *amblyosepala*	128.1	—	A1
Latifoliolatae		*O. amblyosepala* var. *minor*	129.1	—	—
Latifoliolatae		*O. ausensis*	130.1	C2	A1
Latifoliolatae		*O. sonderiana* var. *sonderiana*	131.1	C10	A1

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Latifoliolatae		*O. sonderiana* var. *alba*	132.1	C11	A1
Latifoliolatae		*O. inconspicua*	133.1	C10	—
Latifoliolatae		*O. petraea*	134.1	C11	—
Latifoliolatae		*O. commutata* var. *commutata*	135.1	C10	A1
Latifoliolatae		*O. commutata* var. *concolor*	136.1	C10	—
Latifoliolatae		*O. commutata* var. *montana*	137.1	C11	—
		O. oculifera	302	C10	—
Latifoliolatae		*O. tenella*	138.1	D1	C4
Latifoliolatae		*O. aridicola*	139.1	D1	C4
Latifoliolatae		*O. stokoei*	140.1	D1	—
Latifoliolatae		*O. petiolulata*	141.1	D2	—
Latifoliolatae		*O. callosa* var. *callosa*	142.1	D1	—
Latifoliolatae		*O. callosa* var. *minor*	143.1	D1	—
Latifoliolatae		*O. hirsuta*	144.1	—	A1
Crassulae		*O. fabaefolia*	145.1	C10	A1
Crassulae		*O. cathara*	146.1	C7	A1
Crassulae		*O. pulvinata*	147.1	C10	—
Crassulae		*O. flava*	148.1	C10	A1
Crassulae		*O. flaviuscula* var. *flaviuscula*	149.1	C10	A1
Crassulae		*O. flaviuscula* var. *longifolia*	150.1	C10	—
Crassulae		*O. namaquana*	151.1	C2	A1
Crassulae		*O. louisae*	152.1	C10	—
Crassulae		*O. salteri*	153.1	C10	A1
Angustatae	*Pardalis*	*O. capillacea* var. *capillacea*	154.1	C2	A1
Angustatae	*Pardalis*	*O. capillacea* var. *ternata*	155.1	—	—
Angustatae	*Pardalis*	*O. leptogramma* var. *leptogramma*	156.1	C2	A1
Angustatae	*Pardalis*	*O. leptogramma* var. *brevifolia*	157.1	—	—

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Angustatae	*Pardalis*	*O. leptogramma* var. *lutea*	158.1	C2	—
Angustatae	*Pardalis*	*O. lineolata*	159.1	C2	—
Angustatae	*Pardalis*	*O. massoniana* var. *massoniana*	160.1	C3	A1
Angustatae	*Pardalis*	*O. massoniana* var. *flavescens*	161.1	—	—
Angustatae	*Pardalis*	*O. melanograpta*	162.1	C9	—
Angustatae	*Pardalis*	*O. camelopardalis*	163.1	C2	A1
Angustatae	*Pardalis*	*O. confertifolia* var. *petiolata*	164.1	C2	—
Angustatae	*Pardalis*	*O. confertifolia* var. *lutea*	165.1	C2	—
Angustatae	*Pardalis*	*O. confertifolia* var. *confertifolia*	166.1	C3	A1
Angustatae	*Pardalis*	*O. heidelbergensis*	167.1	C2	A1
Angustatae	*Pardalis*	*O. pardalis*	168.1	C2	A1
Angustatae	*Pardalis*	*O. grammophylla*	169.1	C2	—
Angustatae	*Pardalis*	*O. robinsonii*	170.1	C2	A1
Angustatae	*Sessilifoliatae*	*O. hirta* var. *hirta*	171.1	D1	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *canescens*	172.1	D1	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *tenuicaulis*	173.1	D1	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *intermedia*	174.1; 174.2	D4	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *polioedes*	175.1; 175.2	D1	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *tubiflora*	176.1; 176.2	D4	C4
Angustatae	*Sessilifoliatae*	*O. hirta* var. *secunda*	177.1	—	C4
Angustatae	*Sessilifoliatae*	*O. pseudo-hirta*	178.1	D1	C4
Angustatae	*Sessilifoliatae*	*O. subsessilis*	179.1	D1	—
Angustatae	*Sessilifoliatae*	*O. crocea*	180.1	C7	—
Angustatae	*Sessilifoliatae*	*O. meisneri*	181.1	C9	A1
Angustatae	*Sessilifoliatae*	*O. viscosa*	182.1	C2	A1
Angustatae	*Sessilifoliatae*	*O. porphyriosiphon*	183.1	C9	—

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Angustatae	*Sessilifoliatae*	*O. leipoldtii*	184.1	—	—
Angustatae	*Sessilifoliatae*	*O. giftbergensis*	185.1	C15	A1
Angustatae	*Sessilifoliatae*	*O. macra*	186.1	D	C4
Angustatae	*Sessilifoliatae*	*O. tenuifolia*	187.1	C8	A1
Angustatae	*Sessilifoliatae*	*O. multicaulis* var. *multicaulis*	188.1	C8	A1
Angustatae	*Sessilifoliatae*	*O. multicaulis* var. *stolonifera*	189.1	C8	—
Angustatae	*Sessilifoliatae*	*O. urbaniana* var. *urbaniana*	190.1	C8	A3
Angustatae	*Sessilifoliatae*	*O. urbaniana* var. *leipoldtii*	191.1	—	—
Angustatae	*Sessilifoliatae*	*O. callimarginata*	192.1	C9	—
Angustatae	*Sessilifoliatae*	*O. recticaulis*	193.1	C2	A1
Angustatae	*Xanthotrichae*	*O. pillansiana*	194.1; 194.2	C10	—
Angustatae	*Xanthotrichae*	*O. argillacea*	195.1; 195.2	C10	—
Angustatae	*Xanthotrichae*	*O. adspersa*	196.1	C10	A1
Angustatae	*Linearis*	*O. primuloides*	197.1	D1	—
Angustatae	*Linearis*	*O. linearis*	198.1; 198.2	D3	C4
Angustatae	*Linearis*	*O. quinata*	199.1	D1	C4
Angustatae	*Linearis*	*O. exserta*	200.1	D1	—
Angustatae	*Linearis*	*O. gracilis* var. *gracilis*	201.1	D1	C4
Angustatae	*Linearis*	*O. gracilis* var. *purpurea*	202.1	D1	C4
Angustatae	*Linearis*	*O. gracilis* var. *lilacea*	203.1	D1	C4
Angustatae	*Linearis*	*O. helicoides* var. *helicoides*	204.1	D1	—
Angustatae	*Linearis*	*O. helicoides* var. *alba*	205.1	D1	—
Angustatae	*Linearis*	*O. campicola*	206.1	D1	—
Angustatae	*Linearis*	*O. stenopetala*	207.1	C7	—
Angustatae	*Linearis*	*O. xantha*	208.1	D1	—
Angustatae	*Linearis*	*O. tenuipes* var. *tenuipes*	209.1	C12	—

SECTION	**SUBSECTION**	**TAXON**	**TAXON No.**	**PT**	**HUYNH PT**
Angustatae	*Linearis*	*O. tenuipes* var. *biapiculata*	210.1	C11	—
Angustatae	*Linearis*	*O. phloxidiflora*	211.1	C14	A3
Angustatae	*Linearis*	*O. involuta*	212.1	C8	A1
Angustatae	*Linearis*	*O. goniorrhiza*	213.1	C8	A1
Angustatae	*Linearis*	*O. fragilis* var. *fragilis*	214.1	C2	—
Angustatae	*Linearis*	*O. fragilis* var. *pellucida*	215.1	C2	—
Angustatae	*Linearis*	*O. pallens*	216.1	C2	A1
Angustatae	*Linearis*	*O. glabra*	217.1	C8	A1
Angustatae	*Linearis*	*O. pusilla*	218.1	C2	A1
Angustatae	*Linearis*	*O. leptocalyx*	219.1	C8	A1
Angustatae	*Linearis*	*O. versicolor* var. *versicolor*	220.1	C8	A1
Angustatae	*Linearis*	*O. versicolor* var. *flaviflora*	221.1	C8	—
Angustatae	*Linearis*	*O. versicolor* var. *latifolia*	222.1	C8	—
Angustatae	*Linearis*	*O. polyphylla* var. *polyphylla*	223.1	C7	A1
Angustatae	*Linearis*	*O. polyphylla* var. *pentaphylla*	224.1	C8	—
Angustatae	*Linearis*	*O. polyphylla* var. *heptaphylla*	225.1	C8	—
Angustatae	*Linearis*	*O. polyphylla* var. *pubescens*	226.1	C8	—
Angustatae	*Linearis*	*O. polyphylla* var. *alba*	227.1	C8	—
Angustatae	*Linearis*	*O. polyphylla* var. *minor*	228.1	C9	—
Angustatae	*Linearis*	*O. burtoniae*	229.1	C8	—
Angustatae	*Linearis*	*O. gracilipes*	230.1	C2	—
Angustatae	*Linearis*	*O. falcatula*	231.1	C7	A1
Angustatae	*Linearis*	*O. argyrophylla*	232.1	C8	A1
Angustatae	*Linearis*	*O. perineson*	233.1	C8	—
Angustatae	*Linearis*	*O. stictocheila*	234.1	C8	—
Angustatae	*Linearis*	*O. levis*	235.1	C5	—
Angustatae	*Linearis*	*O. ciliaris* var. *ciliaris*	236.1	D1	C4
Angustatae	*Linearis*	*O. ciliaris* var. *pageae*	237.1	D1	C4
Angustatae	*Linearis*	*O. burkei*	238.1	D1	—
Angustatae	*Linearis*	*O. cuneata*	239.1	D1	C4

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
Angustatae	*Linearis*	*O. oreophila*	240.1	D1	—
Angustatae	*Linearis*	*O. blastorrhiza*	241.1	D1	—
Angustatae	*Linearis*	*O. creaseyi*	242.1	D1	C4
Angustatae	*Linearis*	*O. comptonii*	243.1	C8	—
Angustatae	*Linearis*	*O. reclinata* var. *reclinata*	244.1	D1	C4
Angustatae	*Linearis*	*O. reclinata* var. *micromera*	245.1	D1	C4
Angustatae	*Linearis*	*O. reclinata* var. *quinata*	246.1	D1	C4
Angustatae	*Linearis*	*O. reclinata* var. *gracillima*	247.1	D1	C4
Angustatae	*Linearis*	*O. albiuscula*	249.1	D1	—
Angustatae	*Linearis*	*O. kamiesbergensis*	250.1	D1	—
Angustatae	*Linearis*	*O. oligophylla*	251.1	C8	—
Angustatae	*Glandulosa*	*O. clavifolia*	252.1	C2	A1
Angustatae	*Glandulosa*	*O. deserticola*	253.1	C9	—
Angustatae	*Glandulosa*	*O. droseroides*	254.1	C13	A1
Angustatae	*Glandulosa*	*O. suteroides* var. *suteroides*	255.1	C9	—
Angustatae	*Glandulosa*	*O. suteroides* var. *latituba*	256.1	C7	A1
Angustatae	*Glandulosa*	*O. ebracteata*	257.1	C8	A1
Angustatae	*Glandulosa*	*O. neglecta*	258.1	—	—
Angustatae	*Glandulosa*	*O. tenuis*	259.1	C9	—
Angustatae	*Multifoliolatae*	*O. engleriana*	260.1	C6	—
Angustatae	*Multifoliolatae*	*O. henrici*	261.1	C6	—
Angustatae	*Multifoliolatae*	*O. zeyheri*	262.1	C8	A1
Angustatae	*Multifoliolatae*	*O. amblyodonta*	263.1	C8	A1
Angustatae	*Multifoliolatae*	*O. variifolia* var. *variifolia*	264.1	C9	A1
Angustatae	*Multifoliolatae*	*O. palmifrons*	266.1	C11	—
Angustatae	*Multifoliolatae*	*O. tomentosa*	267.1	C8	A1
TAXA NOT ALLOCATED TO A SPECIFIC SECTION					
		O. monophylla var. *monophylla*	268.1	C10	—

SECTION	SUBSECTION	TAXON	TAXON No.	PT	HUYNH PT
		O. monophylla var. *stenophylla*	269.1	C8	A1
		O. monophylla var. *rotundifolia*	270.1	C11	—
		O. monophylla var. *minor*	271.1	C11	—
POSSIBLE UNDESCRIBED SPECIES					
		O. sp.	279	C2	—
		O. sp.	280	—	—
		O. sp.	281	A	—
		O. sp.	282	C3	—
		O. sp.	283	C2	—
		O. sp.	284	C2	—
		O. sp.	285	C2	—
		O. sp.	286	C2	—
		O. sp.	287	C7	—
		O. sp.	288	C4	—
		O. sp. nov.	289	C8	—
		O. sp. nov.	290	C10	—
		O. sp.	291	D1	—
		O. sp. nov.	292	C10	—
		O. magnifolia MS.	293	C2	—
		O. anaculata MS.	294	C7	—
		O. glauca MS.	295	C10	—
		O. sp.	296	D1	—
		O. sp.	297	D1	—
		O. klaasvoogdensis MS	298	C2	—
		O. heptaphylla MS	299		—
		O. fragrans MS	300		—
		O. bombycina MS	301		—

PT = Pollen type; HUYNH PT = Pollen types identified by Huynh (1969a); MS = Manuscript species. "Groups of related taxa" (Salter 1944) within a given section or subsection are indicated by differential shading.

Table 5.4 Average thickness (µm) of the wall layers of the different pollen types, as determined by TEM analysis.

POLLEN TYPE	**A**	**B**	**C1**	**C2**	**C3**	**C4**	**C5**	**C6**	**C7**	**C8**	**C9**	**C10**	**C11**	**C12**	**C13**	**C14**	**C15**	**D1**	**D2**	**D3**	**D4**
Exine	1.2–1.8	1.8–2.6	1.1–1.2	1.4	1.5–1.6	1.4–1.6	–	1.7–1.8	1.7	1.6–1.7	1.7–1.8	1.6–1.8	1.8	1.8	1.6–1.8	1.8–2.0	2.3–2.8	1.1–1.3	1.6–1.7	1.6–1.7	1.8
Supratectal structure	0.3	0.8–1.4	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	0.7–0.9	1.2–1.3	0.6–1.0	1.2
Tectum	0.2–0.3	0.2	0.4	0.4	0.6	0.4	–	0.4	0.6	0.5	0.5	0.6–0.7	0.7	0.8	0.6	0.5–0.7	0.5–0.7	0.2–0.3	0.3–0.4	0.3–0.4	0.3–0.4
Columellar layer	0.5–0.6	0.4–0.5	0.5	0.6	0.5–0.7	0.6–0.7	–	0.7	0.6–0.7	0.8	0.8	0.7	0.7	0.9	0.7–0.9	0.8–0.9	1.2–1.5	–	–	–	–
Columellae (cross section)	0.5	0.4	0.4	0.5	0.4	0.4	–	0.4	0.3	0.4	0.5	0.4	0.5	0.4–0.5	0.4	0.5	0.5	–	–	–	–
Footlayer	0.3	0.3–0.4	0.2	0.4	0.3	0.3	–	0.3	0.3	0.3	0.3	0.3	0.3	0.3–0.4	0.3	0.3	0.4	0.1	0.15	0.2	0.1–0.2
Endexine	0.3–0.5	0.2	0.1	0.2	0.2	0.1	–	0.2	0.2	0.1	0.3	0.3	0.3	0.4	0.2	0.2	0.3	0.1	0.1	0.1	0.1
Intine	0.1–0.2	–	0.1	0.2	0.5	0.2	–	–	–	0.6	–	–	–	0.5–0.6	0.6	–	–	0.1–0.2	0.5	0.4	0.6

Table 5.5 Summary of the chromosome numbers, level of ploidy, pollen type and grain aberrations encountered in a number of *Oxalis*. taxa. For an explanation of symbols see end of table.

TAXON	**TAXON No.**	**2N***	**X***	**PLOIDY* LEVEL**	**PT**	**3N**	**4N**	**ABERRANT**
O. dentata	12	14	7	2X	C	X		
O. bowiei	16	28	7	4X	C	X		
O. purpurata	17	28; 42	7	4X; 6X	C	X		
O. caprina	29	20	5; 10	4X; 2X	C	X		
O. tragopoda	30	14	7	2X	C	X		
O. incarnata	58	14	7	2X	C	X		
O. smithiana	69	14	7	2X	C	X		
O. purpurea	70	42	7	6X	C	X		
O. cathara	146	14	7	2X	C	X		
O. fabaefolia	145	28	7	4X	C	X		
O. pardalis	168	14	7	2X	C	X		
O. hirta var. *hirta*	171	30	5	6X	D		X	X
O. tenuifolia	187	28	7	2X	C	X		
O. ciliaris var. *ciliaris*	236	40	5;10	8X; 4X	D	X	X	
O. cuneata	239	12	6	2X	D	X	X	X
O. polyphylla	223	30	5	6X	C	X		
O. polyphylla var. *pentaphylla*	224	14	7	2X	C			
O. truncatula	45	28; 42	7	2X; 4X	C	X		

* From Marks (1956); TAXON No. = Taxon number; 2N = Somatic chromosome number; N = Haploid chromosome number; 4N = Tetraploid; 6N = Hexaploid chromosome number; PT = Pollen type

CHAPTER 6
DESCRIPTION OF POLLEN TYPES

6.1 Introduction

Three keys are provided in the first part of this chapter: one to the four main pollen types and two more detailed keys to the subtypes of pollen types C and D respectively. This is followed by formal descriptions of the 21 pollen types and subtypes found in *Oxalis*. The descriptions are based on LM, SEM and TEM results, discussed under separate headings. Diagnostic features are provided for the subtypes of pollen types C and D. SEM and TEM micrographs of the different pollen types are supplied at the end of the chapter (Figures 6.1—6.22).

6.2 Keys to the pollen types

Key 1: Key to the main pollen types

1a Pollen tectate with well-developed supratectal structures **2**
  2a Columellar layer well-developed, exine micro-rugulate or rugulate-reticulate.... ....**3**
    3a Grains pantocolpate (seldom tricolpate), exine rugulate-reticulate with supratectal spinules ....**Type A**
    3b Grains tricolpate, exine micro-rugulate with supratectal spines .... **Type B**
  2b Columellar layer weakly developed, exine supra-areolate on an uneven, verrucate to baculate tectum ....**Type D** (see Key 3 for subtypes)
1b Pollen semitectate, seldom with reduced supratectal structures ....**Type C** (see Key 2 for subtypes)

Key 2: Key to the subtypes of pollen type C

1a Intraluminary bacula absent in the mesocolpium...2
  2a Supratectal spinules absent 3
    3a Lumina isodiametrically rounded ....**Subtype C1**
    3b Lumina oblong, irregularly rounded to angular...4
      4a Tectum micro-reticulate (lumen diameter predominantly < 1 µm); lumina rounded to oblong ....**Subtype C2**
      4b Tectum finely reticulate (lumen diameter predominantly 1.0—1.5 µm) to reticulate (lumen diameter predominantly > 1.5—2.5 µm); lumina rounded to irregularly angular...5
        5a Tectum finely reticulate; lumen diameter predominantly 1.0—1.5 µm ....**Subtype C3**

5b Tectum reticulate; lumen diameter predominantly > 1.5—2.5 µm .... **Subtype C4**

2b Supratectal spinules present .... **Subtype C5**

1b Intraluminary bacula present in the mesocolpium 6

6a Bacula scattered all over lumina floor, rarely clustered along muri 7

7a Supratectal spinules present .... **Subtype C6**

7b Supratectal spinules absent 8

8a Tectum micro-reticulate (lumen diameter predominantly < 1 µm); lumina irregularly rounded to oblong .... **Subtype C7**

8b Tectum finely reticulate (lumen diameter predominantly 1.0—1.5 µm) to reticulate (lumen diameter predominantly > 1.5—2.5 µm); lumina rounded to irregularly angular 9

9a Tectum finely reticulate; lumen diameter predominantly 1.0—1.5 µm .... **Subtype C8**

9b Tectum reticulate; lumen diameter predominantly > 1.5—2.5 µm .... **Subtype C9**

6b Bacula mainly clustered along muri; rarely scattered on lumina floor 10

10a Muri smooth, without perforations 11

11a Tectum finely reticulate (lumen diameter predominantly 1.0—1.5 µm) .... **Subtype C10**

11b Tectum reticulate (lumen diameter predominantly > 1.5—2.5 µm) or coarsely reticulate (lumen diameter predominantly > 2.5—3.5 µm) 12

12a Tectum reticulate (lumen diameter predominantly > 1.5—2.5 µm) .... **Subtype C11**

12b Tectum coarsely reticulate (lumen diameter predominantly > 2.5—3.5 µm) .... **Subtype C12**

10b Muri perforate 13

13a Tectum reticulate (lumen diameter predominantly > 1.5—2.5 µm) .... **Subtype C13**

13b Tectum coarsely to very coarsely reticulate (lumen diameter predominantly > 2.5 µm) 14

14a Tectum coarsely reticulate (lumen diameter predominantly > 2.5—3.5 µm) .... **Subtype C14**

14b Tectum very coarsely reticulate (lumen diameter predominantly > 3.5 µm) .... **Subtype C15**

Key 3: Key to the subtypes of pollen type D

1a Supratectal areolae triangular, rounded to club-shaped, individual elements solitary, clustered or arranged into a negative reticulum **2**
  2a Pollen tricolpate or pantocolpate, supratectal areolae solitary, clustered or seldomly arranged into a vague negative reticulum; intraluminary bacula absent, tectum uneven but not verrucate on outer surface ....**Subtype D1**
  2b Pollen tricolpate, supratectal areolae arranged into a distinct negative reticulum; tectum prominently verrucate to baculate on outer surface **3**
    3a Supratectal areolae angular with an average diameter of 1.8 μm over the entire grain ....**Subtype D2**
    3b Supratectal areolae rounded with an average diameter of 0.89 μm except in the apocolpial areas where they are much enlarged and prominently ridged... ....**Subtype D3**
1b Supratectal areolae rectangular, arranged into a coarse, ridged pattern, ...**Subtype D4**

6.3 Description of the pollen types

6.3.1 Pollen type A

Rugulate-reticulate type (Figure 6.1)

LM

Pollen grains pantocolpate with tricolpate and tetracolpate grains recorded from two taxa only, mostly apolar, spherical, larger grains 38—48 μm and smaller grains 31—37 μm in diameter. Apocolpium reduced in tri- and tetracolpate grains. Colpus ends rounded to acute.

SEM (Figure 6.1 A—D)

Pollen tectate. Tectum rugulate-reticulate covered with small, sharp supratectal spinules. Muri smooth, wide, with numerous constrictions or folds resulting in differences in interstitium thickness; predominant muri thickness 1.2 μm. Lumina irregular, angular to rounded-angular, well defined in places becoming smaller and less prominent in other areas of the same grain due to lateral fusion of the muri; inner walls of the lumina undulate due to constrictions. Nexine floor sometimes randomly beset with small blunt bacula. Colpus membrane smooth, sometimes with granular exine islands within the colpus area.

TEM (Figure 6.1 E, F)

Exine 1.2-1.8 μm thick, consisting of comparatively thick ectexine (supratectal spinules, tectum, columellae, footlayer) and a much thinner endexine. Supratectal spinules triangular, 0.3 μm long, apices rounded to acute. Tectum 0.2—0.3 μm thick, slightly thinner than footlayer; outer tectum surface smooth to undulate; inner tectum surface uneven. Columellae well-developed, a third to half of the total thickness of the exine (0.5—0.6 μm), simplicolumellate; columellae erect, cylindrical (0.5 μm), thickening slightly below the tectum, decreasing in length towards the colpi; intercolumellar spaces relatively broad, partially filled with a dark-stained substance. Footlayer 0.3—0.4 μm thick, uneven, with a distinctly baculate outer surface. Endexine discontinuous, thin with some thickenings interrupted by much thinner areas, maximum thickness 0.3 μm; inner surface very uneven. Intine uneven, about half as thick as footlayer (0.1—0.2 μm), continuous, unstratified but slightly more granular towards the inner surface.

6.3.2 Pollen type B

Micro-rugulate-spinate type (Figure 6.2)

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40 X 48 μm. Apocolpium reduced. Colpus ends acute.

SEM (Figure 6.2 A—D)

Pollen tectate. Tectum micro-rugulate with numerous conical, supratectal spines; predominant spine length 0.84—1.4 μm. Muri smooth. Lumina reduced in the mesocolpial areas, with irregular, rounded micro-lumina visible closer to the colpi. Colpus membrane coarsely granular.

TEM (Figure 6.2 E, F)

Exine 1.5—2.6 μm thick, consisting of comparatively thick ectexine (supratectal spines, tectum, columellae, footlayer) and a much thinner endexine. Supratectal spines triangular, 0.8—1.4 μm long, apices acute. Tectum 0.2 μm thick, slightly thinner than footlayer, traversed by micro-channels; elements of the tectum round to ellipsoid in cross-section; outer and inner tectum surface smooth to undulate. Columellae well-developed, a third or less of the total thickness of the exine (0.4—0.5 μm), simplicolumellate; columellae erect, cylindrical, 0.4 μm in cross-section, thickening towards their bases, decreasing in length towards the colpi, each columella capped by a supratectal spine; intercolumellar spaces broad. Footlayer 0.3—0.4 μm thick, uneven, outer surface distinctly baculate. Endexine discontinuous, thin with some thickenings interrupted by much thinner areas, maximum thickness 0.2 µm; inner surface very uneven. Intine removed by acetolysis.

6.3.3 Pollen type C (Figures 6.3—6.17)
Reticulate type

Pollen subtype C1 (Figure 6.3)

Tectum micro-reticulate; lumina isodiametrically rounded; mesocolpial intraluminary bacula absent.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40—50 X 40—55 µm and smaller grains 28—38 X 36 µm in diameter. Apocolpium reduced. Colpus ends acute.

SEM (Figure 6.3 A—E)

Pollen semitectate. Tectum micro-reticulate, heterobrochate. Lumina isodiametrically rounded, diminishing in size towards the colpi. Predominant lumina diameter 0.64 µm. Muri smooth. Predominant muri thickness 0.44 µm. Nexine floor without visible free-standing bacula in the mesocolpial areas, sometimes with a few scattered blunt bacula in the apocolpial regions.

TEM (Figure 6.3 F)

Exine 1.1—1.2 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of fairly uniform thickness (0.4 µm), twice as thick as footlayer; elements of the tectum rounded in cross-section; outer tectum surface smooth. Columellae well-developed, almost half of the total thickness of the exine (0.5 µm), simplicolumellate; columellae erect, cylindrical, of even diameter (0.5 µm) to slightly broader towards their bases, decreasing in length towards the colpi; intercolumellar spaces narrow. Footlayer 0.2 µm thick, smooth to undulate, uniform, uninterrupted. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.1 µm; inner surface undulate. Intine about half as thick as footlayer (0.1 µm), continuous, even to undulate, unstratified.

Pollen subtype C2 (Figure 6.4)

Tectum micro-reticulate: lumina rounded to oblong to slightly angular; mesocolpial intraluminary bacula absent.

LM

Pollen grains tricolpate or tetracolpate, with a few 6-pantocolpate aberrations in three taxa, mostly isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35—45 X 40—50 and smaller grains 25—35 X 30—40 µm in diameter. Apocolpium mostly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.4 A—D)

Pollen semitectate. Tectum micro-reticulate, heterobrochate. Lumina rounded to oblong, sometimes slightly angular, diminishing in size towards the colpi. Predominant lumina thickness 0.65 µm. Muri mostly smooth, sometimes slightly stratified. Predominant muri thickness 0.49 µm. Nexine floor without visible free-standing bacula in the mesocolpial areas, sometimes with a few scattered blunt bacula in the apocolpial regions. Colpus membrane coarsely granular.

TEM (Figure 6.4 E, F)

Exine 1.4 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of fairly uniform thickness (0.4 µm), as thick as footlayer; elements of the tectum rounded to ellipsoid in cross-section; outer tectum surface smooth to undulate. Columellae well-developed, almost half of the total thickness of the exine (0.6 µm), simplicolumellate; columellae erect, cylindrical,, of even diameter (0.5 µm) to slightly broader towards their bases, decreasing in length towards the colpi; intercolumellar spaces narrow, filled with a dark-stained substance. Footlayer thick (0.4 µm), smooth to undulate, uniform, uninterrupted. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.2 µm; inner surface undulate. Intine about half as thick as footlayer (0.2 µm), continuous, even to undulate, unstratified.

Note: AFM studies revealed two steps of approximately equal dimensions in the muri of this pollen type (see Appendix). These steps are probably equivalent to the striations observed in SEM analysis. Further AFM work is required to determine the stability and taxonomic significance of this character.

Pollen subtype C3 (Figure 6.5)

Tectum finely reticulate; lumina irregularly angular to rounded; mesocolpial intraluminary bacula absent.

LM

Pollen grains tricolpate, with 4-zonocolpate and 4-aperturate aberrations found in two taxa, mostly isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 38—50 X 40—55 µm and smaller grains 25—40 X 30—45 µm in diameter. Apocolpium large to fairly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.5 A—E)

Pollen semitectate. Tectum finely reticulate, heterobrochate. Lumina irregularly angular to slightly rounded, diminishing in size towards the colpi. Predominant lumina diameter 1.14 µm. Muri smooth to slightly stratified. Predominant muri thickness 0.59 µm. Nexine floor without visible free-standing bacula in the mesocolpial areas, sometimes with a few scattered blunt processes in the apocolpial regions. Colpus membrane coarsely granular.

TEM (Figure 6.5 F)

Exine 1.5—1.6 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of uniform thickness (0.6 µm), about twice as thick as footlayer; elements of the tectum round to ellipsoid in cross-section; outer tectum surface smooth to undulate. Columellae well-developed, a third to a half of the total thickness of the exine (0.5—0.7 µm), simplicolumellate; columellae erect, cylindrical, of even diameter (0.4 µm) to slightly broader towards their bases, decreasing in length towards the colpi; intercolumellar spaces narrow. Footlayer relatively thin, 0.3 µm thick, smooth to undulate, uniform, uninterrupted. Endexine discontinuous, mostly very thin with scattered thickened sections, maximum thickness 0.2 µm; inner surface uneven to undulate. Intine well-developed, about one and a half times thicker than footlayer (0.5 µm), continuous, uneven to undulate, unstratified but slightly lighter stained and more stratified towards the inner surface.

Note: AFM studies also revealed two steps in the muri of this pollen type, but in this case the first step is much larger than the second. As in the case of pollen subtype C2, further studies are required to validate the significance of this character.

Pollen subtype C4 (Figure 6.6)

Tectum reticulate; lumina large, irregularly angular to slightly rounded; mesocolpial intraluminary bacula absent.

LM

Pollen grains, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40—50 (68) X 40—50 (68) µm and smaller grains 30—40 (51) X 30—40 (52) µm in diameter. Apocolpium mostly fairly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.6 A—D)

Pollen semitectate. Tectum reticulate, heterobrochate. Lumina irregularly rounded to slightly angular, greatly diminishing in size towards the colpus, resulting in a distinct colpus margin. Predominant lumina diameter 1.58 µm. Muri smooth to slightly stratified. Predominant muri thickness 0.56 µm. Nexine floor without visible free-standing bacula in the mesocolpial areas, sometimes with a few scattered blunt bacula in the apocolpial regions. Colpus membrane coarsely granular.

TEM (Figure 6.6 E, F)

Exine 1.4—1.6 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of uniform thickness (0.5 µm), slightly thicker than footlayer; elements of tectum rounded to slightly ellipsoid in cross-section; outer tectum surface smooth to undulate. Columellae well-developed, almost half of the total thickness of the exine (0.6—0.7 µm), simplicolumellate; columellae erect, cylindrical, of even diameter (0.4 µm) to slightly broader towards their bases, decreasing in length towards the colpi; intercolumellar spaces relatively narrow, filled with a dark-stained substance. Footlayer 0.3 µm thick, smooth, uniform, uninterrupted. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 1 µm; inner surface undulate. Intine about half as thick as footlayer (0.15 µm), continuous, uneven to undulate, with a faintly lighter outer layer and a darker, more granular inner layer. The layering of the intine is, however, not very distinct.

Pollen subtype C5 (Figure 6.7)

Tectum complex, micro-reticulate, consisting of muri on two different levels; lumina isodiametrically rounded to oblong; blunt supratectal spinules present.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and oblate in equatorial view, large grains 42 X 44 and smaller grains 33 X 36 µm in diameter. Apocolpium reduced. Colpus ends rounded.

SEM (Figure 6.6 A—D)

Pollen semitectate. Tectum micro-reticulate, heterobrochate, covered with small, blunt supratectal spinules. Lumina irregular, isodiametrically rounded to oblong, diminishing in size towards the colpi. Predominant lumina diameter 0.56 µm. Muri smooth, on two different levels, with some interconnecting on a lower level than others. Predominant muri thickness 0.58 µm. Colpus membrane coarsely granular.

TEM

Insufficient material available.

Pollen subtype C6 (Figure 6.8)

Tectum a coarse open reticulum; lumina large, irregularly angular; supratectal spinules present; intraluminary bacula scattered on the nexine floor of the entire grain.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 44 X 45 µm and smaller grains 33 X 33 µm in diameter. Apocolpium much reduced. Colpus ends rounded.

SEM (Figure 6.8 A—D)

Pollen semitectate. Tectum a coarse, open, homobrochate reticulum, covered with numerous small, conical supratectal spinules. Lumina large, irregularly angular, slightly diminishing in size towards the colpi and apocolpium. Predominant lumina diameter 2.83 µm. Muri vermiculate, sometimes interrupted. Predominant muri thickness 0.8 µm. Nexine floor scattered with blunt, free-standing bacula over the entire grain. Colpus membrane moderately granular.

TEM (Figure 6.8 E, F)

Exine 1.7—1.8 µm thick, consisting of comparatively thick ectexine (supratectal spinules, tectum, columellae, footlayer) and a much thinner endexine. Supratectal spinules triangular, 0.2 µm long, apices acute. Tectum of fairly uniform thickness (0.4 µm), almost twice as thick as footlayer; elements of the tectum ellipsoid with acute distal ends in cross-section. Columellae well-developed, less than half of the total thickness of the exine (0.7 µm), simplicolumellate; columellae erect, cylindrical, 0.4—0.5 µm in cross-section, decreasing in length towards the colpi; intercolumellar spaces broad. Footlayer 0.3 µm thick, uninterrupted, distinctly baculate, traversed by micro-channels. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.2 µm; inner surface undulate. Intine removed by acetolysis.

Pollen subtype C7 (Figure 6.9)

Tectum micro-reticulate; lumina irregularly rounded to oblong; intraluminary bacula scattered on the nexine floor of the entire grain.

LM

Pollen grains tricolpate with 4-zonocolpate aberrations in one taxon, mostly isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35—50 X 38—53 µm and smaller grains 25—30 (42) X 25—35 (40) µm in diameter. Apocolpium mostly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.9 A—D)

Pollen semitectate. Tectum micro-reticulate, heterobrochate. Lumina irregularly rounded to oblong, sometimes slightly angular, diminishing in size towards the colpi. Predominant lumina diameter 0.77 µm. Muri mostly smooth, sometimes slightly stratified. Predominant muri thickness 0.53 µm. Nexine floor of the entire grain randomly scattered with blunt intraluminary bacula. Colpus membrane coarsely granular.

TEM (Figure 6.9 E, F)

Exine 1.7 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of uniform thickness (0.6 µm), twice as thick as footlayer; elements of tectum ovate to ellipsoid in cross-section. Columellae well-developed, a third to a half of the total thickness of the exine (0.6—0.7 µm), simplicolumellate; columellae erect, cylindrical, slender, 0.3 µm in diameter, thickening slightly below the tectum, decreasing in length towards colpi; intercolumellar spaces narrow. Footlayer 0.3 µm thick, distinctly baculate, uninterrupted. Endexine discontinuous, mostly very thin with scattered thicker sections, maximum thickness 0.2 µm; inner surface uneven. Intine removed by acetolysis.

Pollen subtype C8 (Figure 6.10)

Tectum finely reticulate; lumina irregularly rounded to angular; intraluminary bacula scattered on the nexine floor of the entire grain.

LM

Pollen grains tricolpate with 2-zonocolpate, 4-zonocolpate and 6-pantocolpate aberrations in four taxa, mostly isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35—50 X 40—50 (60) µm and smaller grains 25—40 X 30—40 (48) µm in diameter. Apocolpium large to fairly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.10 A—D)

Pollen semitectate. Tectum finely reticulate, heterobrochate. Lumina irregularly angular to rounded, diminishing in size towards the colpi. Predominant lumina diameter 1.16 µm. Muri mostly smooth, sometimes slightly stratified. Predominant muri thickness 0.53 µm. Nexine floor of the entire grain randomly scattered with blunt intraluminary bacula. Colpus membrane coarsely granular.

TEM (Figure 6.10 E, F)

Exine 1.6—1.7 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of uniform thickness (0.5 µm), slightly thicker than footlayer; elements of tectum ovate to ellipsoid in cross-section; outer tectum surface undulate. Columellae well-developed, about half of the total thickness of the exine (0.8 µm), simplicolumellate; columellae erect, cylindrical, 0.4 µm in diameter, thickening towards their bases, decreasing in length towards colpi; intercolumellar spaces relatively broad, partially filled with a dark-stained substance. Footlayer 0.3 µm thick, distinctly baculate, uninterrupted, coated with a dark-stained substance. Endexine discontinuous, mostly very thin with scattered thicker sections, maximum thickness 0.1 µm; inner surface uneven. Intine well-developed, about twice as thick as footlayer (0.6 µm), continuous, uneven, with a slightly lighter stained outer layer and a darker stained inner layer.

Pollen subtype C9 (Figure 6.11)

Tectum reticulate; lumina angular to rounded; intraluminary bacula scattered on the nexine floor of the entire grain.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35—50 X 40—55 µm and smaller grains 25—35 X 30—40 (45) µm in diameter. Apocolpium mostly fairly reduced. Colpus ends acute to obtuse.

SEM (Figure 6.11 A—D)

Pollen semitectate. Tectum reticulate, homobrochate or heterobrochate. Lumina angular to rounded, diminishing in size towards the colpi, resulting in a distinct colpus margin. Predominant lumina diameter 1.82 µm. Muri smooth or stratified. Predominant muri thickness 0.62 µm. Nexine floor of the entire grain randomly scattered with blunt intraluminary bacula. Colpus membrane coarsely granular.

TEM (Figure 6.11 E, F)

Exine 1.7—1.8 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of fairly uniform thickness (0.5 µm), almost twice as thick as footlayer; elements of the tectum rounded to ellipsoid in cross-section; outer tectum surface smooth to undulate. Columellae well-developed, almost half of the total thickness of the exine (0.8 µm), simplicolumellate; columellae erect, cylindrical, of even thickness (0.5 µm) to slightly thicker towards their bases, decreasing in length towards the colpi; intercolumellar spaces relatively broad. Footlayer thick (0.3 µm), uninterrupted, distinctly baculate, traversed by micro-channels. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.3 µm; inner surface undulate. Intine removed by acetolysis.

Pollen subtype C10 (Figure 6.12)

Tectum finely reticulate; lumina irregularly angular; intraluminary bacula predominantly clustered along the muri.

LM

Pollen grains tricolpate with spiralaperturate aberrations in one taxon, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35—50 X 35—50 µm and smaller grains 25—35 (42) X 25—35 (44) µm in diameter. Apocolpium much reduced. Colpus ends acute to obtuse.

SEM (Figure 6.12 A—D)

Pollen semitectate. Tectum micro-reticulate to reticulate, heterobrochate. Lumina irregularly angular, diminishing in size and becoming more angular towards the colpi to form a distinct colpus margin. Predominant lumina diameter 1.14 µm. Muri smooth to stratified, often interrupted. Predominant muri thickness 0.55 µm. Nexine floor beset with blunt intraluminary bacula, predominantly clustered along the muri. Colpus membrane coarsely granular.

TEM (Figure 6.12 E, F)

Exine 1.6—1.8 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum 0.6—0.7 µm thick, twice as thick as footlayer; elements of the tectum ellipsoid to ovate in cross-section. Columellae well-developed, almost half of the total thickness of the exine (0.7 µm), simplicolumellate; columellae erect, cylindrical, slender, 0.4 µm thick, decreasing in length towards the colpi; intercolumellar spaces relatively broad. Footlayer 0.3 µm thick, distinctly baculate, traversed by micro-channels. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.3 µm. Intine removed by acetolysis.

Note: Specimen 194.1 belongs to this group on the grounds of most of the characters discussed above. It does, however, have extraordinary thick muri (predominant diameter 0.93 µm) which are distinctly stratified. These two characters make it a rather unique species within the group.

Pollen subtype C11 (Figure 6.13)

Tectum reticulate; lumina irregularly angular; intraluminary bacula predominantly clustered along the muri.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 36—43 X 37—44 µm and smaller grains 26—32 X 26—33 µm in diameter. Apocolpium much reduced. Colpus ends acute.

SEM (Figure 6.13 A—D)

Pollen semitectate. Tectum reticulate, homobrochate. Lumina irregularly angular, abruptly diminishing in size towards the colpi, resulting in a very distinct colpus margin with rounded lumina. Predominant lumina diameter 2.0 µm. Muri smooth or stratified. Predominant muri thickness 0.6 µm. Nexine floor beset with blunt intraluminary bacula, predominantly clustered along the muri. Colpus membrane coarsely granular.

TEM (Figure 6.13 E, F)
Exine 1.8 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of fairly uniform thickness (0.7—0.8 µm), three to four times as thick as footlayer; elements of the tectum ellipsoid to ovate in cross-section. Columellae well-developed, slightly less than half of the total thickness of the exine (0.7 µm), simplicolumellate; columellae erect, cylindrical, 0.5 µm in cross-section, becoming slightly broader below the tectum; decreasing in length towards the colpi; intercolumellar spaces relatively narrow. Footlayer thick (0.2 µm), uninterrupted, distinctly baculate, traversed by micro-channels. Endexine discontinuous, of differential thickness with very thin areas alternating with thickened sections, maximum thickness 0.2 µm; inner surface undulate. Intine removed by acetolysis.

Pollen subtype C12 (Figure 6.14)

Tectum coarsely reticulate; lumina irregularly angular; intraluminary bacula clustered along the muri.

LM
Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 42 X 45 µm and smaller grains 32 X 34 µm in diameter. Apocolpium reduced. Colpus ends obtusely rounded.

SEM (Figure 6.14 A—D)
Pollen semitectate. Tectum coarsely reticulate, homobrochate. Lumina irregularly angular, abruptly diminishing in size towards the colpi resulting in a distinct colpus margin with rounded lumina. Predominant lumina diameter 2.9 µm. Muri stratified. Predominant muri thickness 0.8 µm. Nexine floor beset with blunt intraluminary bacula, predominantly clustered along the muri. Colpus membrane coarsely granular.

TEM (Figure 6.14 E, F)
Exine 1.8 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum 0.8 µm thick, twice as thick as footlayer; elements of the tectum ellipsoid to ovate in cross-section. Columellae well-developed, about half of the total thickness of the exine (0.9 µm), simplicolumellate; columellae erect, cylindrical, 0.4—

0.5 µm in cross-section, thickening towards their bases, decreasing in length towards the colpi; intercolumellar spaces broad, mostly filled with a dark-stained substance. Footlayer 0.3—0.4 µm thick, uninterrupted, distinctly baculate, traversed by micro-channels; outer surface (bacula) coated with a dark-stained substance. Endexine discontinuous, mostly very thin but with scattered thickened sections, maximum thickness 0.4 µm; inner surface very uneven. Intine well developed, about twice as thick as footlayer (0.5—0.6 µm), continuous, uneven, unstratified.

Pollen subtype C13 (Figure 6.15)

Tectum rugose reticulate; muri thick, distinctly perforated; lumina irregularly angular; intraluminary bacula clustered along the muri.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and oblate in equatorial view, large grains 44 X 45 µm and smaller grains 35 X 36 µm in diameter. Apocolpium much reduced. Colpus ends acute.

SEM (Figure 6.15 A—D)

Pollen semitectate. Tectum rugulose-reticulate, heterobrochate. Lumina irregularly angular to rounded, gradually diminishing in size towards the colpi, resulting in a distinct colpus margin with rounded lumina. Predominant lumina diameter 1.65 µm. Muri wide (1.02 µm), smooth, distinctly perforate, with the perforations less prominent in the apocolpial area. Nexine floor beset with blunt intraluminary bacula predominantly clustered along the muri. Colpus membrane moderately granular.

TEM (Figure 6.15 E, F)

Exine 1.6—1.8 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum of fairly uniform thickness (0.6 µm), twice as thick as footlayer; elements of the tectum ellipsoid to ovate in cross-section; outer tectum surface smooth to undulate. Columellae well-developed, about half of the total thickness of the exine (0.7—0.9 µm), complex, pluricolumellate; columellae erect to slightly tilted, cylindrical, 0.4 µm in cross-section but thickening below the tectum, decreasing in length towards the colpi; intercolumellar spaces of varying widths, narrow within the pluricolumellate complex and much wider between adjacent complexes, partially filled with a dark-stained substance. Footlayer 0.3 µm thick, traversed by micro-channels, very uneven with a distinctly baculate outer surface; bacula predominantly clustered around pluricolumellar complexes. Endexine discontinuous, very thin with a few thickened sections, maximum thickness 0.2 µm; inner surface uneven. Intine well-developed, twice as thick as footlayer (0.6 µm), uneven, stratified with a light-stained outer layer and a more granular, dark-stained inner layer.

Note: Although specimens [254.1] and [254.2] revealed the same basic pollen type, the average lumina diameter of the latter is much larger than that of the first (Figure 6.15). These variations could be indicative of a rather variable species.

Pollen subtype C14 (Figure 6.16)

Tectum coarsely reticulate; muri thin, sometimes perforated; lumina irregularly angular; intraluminary bacula clustered along the muri.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 35 X 35 µm and smaller grains 28 X 28 µm in diameter. Apocolpium reduced. Colpus ends acute to rounded.

SEM (Figure 6.16 A—D)

Pollen semitectate. Tectum coarsely reticulate, heterobrochate. Lumina irregularly angular to rounded, gradually diminishing in size towards the colpi, resulting in a distinct colpus margin with rounded lumina. Predominant lumina diameter 2.7 µm. Muri relatively thin (0.69 µm), smooth, with numerous perforations. Nexine floor beset with blunt intraluminary bacula, predominantly clustered along the muri. Colpus membrane moderately granular.

TEM (Figure 6.16 E, F)

Exine 1.8—2.0 µm thick, consisting of comparatively thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum 0.5—0.7 µm thick, twice as thick as footlayer; elements of the tectum rounded to ellipsoid in cross-section, tectal layer forming triangular domes over the pluricolumellate complexes. Columellae well-developed, about half of the total thickness of the exine (0.7—0.9 µm), complex, pluricolumellate; columellae erect to slightly tilted, cylindrical, 0.5 µm in cross-section but thickening below the tectum, decreasing in length towards the colpi; intercolumellar spaces of varying widths, narrow within the pluricolumellate complex and much wider between adjacent complexes. Footlayer 0.3 µm thick, traversed by micro-channels, very uneven with a distinctly baculate outer surface; bacula predominantly clustered around pluricolumellar complexes. Endexine discontinuous, very thin with a few thickened sections, maximum thickness 0.2 µm; inner surface uneven. Intine removed by acetolysis.

Pollen subtype C15 (Figure 6.17)

Tectum very coarsely reticulate; muri relatively thin, sometimes perforated; lumina large, irregularly angular; intraluminary bacula clustered along the muri.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 39 X 41 µm and smaller grains 25—35 X 34—35 µm in diameter. Apocolpium small. Colpus ends acute to rounded.

SEM (Figure 6.17 A—D)

Pollen semitectate. Tectum very coarsely reticulate, homobrochate. Lumina irregularly angular, abruptly diminishing in size near the colpi, resulting in a distinct colpus margin with rounded lumina. Predominant lumina diameter 3.7 µm. Muri thick (1.06 µm), smooth, on a slightly higher level where the muri meet than in between crossings; with numerous perforations, especially near the colpi and in the apocolpial regions. Nexine floor beset with blunt intraluminary bacula, predominantly clustered along the muri. Colpus membrane granular.

TEM (Figure 6.17 E, F)

Exine 2.6—2.8 µm thick, consisting of thick ectexine (tectum, columellae, footlayer) and a much thinner endexine. Tectum 0.5—0.7 µm thick, almost twice as thick as footlayer; elements of the tectum ellipsoid to ovate in cross-section, tectal layer forming triangular domes over the pluricolumellate complexes. Columellae well-developed, about half of the total thickness of the exine (1.2—1.5 µm), complex, pluricolumellate; columellae erect to slightly tilted, cylindrical, slender, 0.5 µm in cross-section, thickening towards their bases; intercolumellar spaces of varying widths, narrow within the pluricolumellate complex and very wide between adjacent complexes. Footlayer 0.4 µm thick, very uneven, traversed by micro-channels, prominently baculate; bacula up to 0.7 µm tall. Endexine discontinuous, very thin with a few thickened sections, maximum thickness 0.3 µm; inner surface uneven. Intine removed by acetolysis.

6.3.4 Pollen type D

Supra-areolate type (Figures 6.18—8.22)

Pollen subtype D1 (Figure 6.18—6.19)

Supratectal areolae solitary, clustered or arranged into a obscure negative reticulum; individual areolae 0.75—2.00 µm in diameter.

LM

Pollen grains tri-, tetra- or pantocolpate, often with 6-pantocolpate, 12-pantocolpate, 4-aperturate, spiralaperturate and 3-zonocyclicolpate aberrations in various taxa, apolar or isopolar, apolar grains spherical, polar grains triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40—55 (62) X 40—60 µm and smaller grains 30—40 X 30—45 µm in diameter. Apocolpium reduced in tri- and tetracolpate grains. Colpus ends acute to tattered.

SEM

Pollen tectate. Sexine characterised by free-standing supratectal areolae on an uneven tectum traversed by channels. Supratectal areolae 0.75—2.00 µm in diameter, irregular, triangular to rounded or club-shaped, each terminating in a central spinule; solitary, clustered into small groups or arranged into a obscure negative reticulum. Individual areolae smaller and more densely clustered towards the colpi. Outer tectum surface uneven to verrucate. Colpus membrane smooth to granular with exine islands visible within the colpus (Figure 6.18 A, B & C).

TEM

Exine 1.1—1.3 µm thick, consisting of a comparatively thick ectexine (supratectal areolae, tectum, columellae, footlayer) and a much thinner endexine. Supratectal areolae large, 0.7—0.9 µm tall, cylindrical to club-shaped with angular to spear-shaped apices terminating in a central spinule. Tectum 0.2—0.3 µm thick, two to three times as thick as the footlayer, traversed by micro-channels, uneven; outer tectum surface coarsely verrucate. Columellae weakly developed, extremely thin, simplicolumellate; individual columellae only vaguely distinguishable; intercolumellar space uneven, filled with a dark-stained material. Footlayer 0.1 µm thick, uneven, traversed by micro-channels. Endexine discontinuous, maximum thickness 0.1 µm; inner surface uneven. Intine (0.1—0.2 µm) thick, as thick as footlayer too much thicker in areas where the areolae are less densely clustered, continuous, uneven, with a darker stained outer layer separated from a light-stained, granular inner layer.

In the colpial regions the endexine disappears and the intine is much thickened. Complete ectexine islands, composed of all the above mentioned layers, occur isolatedly within the colpi. The intercolumellar spaces within these islands are enlarged, raising both the tectum and the supratectal areolae to form an almost dome-shaped structure (Figure 6.19 E).

Pollen subtype D2 (Figure 6.20)

Supratectal areolae irregular, triangular, arranged into a distinct negative reticulum; individual areolae large (1.8 µm in diameter).

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40 X 41 µm and smaller grains 30 X 31 µm in diameter. Apocolpium much reduced. Colpus ends acute.

SEM (Figure 6.20 A—D)

Pollen tectate. Sexine characterised by free-standing supratectal areolae on an uneven tectum traversed by channels. Supratectal areolae fairly large (1.8 µm in diameter), irregular, triangular to rounded or club-shaped, each terminating in a central spinule; arranged into a distinct negative reticulum, forming large, irregular lumina. Outer tectum surface uneven to distinctly baculate. Colpus membrane smooth to granular with exine islands visible within the colpus.

TEM (Figure 6.20 E, F)

Exine 1.6—1.7 µm thick, consisting of a thick ectexine (supratectal areolae, tectum, columellae, footlayer) and a much thinner endexine. Supratectal areolae large, 1.2—1.3 µm tall, cylindrical becoming wider towards the apex, apices angular to arrow-shaped terminating in a central spinule. A dark-stained substance surrounds the individual areolae. Tectum thick (0.3—0.4 µm), two to three times as thick as footlayer, traversed by micro-channels, uneven; outer tectum surface coarsely verrucate to baculate. Columellae weakly developed, extremely thin; individual columellae not distinguishable; intercolumellar space uneven, filled with a dark-stained substance. Footlayer 0.15 µm thick, uneven, interrupted, traversed by micro-channels. Endexine discontinuous, thin with some local thickenings, maximum thichness 0.1 µm; inner surface undulate. Intine relatively thick (0.5 µm), almost five times thicker than footlayer, continuous, relatively smooth, with a lighter stained outer layer separated from a more granular, darker stained inner layer.

In the colpial regions the endexine disappears and the intine is much thickened. Complete ectexine islands, composed of all the above mentioned layers, occur isolatedly within the colpi. The intercolumellar spaces within these islands are enlarged, raising both the tectum and the supratectal areolae to form an almost dome-shaped structure.

Pollen subtype D3 (Figure 6.21)

Supratectal areolae rounded, arranged into a distinct negative reticulum; individual areolae small (0.89 µm in diameter) but prominently enlarged in apocolpial region.

LM

Pollen grains tricolpate, isopolar, triangularly rounded in polar view and spherical to oblate in equatorial view, large grains 40 X 41 µm and smaller grains 30 X 31 µm in diameter. Apocolpium well-defined. Colpus ends rounded to tattered.

SEM (Figure 6.21 A—D)

Pollen tectate. Sexine characterised by free-standing supratectal areolae on an uneven tectum traversed by channels. Supratectal areolae mostly small (0.89 µm), rounded to club-shaped, each terminating in a central spinule; arranged into a distinct negative reticulum, resulting in large irregular lumina that decrease in size towards the colpi. Areolae in apocolpial area very much enlarged to form a prominently ridged pattern, a feature unique to this subtype. Outer tectum surface uneven to distinctly verrucate. Colpus membrane smooth to granular with exine islands visible within the colpus.

TEM (Figure 6.21 E, F)

Exine 1.6—1.7 µm thick, consisting of a comparatively thick ectexine (supratectal areolae, tectum, columellae, footlayer) and a much thinner endexine. Supratectal areolae 0.6—1.0 µm tall, club-shaped with angular to spear-shaped apices terminating in a central spinule. Tectum 0.3—0.4 µm thick, twice as thick as the footlayer, traversed by micro-channels, uneven; outer tectum surface coarsely verrucate. Columellae weakly developed, extremely thin; individual columellae not distinguishable; intercolumellar space uneven, filled with a dark-stained material. Footlayer 0.2 µm thick, uneven, traversed by micro-channels. Endexine discontinuous; inner surface uneven, maximum thickness 0.1 µm. Intine (0.1—0.2 µm) thick, as thick as footlayer too much thicker in areas where the areolae are less densely clustered, continuous, uneven, with a darker stained outer layer separated from a lighter, granular inner layer.

In the colpial regions the endexine disappears and the intine is much thickened. Complete ectexine islands, composed of all the above mentioned layers, occur isolatedly within the colpi. The intercolumellar spaces within these islands are enlarged, raising both the tectum and the supratectal areolae to form an almost dome-shaped structure (Figure 6.21 F).

Pollen subtype D4 (Figure 6.22)

Supratectal areolae irregular, rectangular, arranged into a coarse ridged pattern; individual areolae large (2.27 X 0.98 µm).

LM

Pollen grains tri- or tetracolpate with numerous 12-pantocolpate aberrations, normal grains isopolar, isodiametrical in both polar and equatorial view, large grains 75—82 X 75—82 µm and smaller grains 44—58 X 44—58 µm in diameter. Apocolpium poorly defined. Colpus ends rounded to tattered.

SEM (Figure 6.22 A—D)

Pollen tectate. Sexine characterised by free-standing supratectal areolae on an uneven tectum traversed by channels. Supratectal areolae irregular, triangular to club-shaped, each terminating in a central spinule; individual areolae larger (2.27 X 0.98 µm) than in subtype D1, arranged into a coarse, ridged pattern (negative reticulum) with elongated lumina. Colpi fringed by elongated areolae which form a distinct margin. Colpus membrane smooth to granular with exine islands visible within the colpus.

TEM (Figure 6.22 E, F)

Exine 1.8 µm thick, consisting of comparatively thick ectexine (supratectal areolae, tectum, columellae, footlayer) and a much thinner endexine. Supratectal areolae very large, elongated (1.2 µm tall), cylindrical to oblong with angular to spear-shaped apices terminating in a central spinule. A dark-stained material surrounds the individual areolae. Tectum 0.3—0.4 µm thick, two to three times as thick as footlayer, traversed by micro-channels, uneven; outer tectum surface coarsely verrucate to baculate. Columellae weakly developed, extremely thin, simplicolumellate; individual columellae only vaguely distinguishable; intercolumellar space uneven, filled with a dark-stained substance. Footlayer 0.1—0.2 µm thick, uneven, interrupted, traversed by micro-channels. Endexine discontinuous, fragmented, thin with some local thickenings interrupted by much thinner areas, maximum thickness 0.1 µm; inner surface uneven to undulate. Intine relatively thick (0.6 µm), almost six times thicker than footlayer, continuous, uneven, with a lighter stained outer layer separated from a much darker inner layer.

In the colpial regions the endexine disappears and the intine is much thickened. Complete exine islands, composed of all the above mentioned layers, occur isolatedly within the colpi. The intercolumellar spaces within these islands are enlarged, raising both the tectum and the supratectal areolae to form an almost dome-shaped structure.

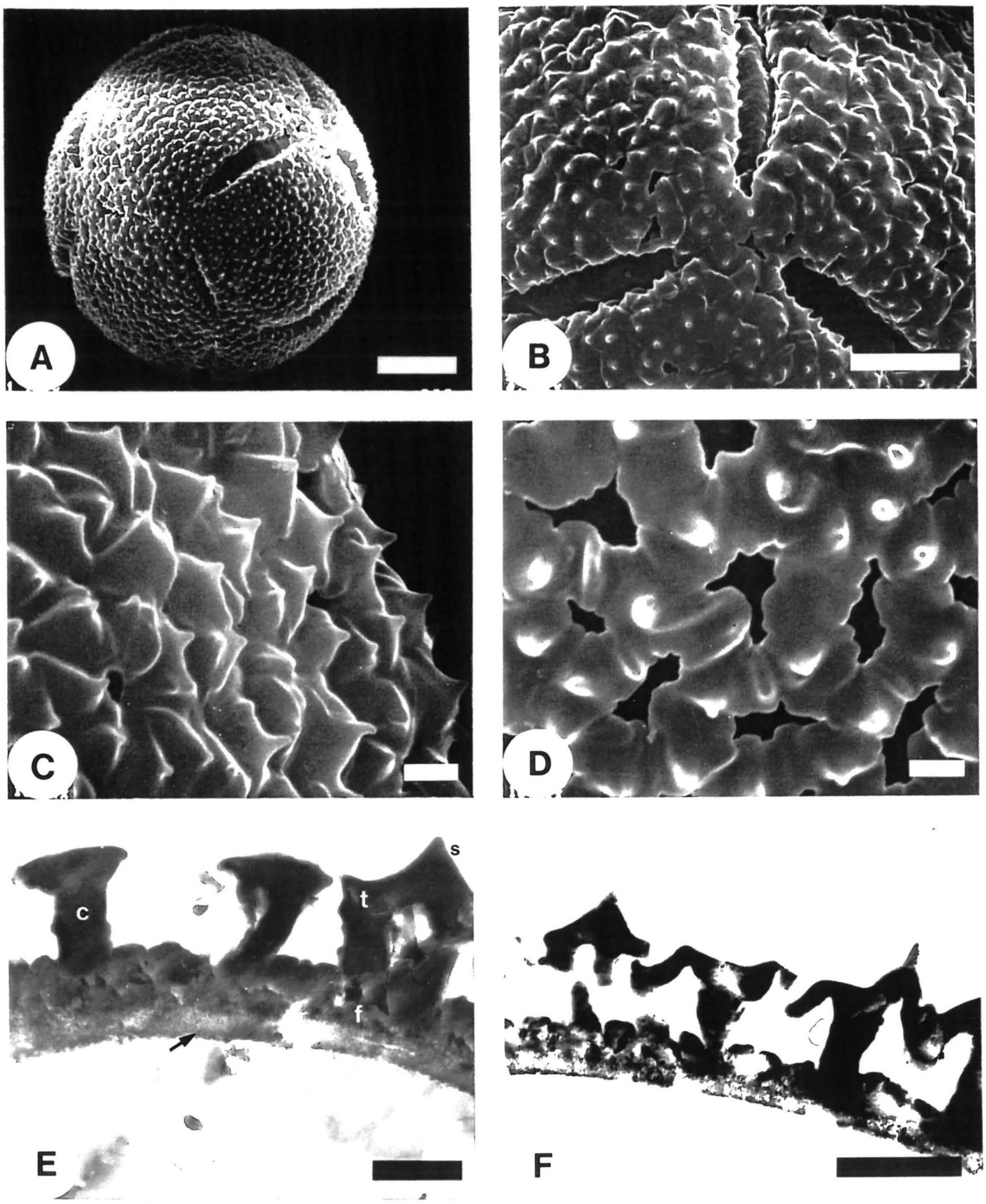


Figure 6.1 A—F. *Oxalis* pollen type A. A, B: *O. minuta* var. *minuta* [108.1]. (A) Pantocolpate grain, SEM. (B) Apertural area showing the meeting point of three colpi, SEM. (C) *O. nidulans* var. *denticulata*, oblique view of rugulate-reticulate tectum showing supratectal spinules (s), SEM. (D) *O. eckloniana* var. *sonderi* [114.1], mesocolpial portion of sexine showing rugulate-reticulate tectum with irregular lumina and constricted muri, SEM. (E) *O. microdonta* [105.1], wall section showing supratectal spinules (s), tectum (t), columellae (c), footlayer (f) and endexine (arrow), TEM. (F) *O. eckloniana* var. *sonderi* [114.1], wall section, TEM. Scale bars: A = 10 μm. B—F = 1 μm.

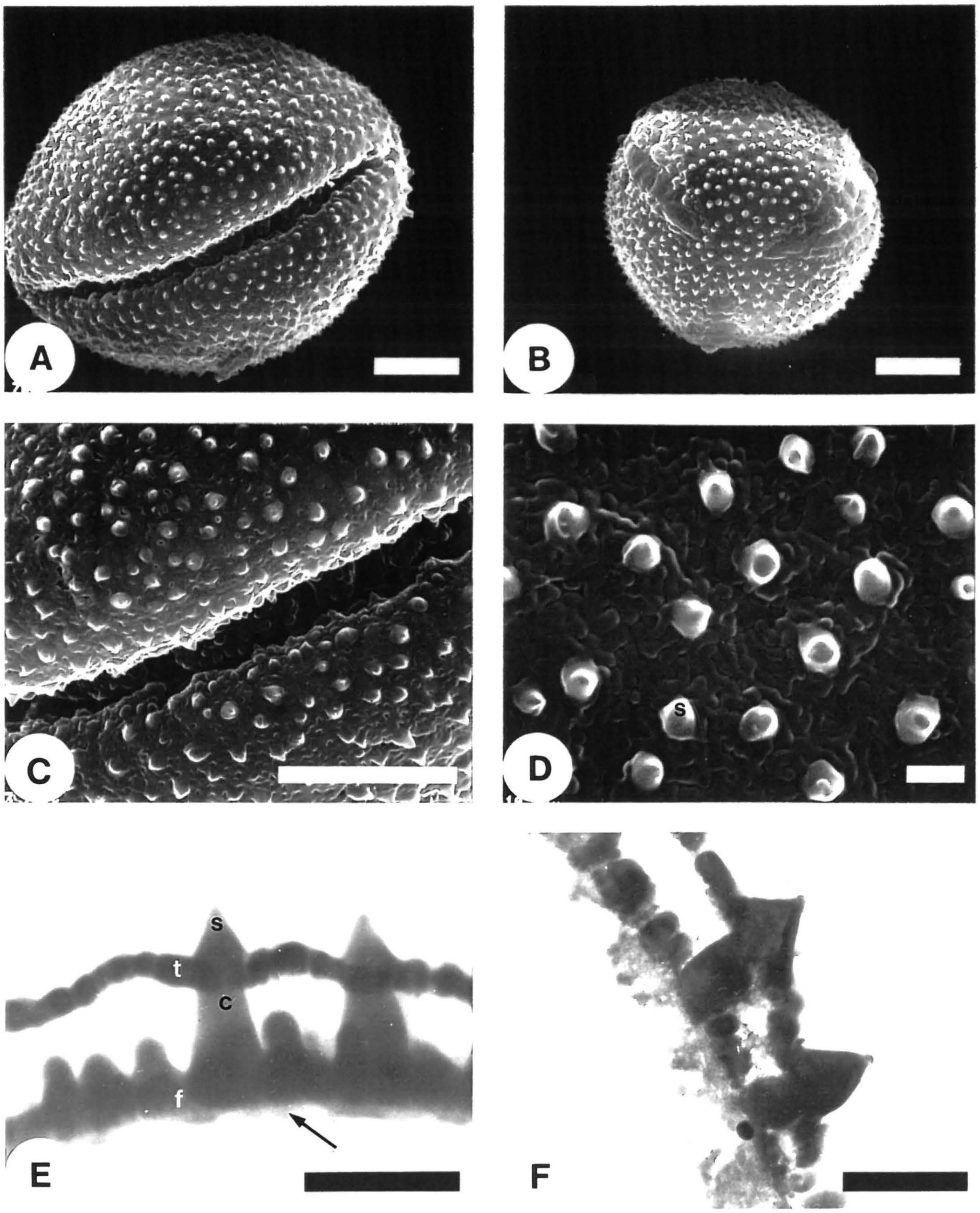


Figure 6.2 A—F. *Oxalis* pollen type B. A—E: *O. fibrosa* [104.1]. (A) Equatorial face view, SEM. (B) Subpolar view showing reduced apocolpium and three colpi with acute ends, SEM. (C) Apertural area showing coarsely granular colpus membrane, SEM. (D) Mesocolpial portion of sexine showing micro-rugulate-spinate tectum and supratectal spines (s), SEM. (E) Wall section showing supratectal spines (s), tectum (t), columellae (c), baculate footlayer (f) and endexine (arrow), TEM. (F) *O. fibrosa* [104.2], wall section, TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

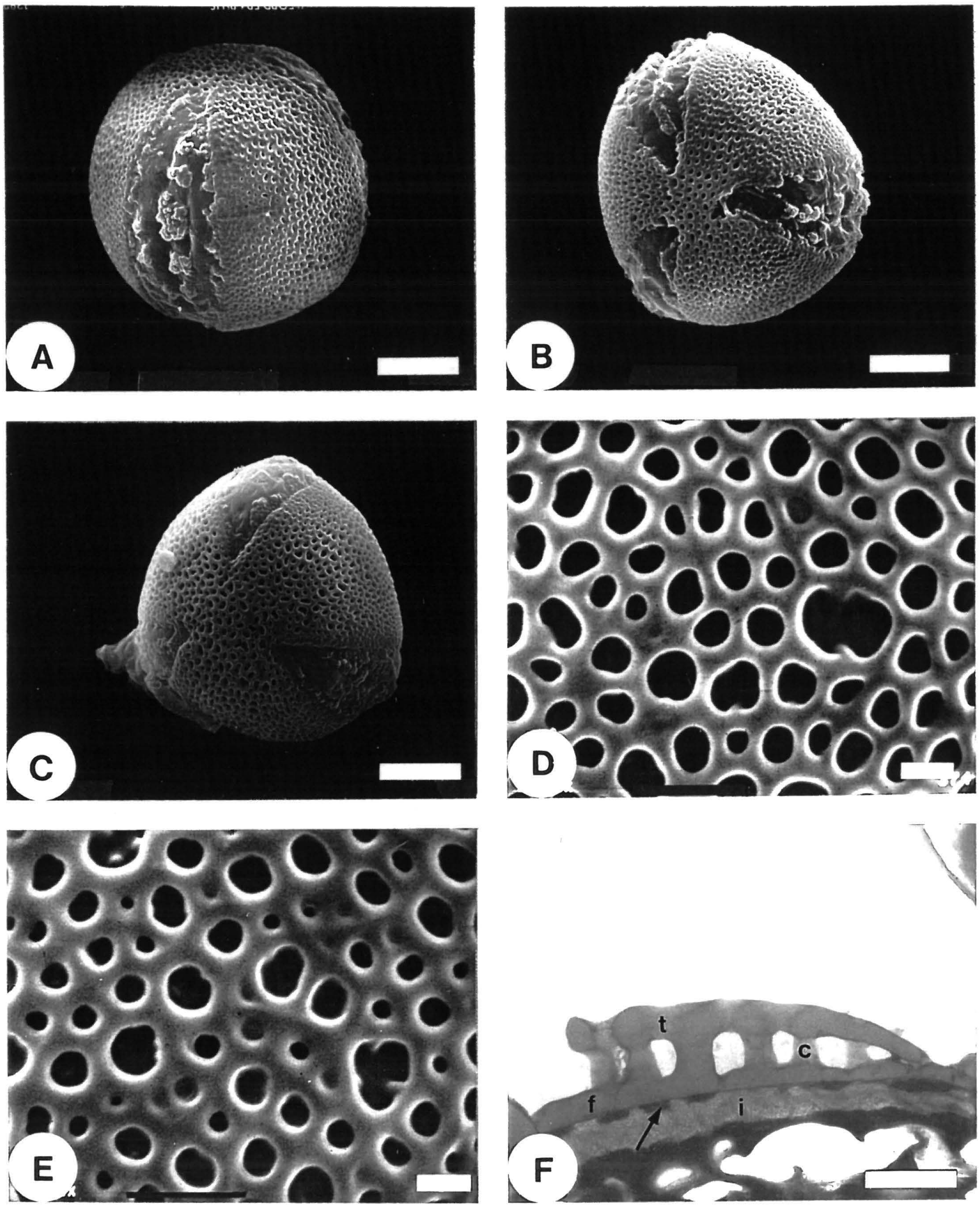


Figure 6.3 A—F. *Oxalis* pollen subtype C1. A, B: *O. stellata* var. *montaguensis* [25.1]. (A) Equatorial view with aperture, SEM. (B) Polar view, note reduced apocolpium and granular colpus membranes, SEM. (C) *O. bowiei* [17.1], subpolar view, SEM. (D) *O. tragopoda* [30.1], mesocolpial portion of sexine showing micro-reticulate tectum with isodiametrically rounded lumina, SEM. E, F: *O. psilopoda* [32.1]. (E) Mesocolpial portion of sexine showing micro-reticulate tectum with isodiametrically rounded lumina, SEM. (F) Wall section of apertural region showing tectum (t), columellae (c), uniform footlayer (f), endexine (arrow) and intine (i); note the reduction in columella length towards the colpus, TEM. Scale bars: A—D = 10 µm. E, F = 1 µm.

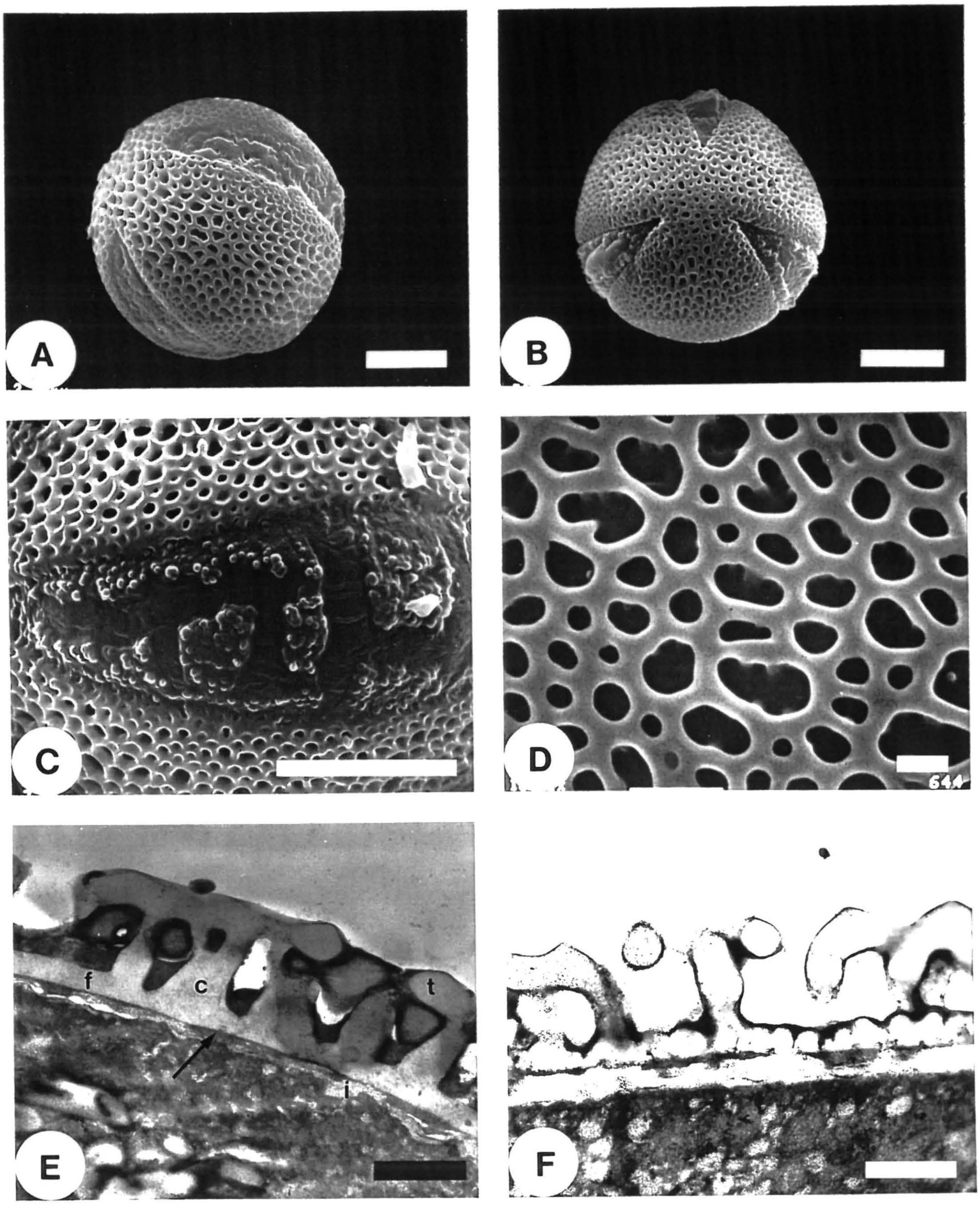


Figure 6.4 A—F. *Oxalis* pollen subtype C2. (A) *O. gracilipes* [230.1], equatorial view with aperture, SEM. (B) *O. bifurca* var. *bifurca* [63.1], polar view, SEM. (C) *O. furcillata var. furcillata* [102.1], apertural area showing granular colpus membrane and reduction in average lumina diameter towards the colpus, SEM. (D) *O. sp.* [285], mesocolpial portion of sexine showing micro-reticulate tectum with rounded to oblong muri, SEM. E, F *O. davyana* [21.1]. (E) Wall section showing the tectum (t), columellae (c), uniform footlayer (f), endexine (arrow) and intine (i), TEM. (F) Wall section showing rounded tectum cross-sections, TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

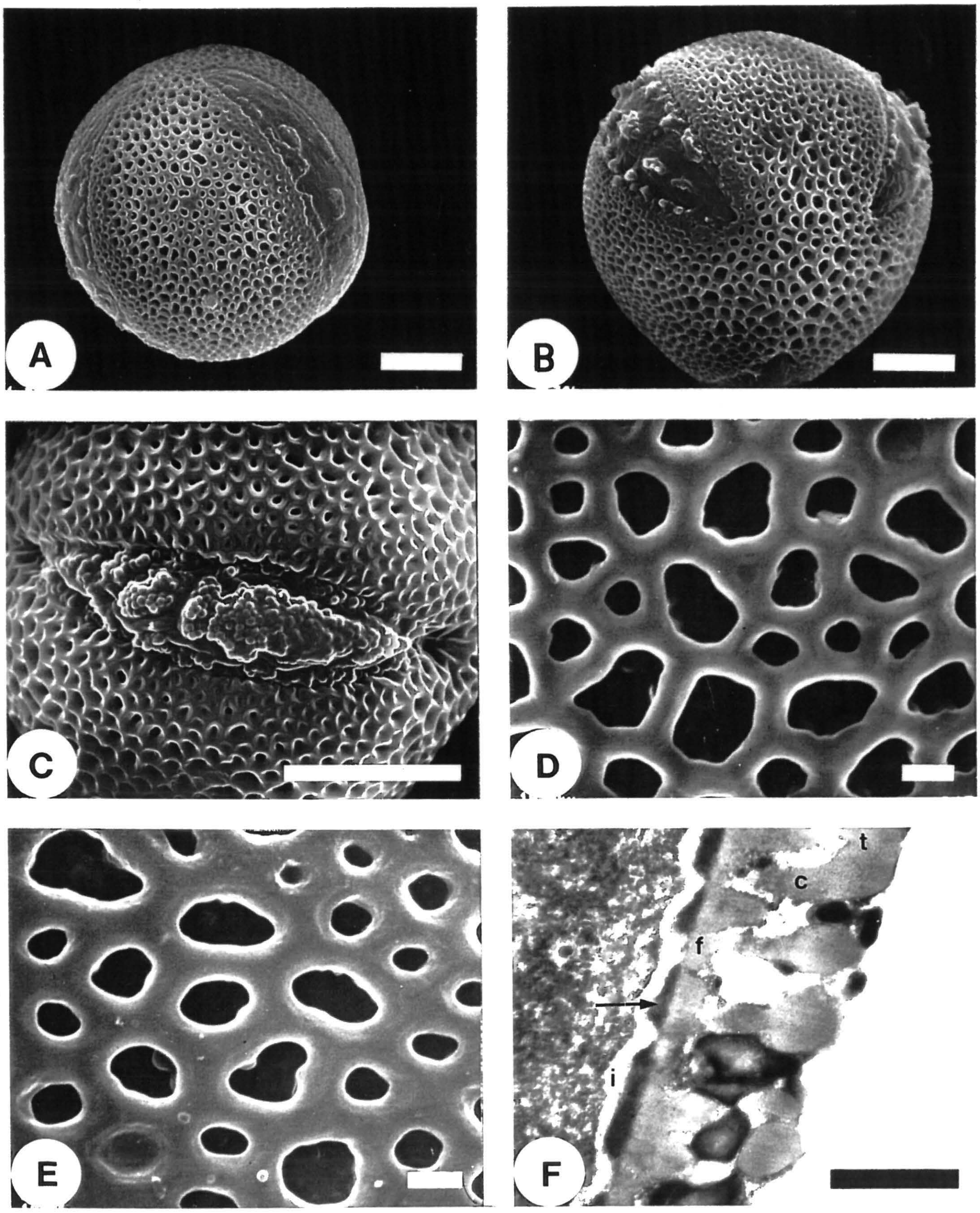


Figure 6.5 A—F. *Oxalis* pollen subtype C3. (A) *O. senecta* [100.1], equatorial view with apertures, SEM. (B) *O. fourcadei* [96.1], subpolar view, SEM. (C) *O. ambiqua* var. *ambiqua* [50.1], apertural area showing granular colpus membrane, SEM. (D) *O. knuthiana* [10.1], mesocolpial portion of sexine showing finely reticulate tectum with slightly angular muri, SEM. (E) *O. sp.* [285], mesocolpial portion of sexine showing finely reticulate tectum with thicker, more rounded muri, SEM. (F) *O. purpurea* [70.2], wall section showing tectum (t), columellae (c), uniform footlayer (f), endexine (arrow) and intine (i), TEM. Scale bars: A—D = 10 μm. E—F = 1 μm.

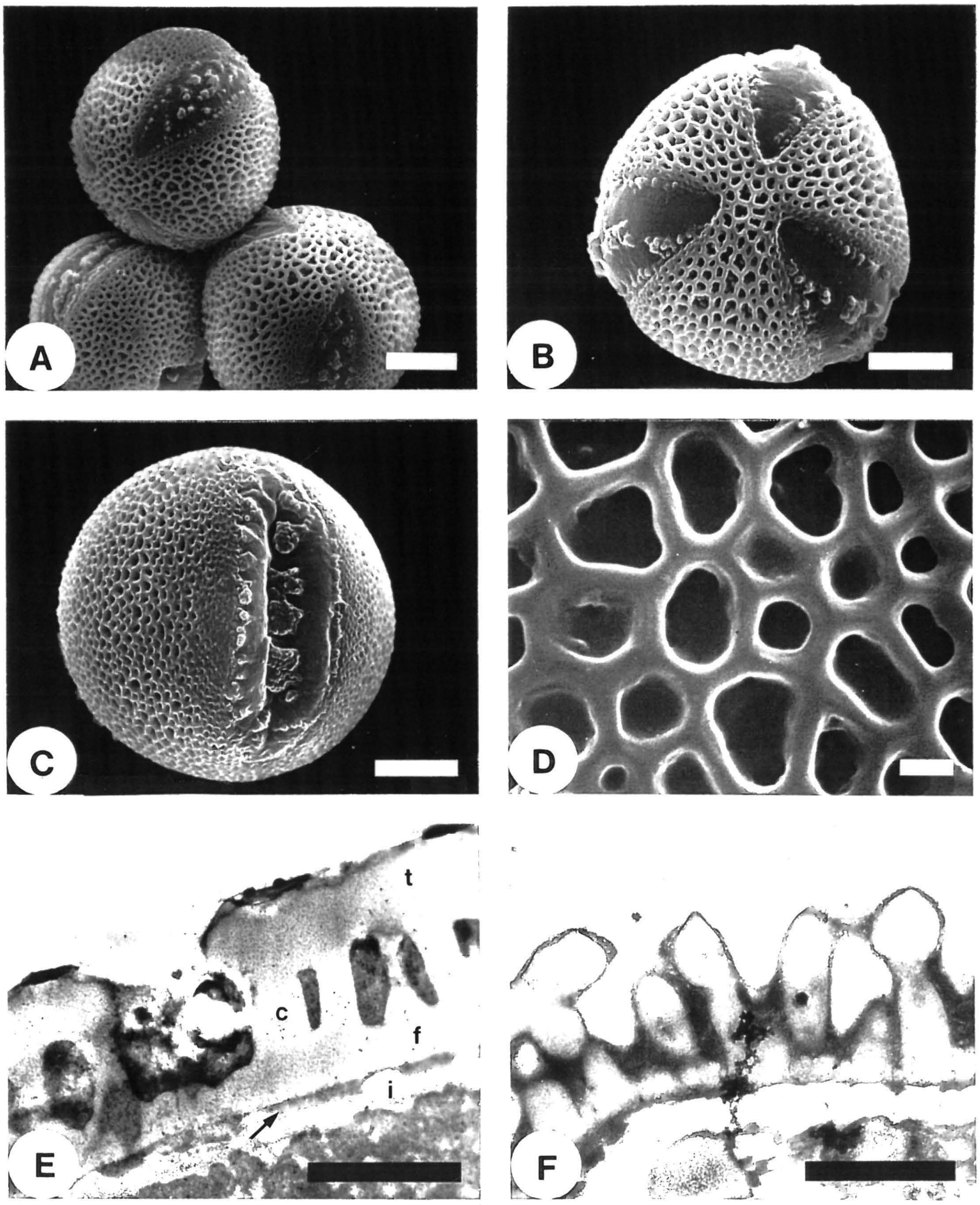


Figure 6.6 A—F. *Oxalis* pollen subtype C4. A, B: *O. heterophylla* [61.1]. (A) Equatorial and polar view of a few grains, SEM. (B) Polar view, note reduced apocolpium, SEM. C, D: *O. densa* [101.1]. (C) Apertural area showing granular colpus membrane and a reduction in average lumina diameter towards the colpus, SEM. (D) Mesocolpial portion of sexine showing reticulate tectum with rounded to angular muri, SEM. E, F *O. inaequalis* [91.1]. (E) Wall section showing uniform tectum (t), columellae (c), footlayer (f), endexine (arrow) and intine (i), TEM. (F) Oblique wall section, TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

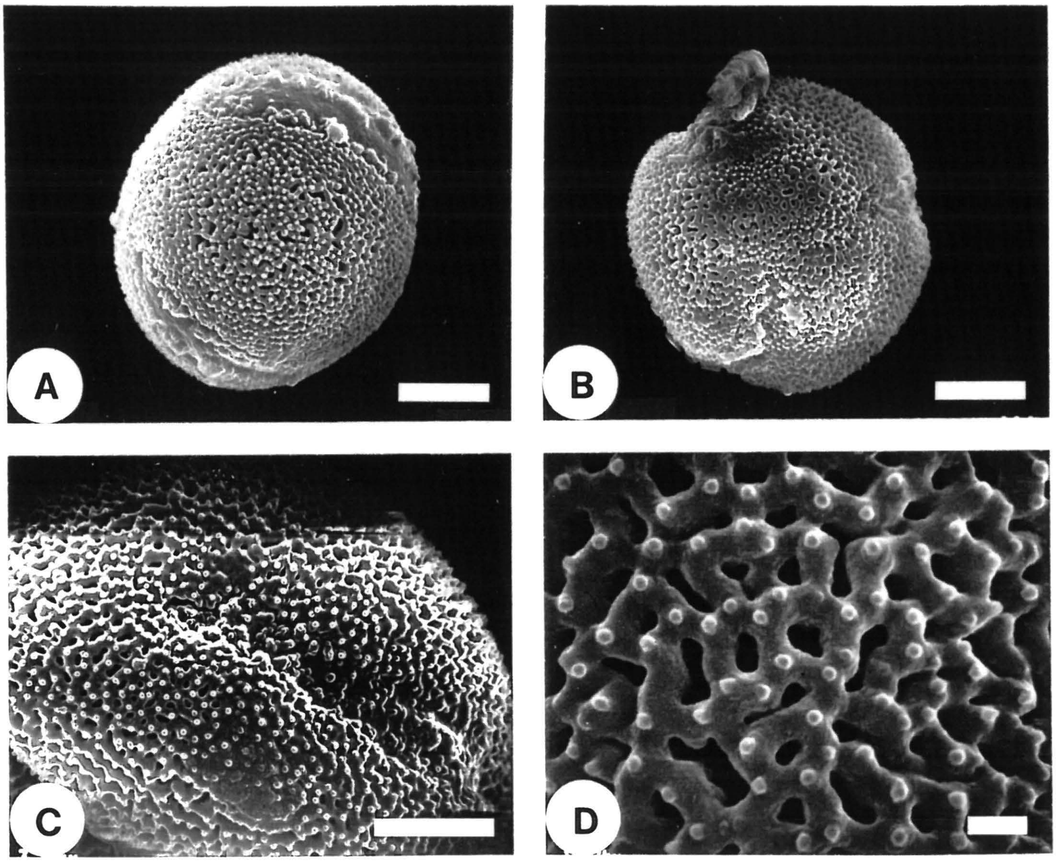


Figure 6.7 A—D. *Oxalis* pollen subtype C5. A—E: *O. levis* [235.1]. (A) Equatorial view, SEM. (B) Polar view, SEM. (C, D) Mesocolpial portion of sexine showing micro-reticulate tectum with blunt supratectal spinules; note the arrangement of muri on two different levels, SEM. Scale bars: A—C = 10 μm. D = 1 μm.

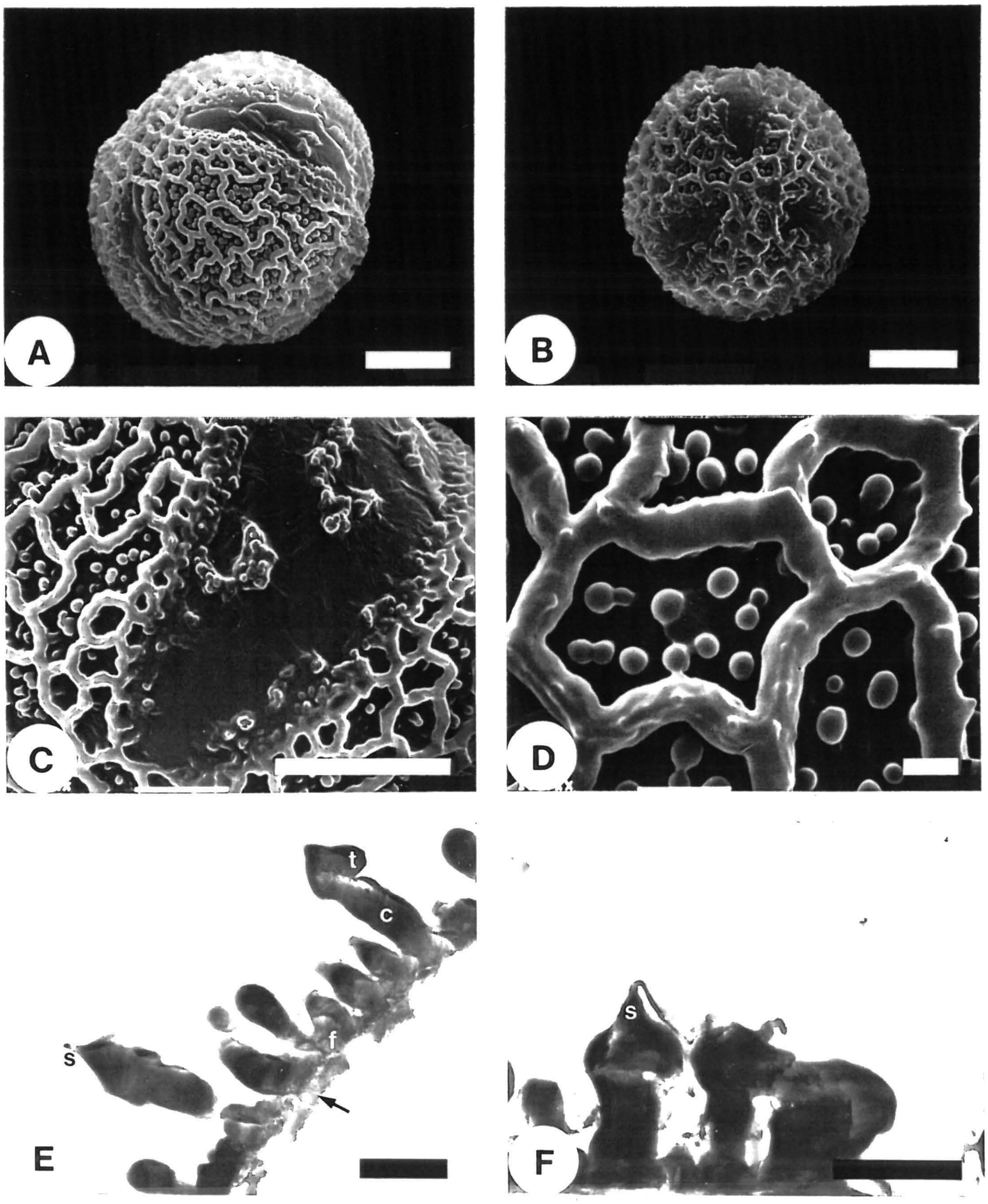


Figure 6.8 A—F. *Oxalis* pollen subtype C6. (A) *O. henrici* [261.1], equatorial view showing open reticulum and two colpi, SEM. (B) *O. engleriana* [260.1], polar view displaying the reduced apocolpium, SEM. C—F: *O. henrici* [261.1]. (C) Apertural area showing granular colpus membrane and a reduction in average lumina diameter towards the colpus, SEM. (D) Mesocolpial portion of sexine showing coarse, reticulate tectum with supratectal spinules; also note the prominent, free-standing intraluminary bacula, SEM. (E) Wall section showing supratectal spinules (s), portions of the tectum (t), columellae (c), uneven footlayer (f) and endexine (arrow), TEM. (F) Wall section showing supratectal spines (s) on underlying columellae (c), TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

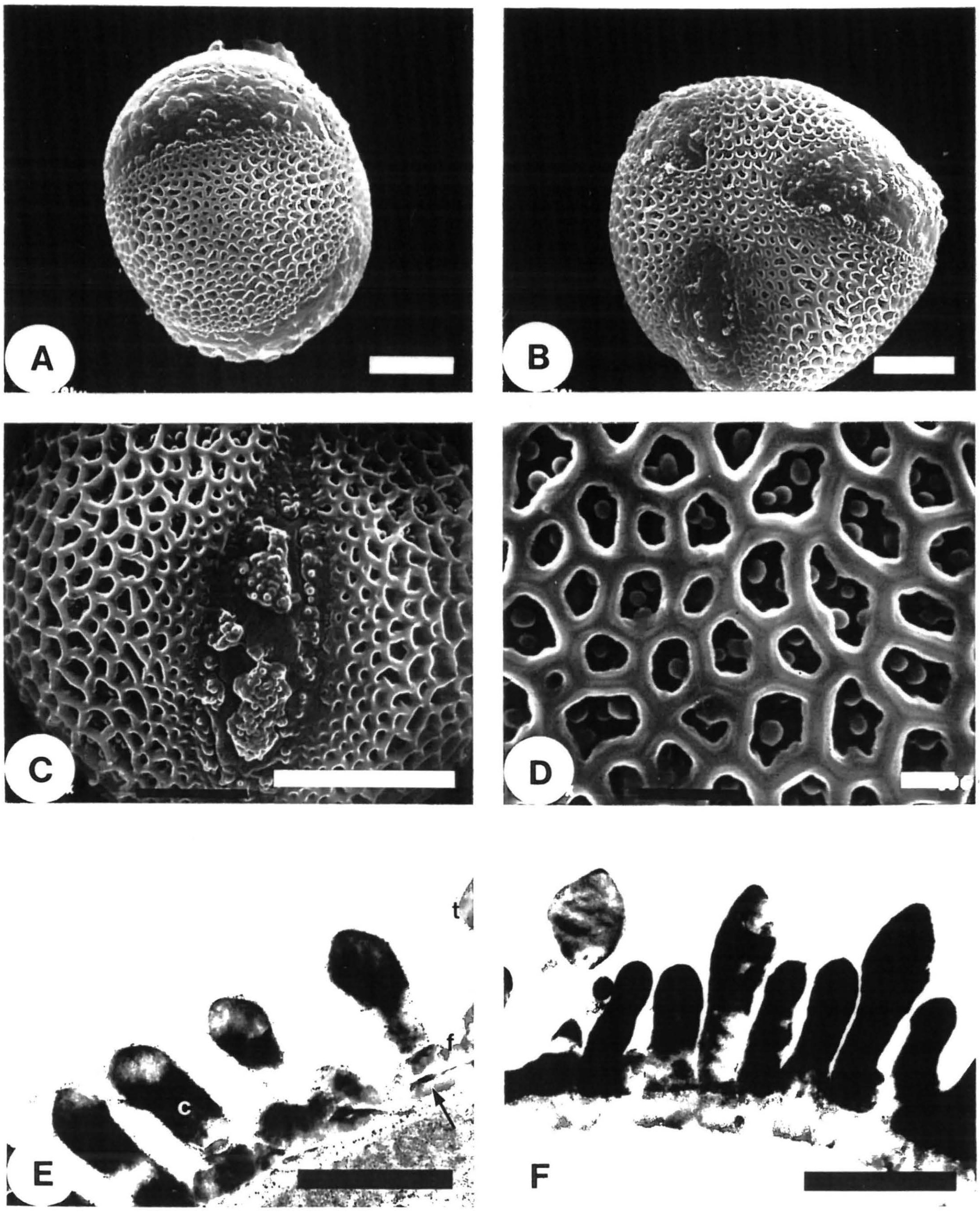


Figure 6.9 A—F. *Oxalis* pollen subtype C7. A, B: *O. polyphylla* var. *polyphylla* [223.1]. (A) Equatorial view, SEM. (B) Polar view, SEM. C—E: *O. suteroides* var. *latituba* [256.1]. (C) Apertural area showing granular colpus membrane and reduction in average lumina diameter towards the colpus, SEM. (D) Mesocolpial portion of sexine showing micro-reticulate tectum with rounded to angular muri; note the randomly scattered intraluminary bacula on the nexine floor, SEM. (E) Wall section showing portions of the tectum (t), columellae (c), uneven footlayer (f) and endexine (arrow), TEM. (F) *O. caprina* [29.1], wall section, TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

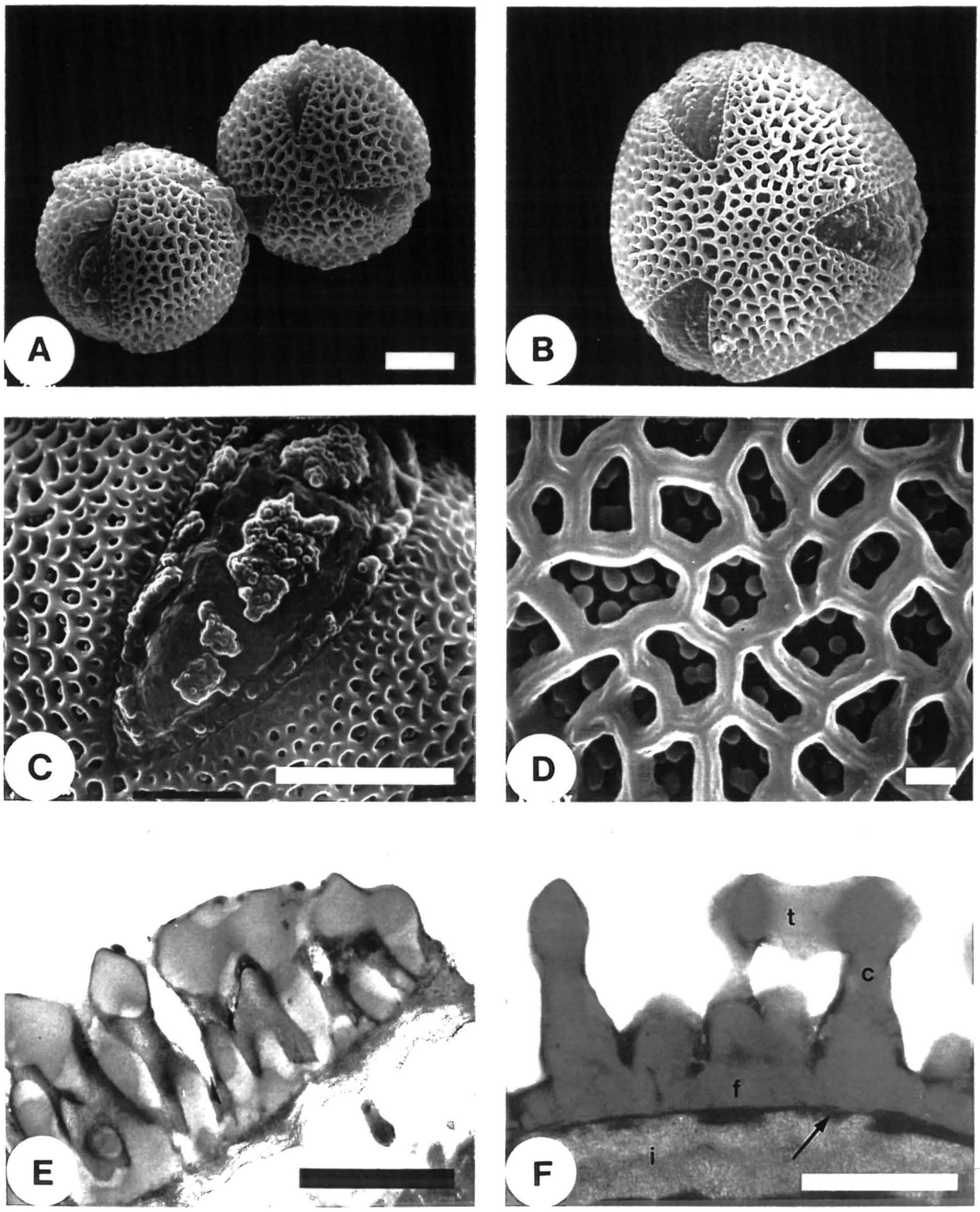


Figure 6.10 A—F. *Oxalis* pollen subtype C8. (A) *O. versicolor* var. *versicolor* [220.1], equatorial and polar views, SEM. (B) *O. glabra* [217.1], polar view showing acute colpus ends and granular colpus membrane, SEM. (C) *O. orbicularis* [39.1], apertural area showing granular colpus membrane, note reduction in average lumina diameter towards the colpus, SEM. (D) *O. comptonii* [243.1], mesocolpial portion of sexine showing reticulate tectum with angular muri, SEM. (E) *O. campylorrhiza* [127.1], wall section of apertural region showing a reduction in columella length towards the colpus, TEM. (F) *O. stictocheila* [234.1], wall section showing portions of the tectum (t), columellae (c), footlayer (f), endexine (arrow) and intine (i), TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

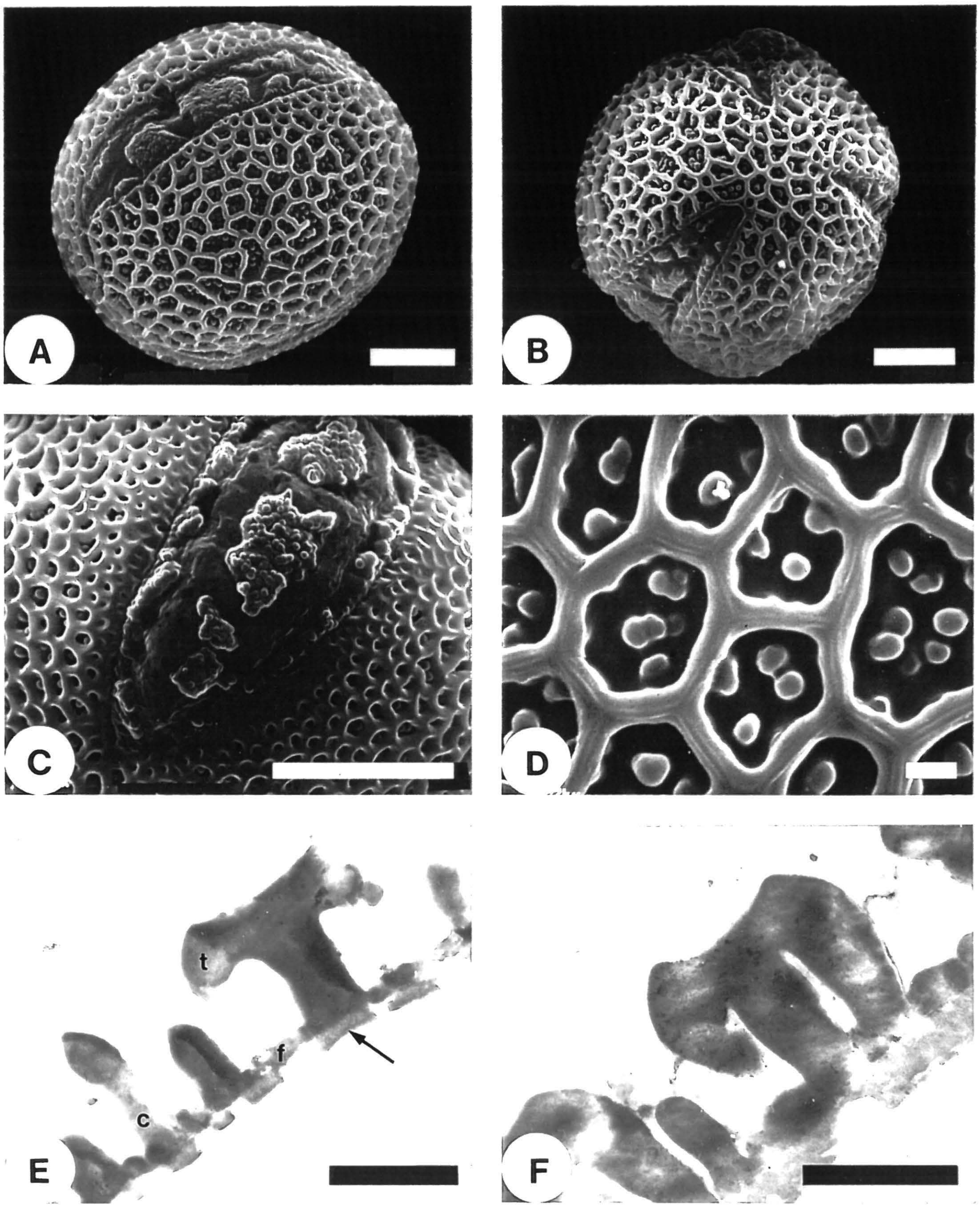


Figure 6.11 A—F. *Oxalis* pollen subtype C9. A, B: *O. deserticola* [253.1]. (A) Equatorial view showing open reticulum, SEM. (B) Polar view, note reduced apocolpium, SEM. (C) *O. tenuis* [259.1], apertural area showing granular colpus membrane, SEM. (D) *O. polyphylla* var. *minor* [228.1], mesocolpial portion of sexine showing reticulate tectum with angular to rounded muri, SEM. E, F: *O. deserticola* [253.1]. (E) Wall section showing tectum (t), columellae (c), uneven footlayer (f) and endexine (arrow), TEM (F) Wall section, TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

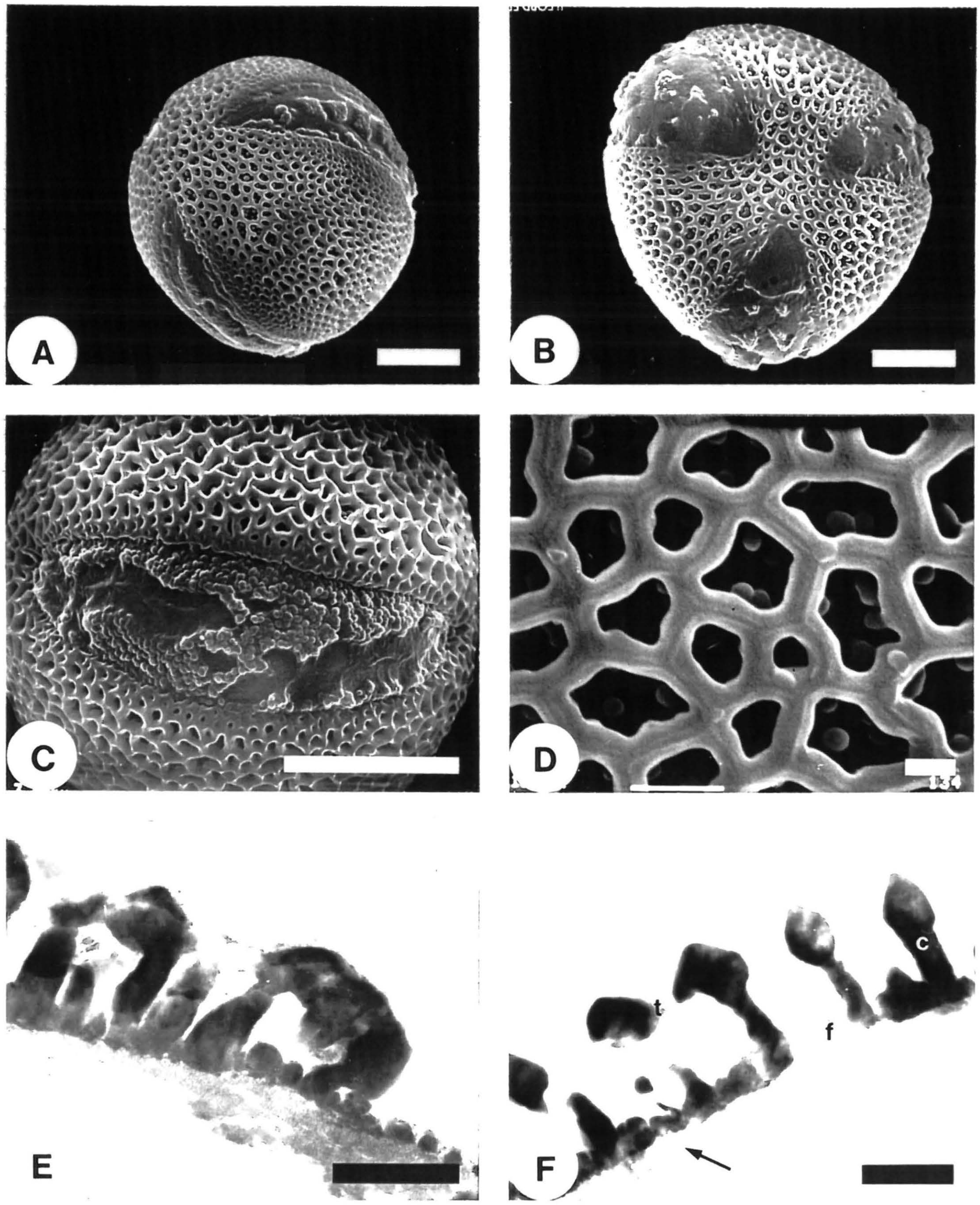


Figure 6.12 A—F. *Oxalis* pollen subtype C10. (A) *O. disticha* var. *alba* [118.1], equatorial view showing colpus with granular colpus membrane, SEM. (B) *O. louisae* [152.1], polar view showing reduced apocolpium, SEM. (C) *O. flaviuscula* var. *flaviuscula* [149.1], apertural area, note reduction in average lumina diameter towards the colpus, SEM. (D) *O. fabaefolia* [145.1], mesocolpial portion of sexine showing reticulate tectum with angular muri and clustered intraluminary bacula, SEM. E, F: *O. pillansiana* [194.1] (E) Wall section of apertural region showing thickened endexine (e), TEM. (F) Mesocolpial wall section showing tectum (t), columellae (c), uneven footlayer (f) and endexine (arrow), TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

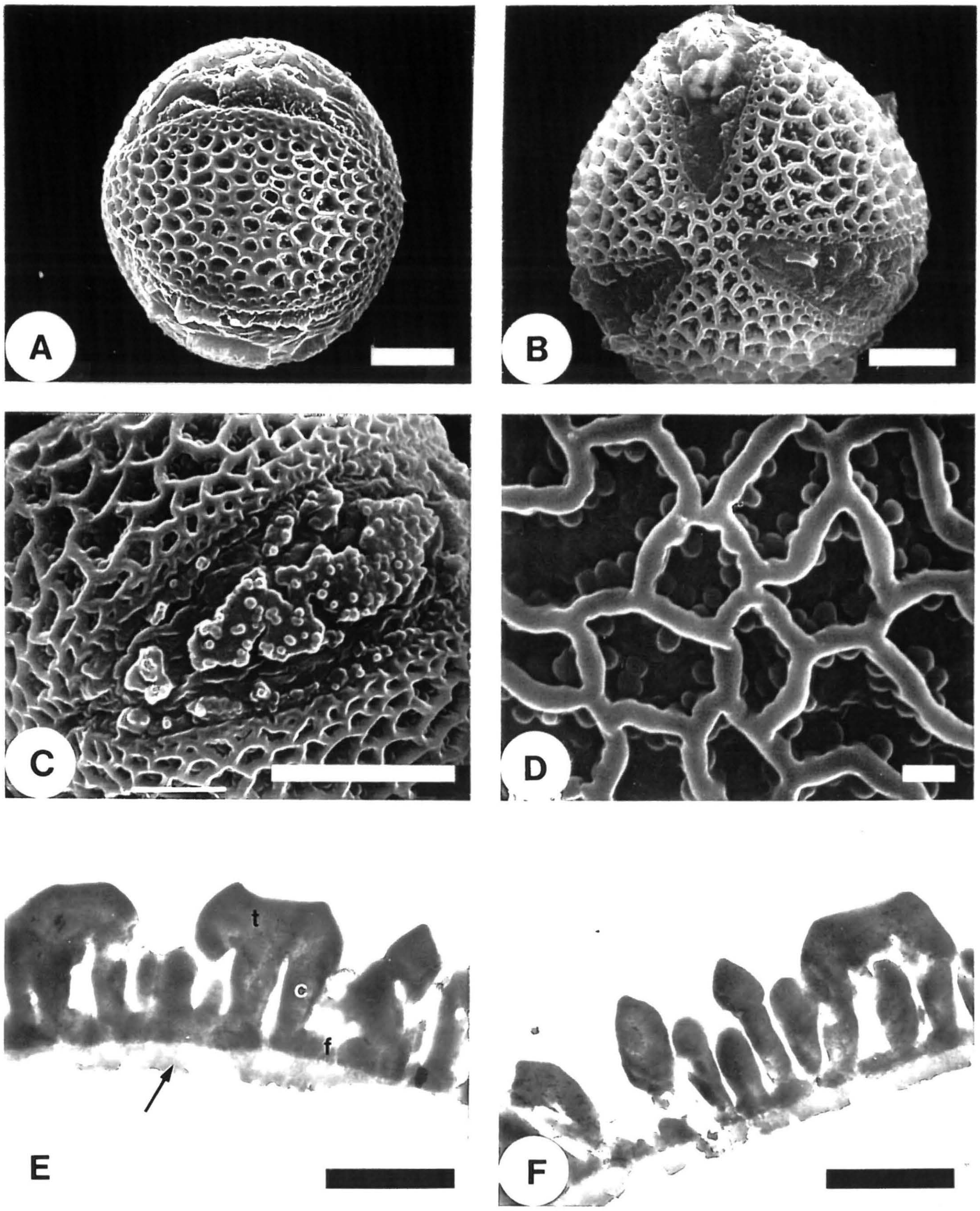


Figure 6.13 A—F. *Oxalis* pollen subtype C11. (A) *O. tenuipes* var. *biapiculata* [210.1], equatorial view, SEM. (B) *O. monophylla* var. *minor* [271.1], polar view showing reduced apocolpium, SEM. (C) *O. monophylla* var. *rotundifolia* [270.1], apertural area showing granular colpus membrane, note reduction in average lumina diameter towards the colpus, SEM. (D) *O. sonderiana* var. *alba* [132.1], mesocolpial portion of sexine showing reticulate tectum with irregularly angular muri and clustered intraluminary bacula, SEM. (E) *O. monophylla* var. *minor* [271.1], wall section showing tectum (t), columellae (c), uneven footlayer (f) and endexine (arrow), TEM. (F) *O. polyphylla* var. *pubescens* [226.1], wall section, TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

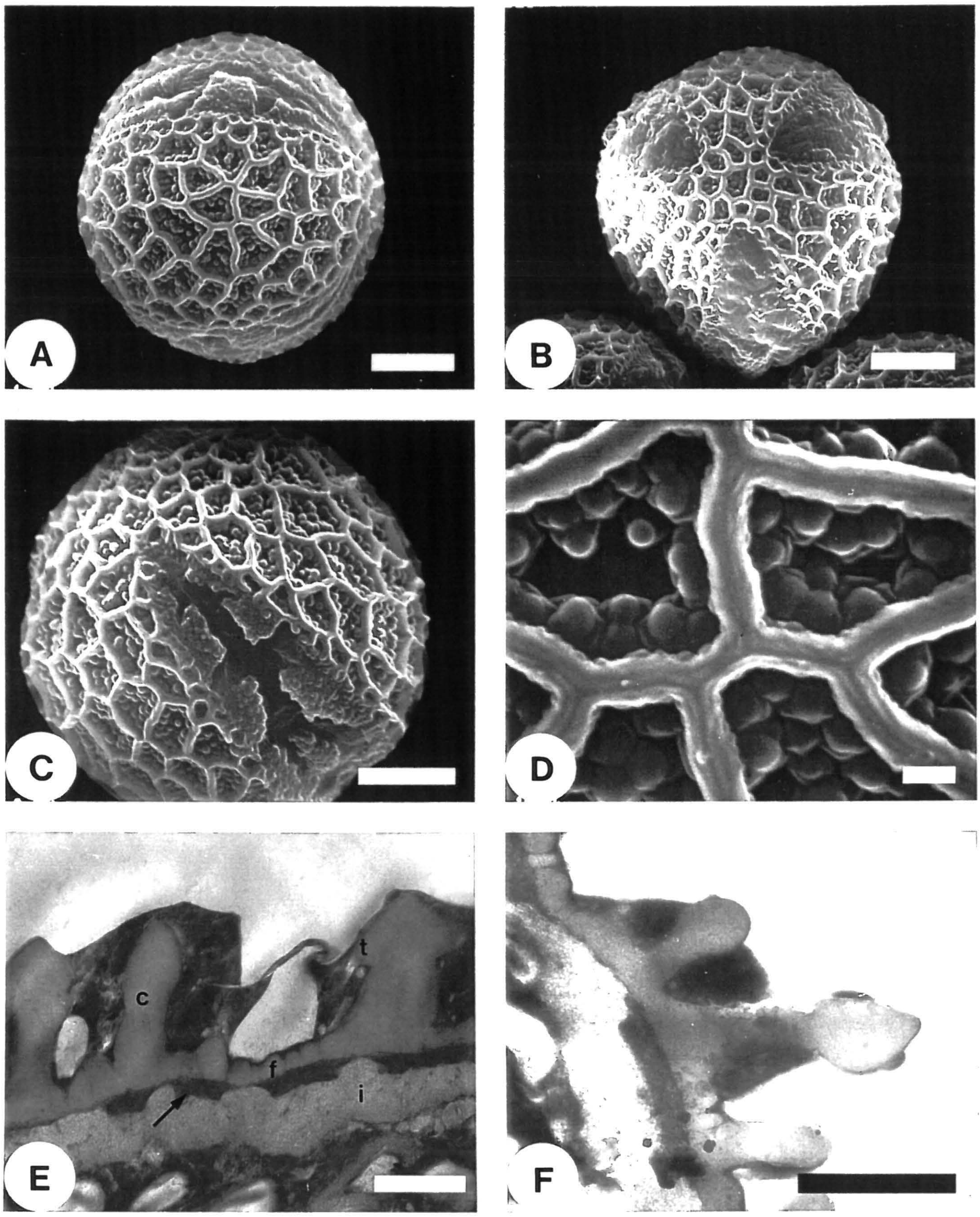


Figure 6.14 A—F. *Oxalis* pollen subtype C12. A—F: *O. tenuipes* var. *tenuipes* [209.1]. (A) Equatorial view showing open reticulum with prominent intraluminary bacula, SEM. (B) Polar view showing reduced apocolpium, SEM. (C) Apertural area, note abrupt reduction in average lumina diameter near the colpus, SEM. (D) Mesocolpial portion of sexine showing reticulate tectum with irregularly angular muri and clustered intraluminary bacula, SEM. (E) Wall section showing tectum (t), columellae (c), uneven footlayer (f), endexine (arrow) and intine (i), TEM. (F) Wall section, TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

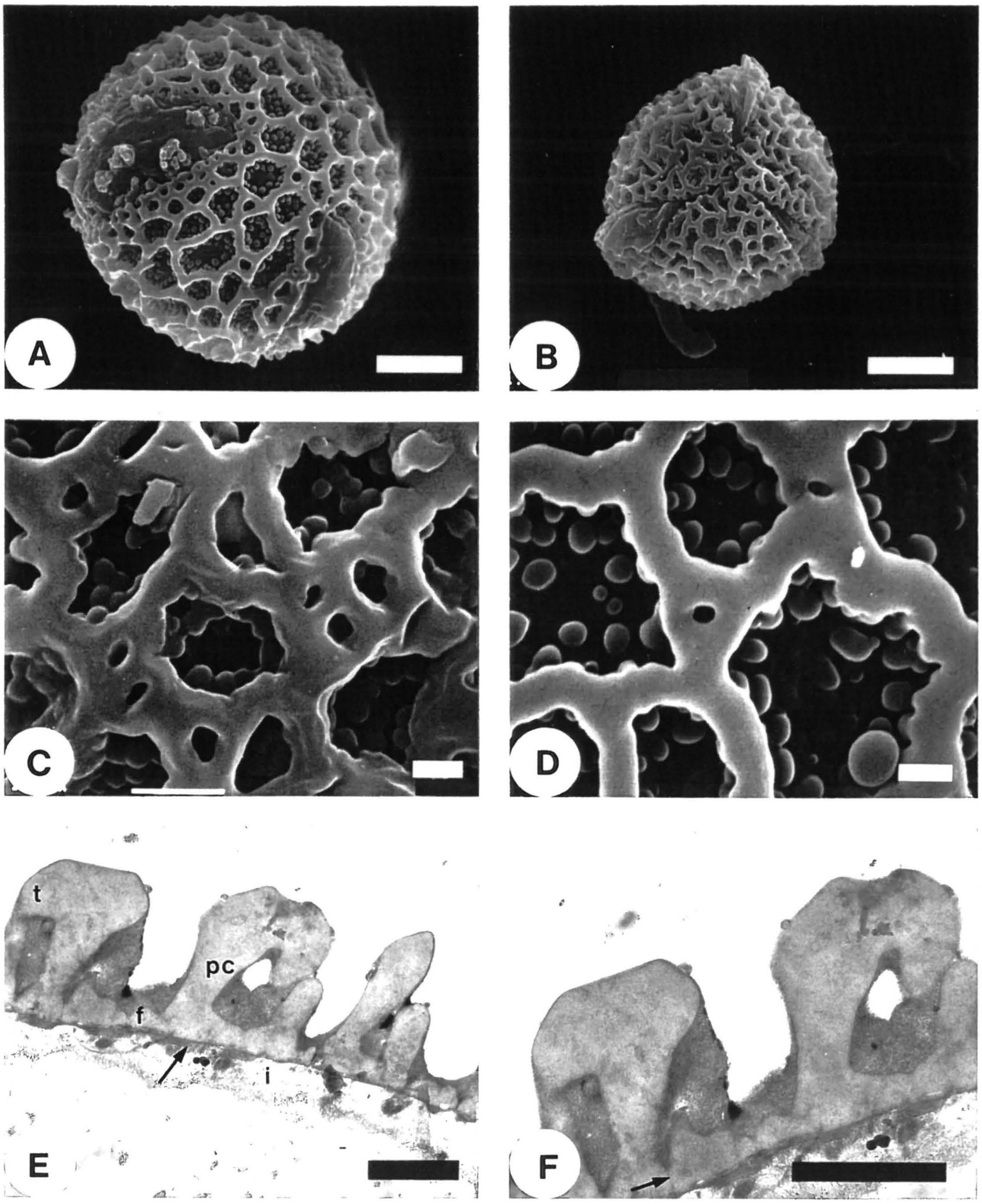


Figure 6.15 A—F. *Oxalis* pollen subtype C13. (A) *O. droseroides* [254.2], large grain showing tectum and two colpi, SEM. B, C: *O. droseroides* [254.1] (B) polar view of small grain, SEM. (C) Mesocolpial portion of sexine showing reticulate tectum with wide, perforated muri, SEM. (D) *O. droseroides* [132.2], mesocolpial portion of sexine, note the larger average lumina diameter of this specimen, SEM. (E) *O. monophylla* var. *minor* [271.1], wall section showing tectum (t), columellae in pluricolumellate complexes (pc), uneven footlayer (f), endexine (arrow) and intine (i), TEM. (F) *O. tenuipes* var. *tenuipes* [209.1], wall section, note micro-channels in footlayer (arrow), TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

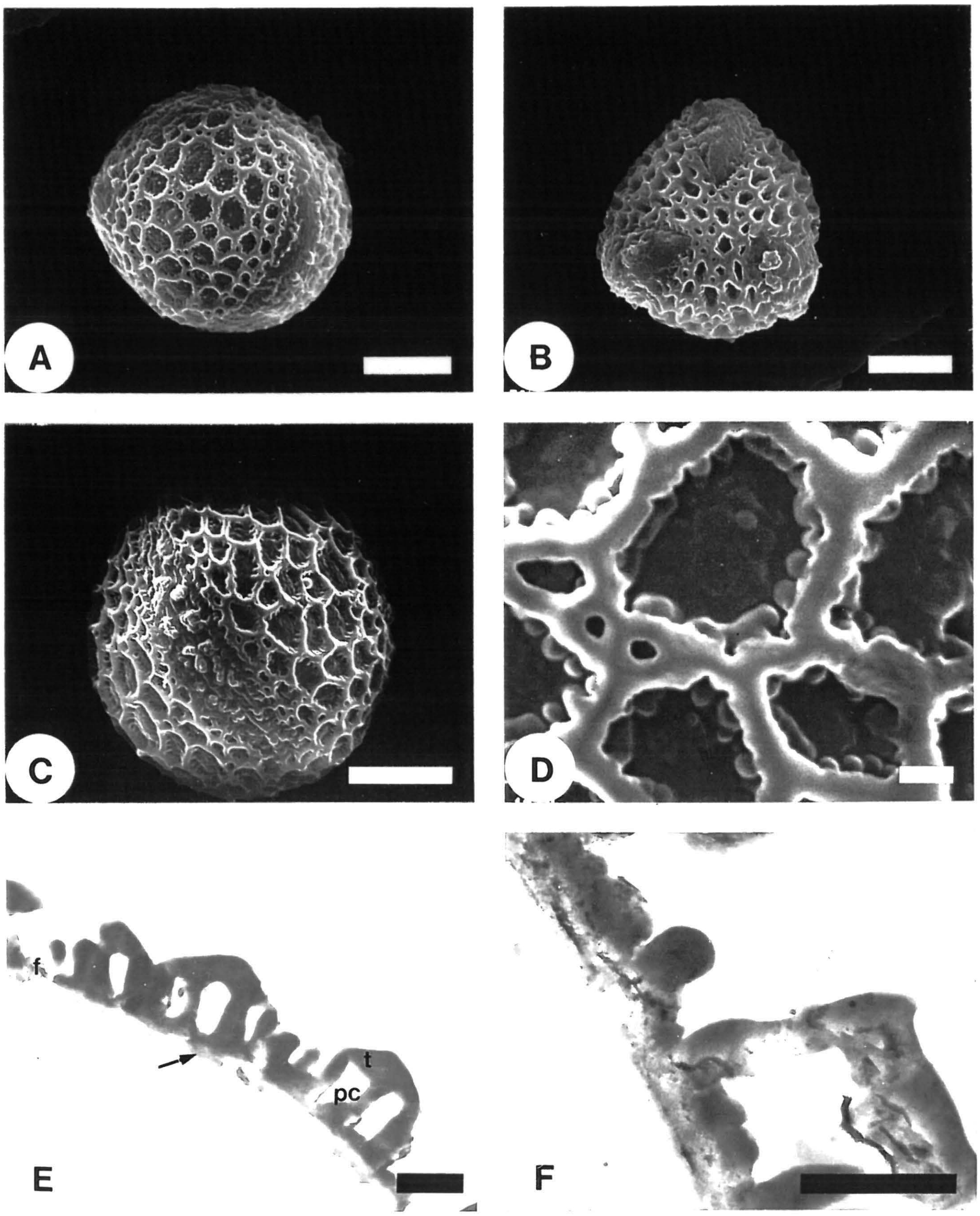


Figure 6.16 A—F. *Oxalis* pollen subtype C14. A—F: *O. phloxidiflora* [211.1]. (A) Equatorial view showing open reticulum and perforated muri, SEM. (B) Polar view showing reduced apocolpium, SEM. (C) Apertural area, note abrupt reduction in average lumina diameter near the colpus, SEM. (D) Mesocolpial portion of sexine showing reticulate tectum with perforated, irregularly angular to rounded muri, SEM. (E) Wall section showing tectum (t), columellae in pluricolumellate complexes (pc), footlayer (f) and endexine (arrow), TEM. (F) Enlarged wall section, note uneven footlayer, TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

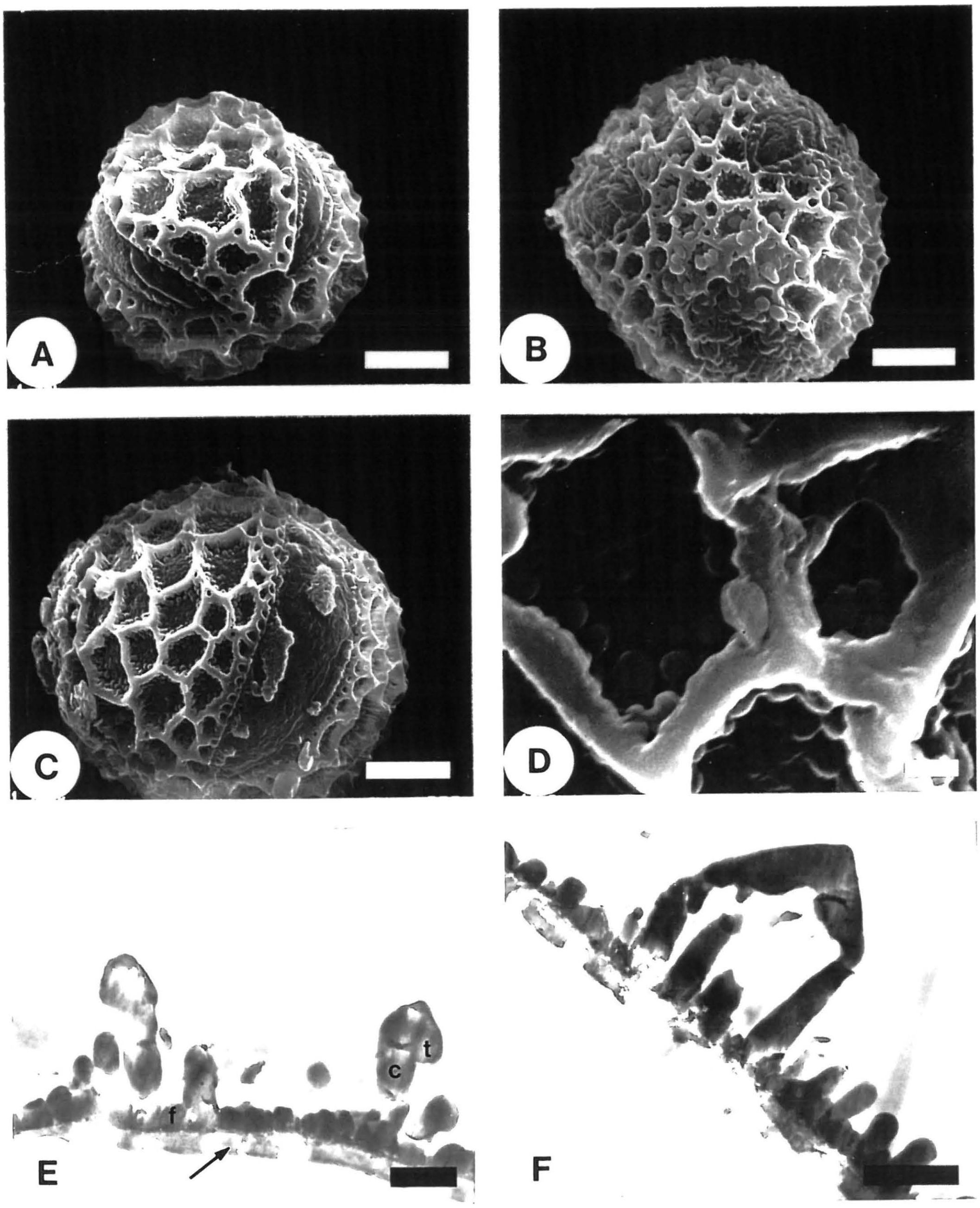


Figure 6.17 A—F. *Oxalis* pollen subtype C15. A—F: *O. giftbergensis* [185.1]. (A) Grain showing coarsely reticulate tectum, reduced apocolpium and perforated muri, SEM. (B) Polar view, SEM. (C) Apertural area, note abrupt reduction in average lumina diameter near the colpus, SEM. (D) Mesocolpial portion of sexine showing coarsely reticulate tectum and intraluminary bacula clustered along the muri, SEM. (E) Wall section showing tectum (t), columellae (c), footlayer (f) and endexine (arrow), TEM. (F) Wall section showing a pluricolumellate complex and footlayer, TEM. Scale bars: A—C = 10 µm. D—F = 1 µm.

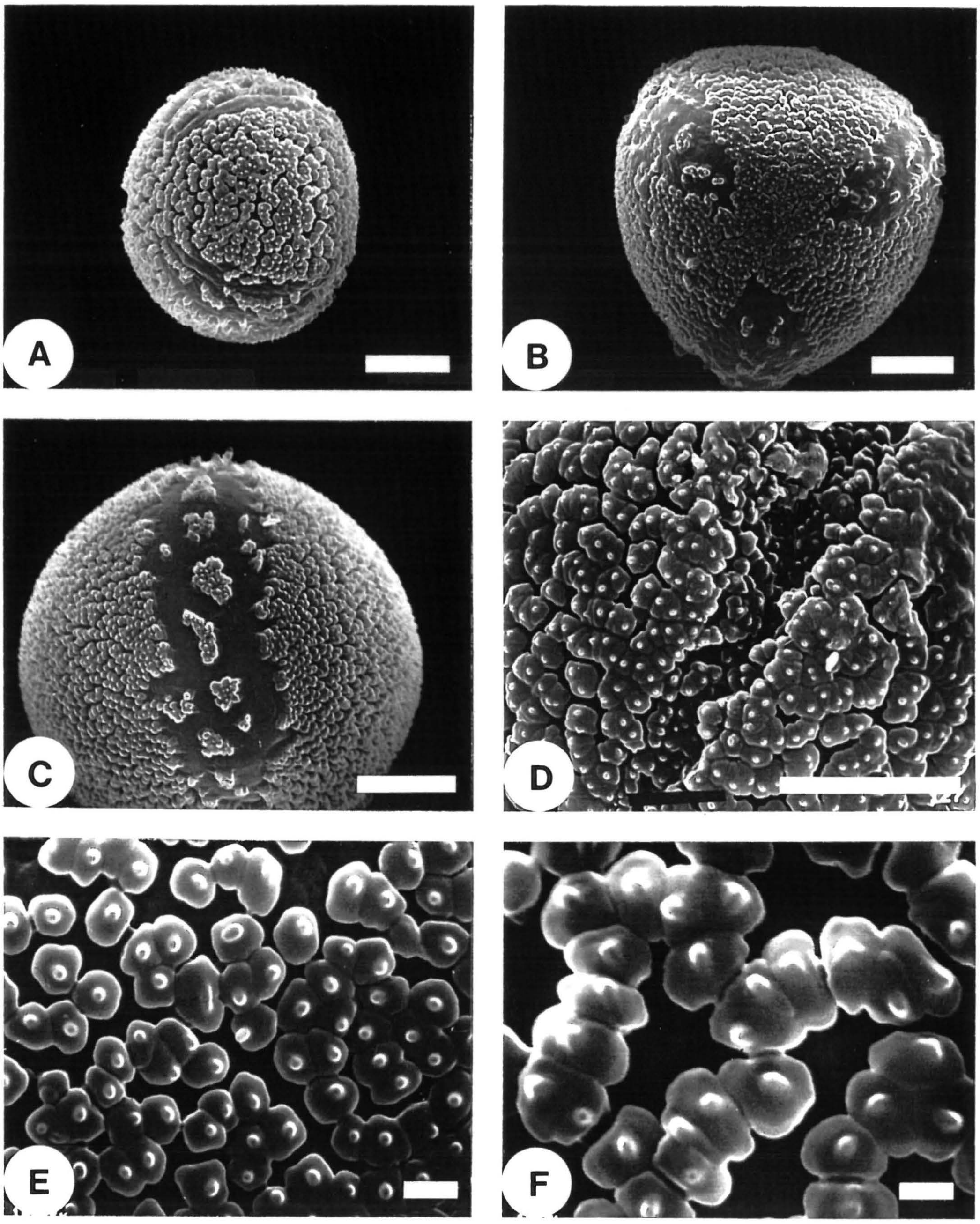


Figure 6.18 A—F. *Oxalis* pollen subtype D1. (A) *O. callosa* var. *minor* [143.1], equatorial view showing clustered supratectal areolae, SEM. (B) *O. ciliaris* var. *pageae* [237.1], polar view, SEM. (C) *O. pseudo-hirta* [178.1], apertural area, note tattered colpus margin and sexine islands within the colpus, SEM. D, E: *O. reclinata* var. *reclinata* [244.1]. (D) Apertural area, SEM. (E) Mesocolpial portion of sexine showing clustered supratectal areolae, SEM. (F) *O. ciliaris* var. *pageae* [237.1], mesocolpial portion of sexine showing supratectal areolae arranged to form a negative reticulum, SEM. Scale bars: A—D = 10 μm. E, F = 1 μm.

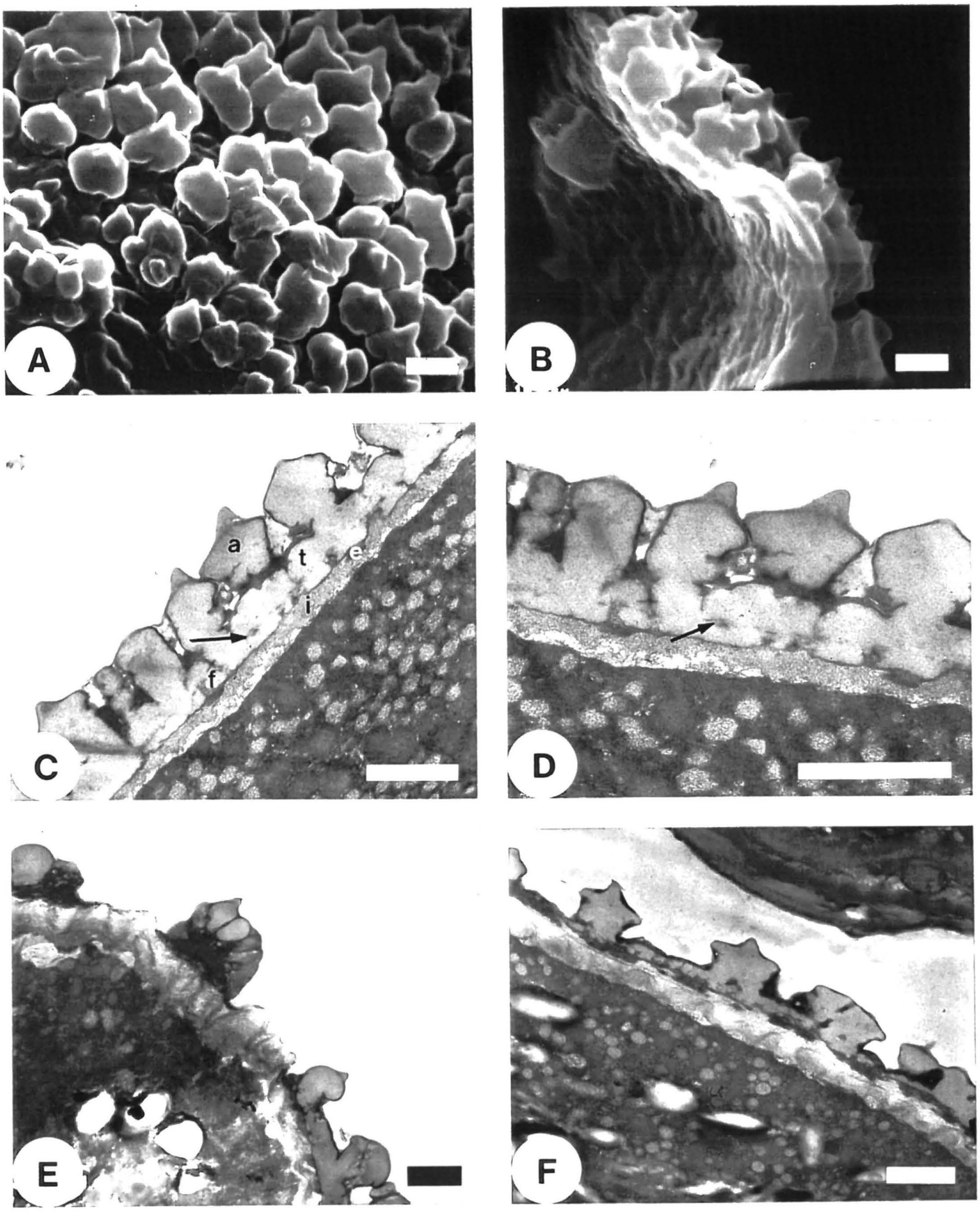


Figure 6.19 A—F. *Oxalis* pollen subtype D1. (A) *O. ciliaris* var. *ciliaris* [236.1], oblique view of sexine providing a side view of the supratectal areolae, note each areola terminating in a central spinule, SEM. (B) *O. xantha* [208.1], section through portion of mesocolpium, SEM. C—E: *O. hirta* var. *hirta* [171.1]. (C) Wall section showing supratectal areolae (a), tectum (t), columellae (arrow), footlayer (f), endexine (e) and intine (i), TEM. (D) Wall section, note reduced columellae (arrow), TEM. (E) Wall section of apertural region showing a sexine island within the colpus, TEM. (F) *O. albiuscula* [249.1], mesocolpial wall section, TEM. Scale bars = 1 μm.

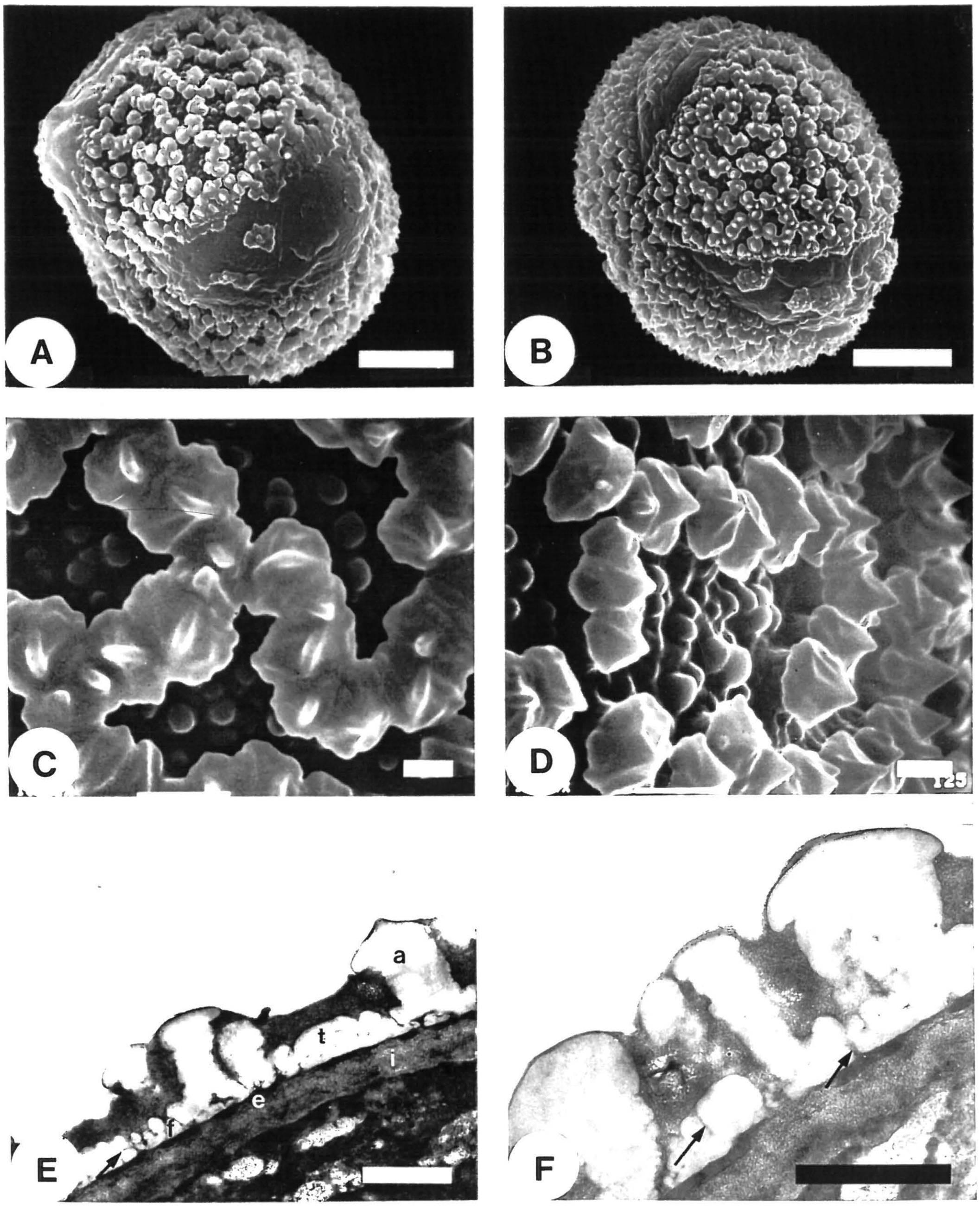


Figure 6.20 A—F. *Oxalis* pollen subtype D2. A—F: *O. petiolulata* [141.1]. (A) Equatorial view, SEM. (B) Oblique polar view showing three colpi with sexine islands and areolae forming a negative reticulum, SEM. (C) Mesocolpial portion of the sexine, SEM. (D) Oblique view of portion of sexine, note the verrucate to baculate outer tectum surface. (E) Mesocolpial wall section showing supratectal areolae (a), tectum (t), reduced columellae (arrow), footlayer (f), endexine (e) and intine (i), TEM. (F) Wall section, note micro-channels in both tectum and footlayer (arrows), TEM. Scale bars: A, B = 10 µm. C—F = 1 µm.

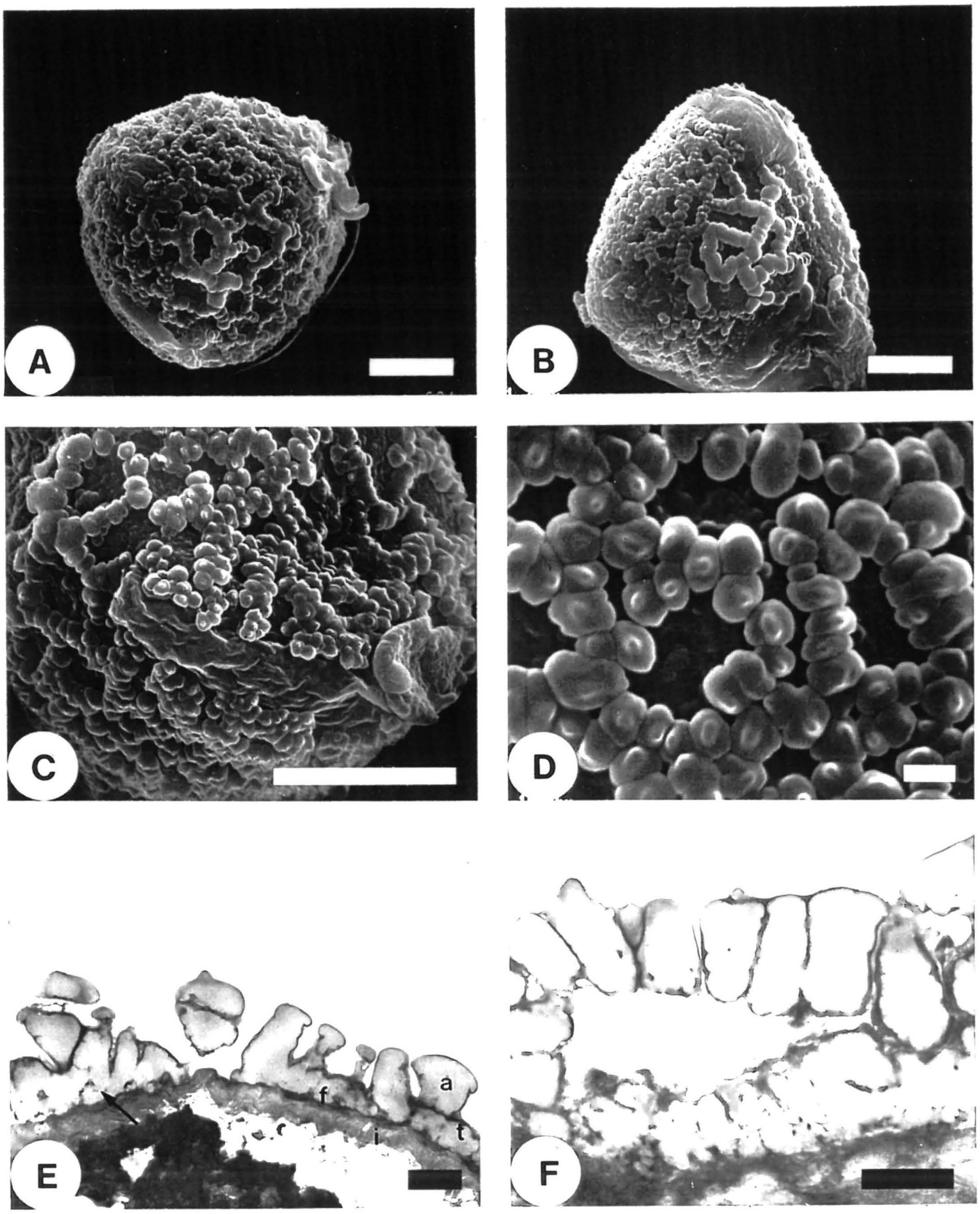


Figure 6.21 A—F. *Oxalis* pollen subtype D3. A—F: *O. linearis* [198.1]. (A) Polar view showing areolae arranged to form negative reticulum, SEM. (B) Polar view, note enlarged areolae in apocolpial area, SEM. (C) Apertural area, SEM. (D) Mesocolpial portion of sexine, note relatively small areolae and verrucate outer tectum surface, SEM. (E) Wall section showing supratectal areolae (a), tectum (t), reduced columellae (arrow), footlayer (f) endexine and intine (i), TEM. (F) Wall section in apertural area, TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

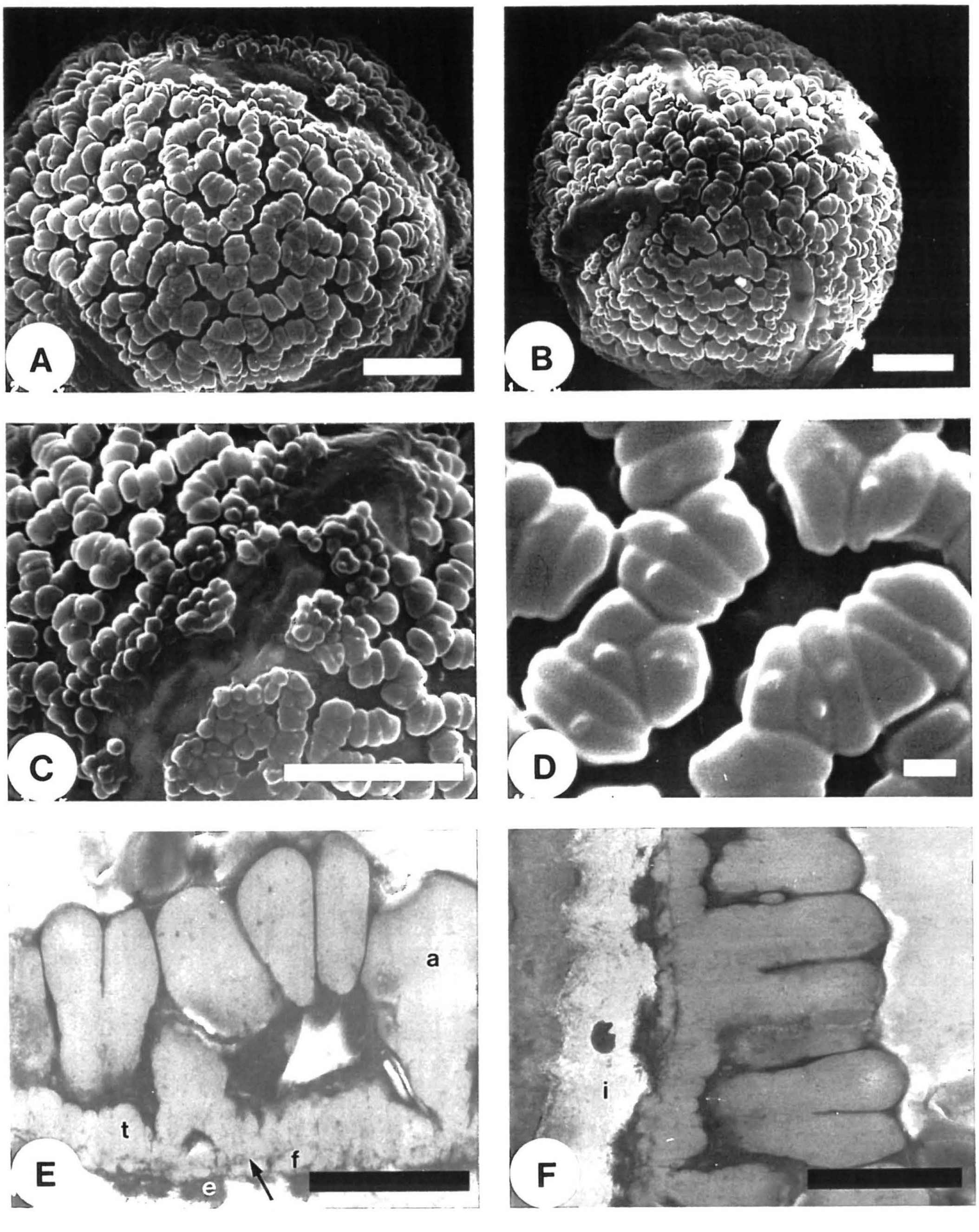


Figure 6.22 A—F. *Oxalis* pollen subtype D4. A—F: *O. hirta* var. *intermedia* [174.1]. (A) Grain showing aberrant apertural configuration, SEM. (B) Subpolar view, note distinctly ridged formation of areolae, SEM. (C) Apertural area showing tattered colpus margins and a reduction in areolae diameter towards the colpi, SEM. (D) Mesocolpial portion of sexine showing ridged negative reticulum, SEM. (E) Wall section showing supratectal areolae (a), baculate tectum (t), reduced columellae (arrow), footlayer (f) and endexine (e), TEM. (F) Wall section; note thick intine (i), TEM. Scale bars: A—C = 10 μm. D—F = 1 μm.

CHAPTER 7

DISCUSSION

7.1 Introduction

Results of the present study emphasise the taxonomic value of palynology within *Oxalis*, and suggest that pollen features can contribute substantially towards a better understanding of the interrelationship among the southern African members of the genus. Although palynology alone cannot form the basis of a new classification, numerous taxonomic deductions can be made from the results. These are so wide and diverse that they are here discussed under five separate headings. In the first section (7.2) palynological results from the present study are compared to those of Huynh (1969a & b). This is followed by an evaluation of the most widely used taxonomic classification of *Oxalis* (Salter 1944) in the light of palynological evidence (7.3). In section 7.4 the situation is viewed in reverse by evaluating the taxonomic significance of the 21 pollen types recognised in the present study. Section 7.5 is essentially an evolutionary discussion, culminating in an evaluation of the evolutionary significance of the different pollen types. To see these evolutionary trends in wider context, it was necessary to take a look at the genus as a whole. The section starts with a discussion of the morphological diversity within *Oxalis* (7.5.1), followed by speculations as to how this could have evolved. Biogeography (7.5.2), means of speciation (7.5.3), reproductive isolation (7.5.4) and pollination (7.5.5) are considered under separate headings. Evolutionary trends within palynology (7.5.6) are evaluated against this backdrop. A hypothesis on the evolution of pollen types is set forward (7.5.6.1), followed by an assessment of the phylogenetic implications of palynological features (7.5.7). To facilitate reference to the taxa listed in Table 5.3, taxon numbers are supplied in square brackets.

7.2 Evaluation of the palynological classification proposed by Huynh (1969a & b)

Based solely on LM observations, Huynh (1969a) recognised 13 principal pollen types in *Oxalis,* which she arranged into four groups (A, B, C & D). She found only two of these groups (A and C) represented among the southern African taxa. To avoid confusion, all references to pollen groups or types proposed by Huynh (1969a & b) are printed in **bold**. Those in normal type face refer to the classification proposed in the present study.

Group A includes tricolpate (or rarely 4- or 5-colpate and/or 6-pantocolpate) grains with a distinct suprareticulum. Four pollen types were identified within the group, with types **A1** and **A3** represented in southern Africa.

A1: Pollen finely reticulate. Grains 48 x 39 µm. Lumina smaller than 3 x 2.5 µm, with a decrease in size towards the colpi. Muri 0.5 µm thick. Wall bacula clearly visible. Exine very thin, ca. 2 µm thick. (Huynh 1969a regards this as a very common pollen type found in most taxonomic sections from both southern Africa and America).

A3: Pollen coarsely reticulate. Grains 58 x 42 µm. Lumina larger than 4 x 6.5 µm with many intraluminary bacula. Muri more than 6.6 µm thick. Exine of medium thickness, ca. 3.0 µm. (Although this type is described as being fairly common, Huynh (1969a) recorded it from two southern African taxa only).

Group C includes 3-, 4- or pantocolpate grains in which the existence of a suprareticulum is doubtful. The infrareticulum can be simple (**C1, C2, C3**) or absent (**C5, C6**). Of the six pollen types identified in this group, **C1, C2, C3, C4** and **C5** are represented in southern Africa.

C1: Tricolpate. Grains 42 x 42 µm. Suprareticulum absent, replaced by mamillae which shine in LM analysis. The mamillae are extensions of some (but not all) of the wall bacula of the infrareticulum. The wall bacula are ovoid (never angular) in transection and never more than 1 µm in diameter. A faint reticulum is visible, with lumina not larger than 3.5 x 4—5 µm. Intraluminary bacula are absent. (This is a distinct and rare pollen type, which Huynh (1969a) found in four southern African taxa only).

C2: Tetracolpate. Grains 42 x 42 µm. This type differs from **C1** only in having four apertures which are dispersed following four of the six lines of a regular tetrahedron, such that their extremities join two by two at four different points. (Huynh (1969a) found this very rare type in *O. microdonta* only).

C3: Pantocolpate with 12, 15 or 18 apertures. Grains 44 x 46 µm. Apart from these features this type agrees with type **C1**. Pollen type **C3** was only recorded in section *Sagittatae*.

Note: Huynh (1969a) regards the latter three types as being closely related, with the affinity between **C1** and **C2** being the closest. These affinities are allegedly also reflected in the morphology of the relevant taxa.

C4: Tricolpate. Grains 58 x 48 µm. Intectate. Suprareticulum absent, replaced by mamillae which shine in LM analysis. The mamillae are extensions of thick wall bacula which form a faint infrareticulum. Huynh (1969a) recorded this pollen type in a few southern African taxa only.

C5: Tricolpate. Completely areticulate. Grains 48 x 40 µm. Surface covered with hemispherical mamillae, usually 0.8 µm thick and 80.4 µm high. The mamillae are similar to infratectal bacula, but more numerous and slender. They are regularly scattered on the footlayer. Exine 2 µm thick. This special pollen type was recorded in *O. fibrosa* only.

Table 7.1 Pollen types identified by Huynh (1969a) compared with pollen types identified in the present study.

POLLEN GROUPS RECOGNISED BY HUYNH (1969a).	**POLLEN TYPES IDENTIFIED IN THE PRESENT STUDY**
A1	C1, C2, C3, C4, C7, C8, C9, C10, C11, C13, C15
A3	C8, C14
C1	A
C2	A
C3	A
C4	D1, D2, D3, D4
C5	B

Although Huynh's (1969a) descriptions and interpretation of pollen types are different to those in the present study, she essentially recorded the same palynological variation as was found here. From Table 7.1 it is clear that her **group A** corresponds to pollen type C. Pollen type **A1** appears to be widely defined, including 11 of the 15 subtypes of pollen type C as defined in the present study. Her pollen type **A3** includes the two seemingly unrelated pollen subtypes C8 and C14. Note that pollen subtype C8 is represented in both her pollen types **A1** and **A3**. She does, however, mention that type **A3** is poorly defined, and therefore probably of limited taxonomic significance. **Group C** includes pollen types A, B, and D, with **C1—C3** being equivalent to pollen type A, **C4** to pollen subtypes D1—D4 and **C5** to pollen type B. Her pollen types **C1, C2** and **C3** are essentially similar and were merely separated on differences in the number of colpi.

Since Huynh's study was limited to a LM analysis, she did not notice much of the finer sculptural detail. To some extent this could explain the lumping of 12 currently proposed subtypes of pollen type C into a single pollen type **A1**. She does mention an evolutionary tendency towards an increase in lumina diameter, but omits using this character in the delimitation of subtypes within her inclusive pollen type **A1**.

Limitations imposed by the LM probably also led to the doubtful interpretation of the currently recognised pollen types A, B and D. They were all placed in **Group C** based on the "doubtful existence of a suprareticulum". Huynh (1969) regarded her types **C1**, **C2** and **C3** (different forms of pollen type A) as transitional stages in the process of tectum destruction. This reduction is continued in **C4** (pollen type D) and culminates in her type **C5** (pollen type B) where the tectum is completely lost. She therefore proposes the following progression of pollen types: C→A→D→B

The SEM and TEM results of the present study contradict this hypothesis. Pollen type A has a distinct rugulate tectum. What she refers to as mamillae are in fact small supratectal spinules. Similarly pollen type B is not intectate, but has a conspicuous micro-rugulate tectum. What she perceived as mamillary bacula scattered on the footlayer are actually large supratectal spines. From the TEM results it seems unlikely that pollen type D represents a transitional stage between pollen types A and B. It has a fully developed tectum and what Huynh (1969a) regards as columellar remains are really massive supratectal areolae. These results reject Huynh's hypothesis of gradual tectum destruction and favours a gradual increase in tectum complexity instead. If the development of supratectal structures represents a progressive line, then results from the present study support quite a different developmental continuity. This will be discussed in more detail in section 7.5.6.

Note: The taxonomic significance of aperture number in *Oxalis* was discussed in some detail in Chapter 5. The possibility to follow Huynh (1969a) and subdivide pollen type A on the basis of aperture number was therefore considered here. The idea was, however, rejected due to the variation in aperture numbers between clearly related species and even between varieties of the same species with this pollen type.

7.3 Palynological evaluation of the current taxonomic classification of *Oxalis*

In this section Salter's (1944) taxonomic classification of *Oxalis*, which is currently followed in southern African herbaria, is compared with the pollen types identified in the present study. Each section or subsection is discussed under a separate heading, with the following layout:

morphological/taxonomical summary; palynology; resultant taxonomic implications. Reference is also given to personal comments kindly provided by Mr M.B. Bayer[1]. Taxa and pollen types are compared in Table 5.3.

SECTION *CORNICULATAE*: Taxon 1

The American section *Corniculatae* is represented in southern Africa only by the exotic species *O. corniculata.* This variable, cosmopolitan species is well known as a common garden weed. It has micro-reticulate pollen of the subtype C1.

SECTION *IONOXALIS*: Taxon 2

Section *Ionoxalis* is regarded as rather 'primitive' and is only represented in southern Africa by the introduced Mexican species *O. latifolia.* This species has reticulate pollen of the subtype C7.

SECTION *CERNUA*: Taxa 3—31
SECTION *OPPOSITAE*: Taxa 32—69
SECTION *STICTOPHYLLAE*: Taxa 70—73
SECTION *FOVEOLATAE*: Taxa 74—103

According to Salter (1944) the sections *Cernuae*, *Oppositae*, *Stictophyllae* and *Foveolatae* are all morphologically well-defined. Taxa included in the section *Cernuae* have pedunculate, many-flowered inflorescences and bilobed or conspicuously incised leaflets. Section *Oppositae* is characterised by opposite bracts set at an upper or second articulation of the peduncle. Section *Stictophyllae* includes taxa with broad leaflets which become black-dotted (striolate) in the dried state. With the exception of *O. densa* and *O. furcillata*, the taxa included in section *Foveolatae* have three rather fleshy leaflets with large epidermal cells which become punctate in the dried state. They have pedunculate, many-flowered inflorescences. Bayer (pers. comm.) doubts the integrity of these four sections, especially the subsections defined within the first two. In his opinion, section *Oppositae* could be one of the poorest defined by Salter. Nevertheless, these four sections share one character which separates them from the rest of the genus. With the exception of *O. furcillata*, they all have endospermous seed as opposed to the exendospermous state in the other southern African

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[1] M.B. Bayer, 29 Weltevreden Street, Paarl, 7646. Mr Bayer was previously employed by the NBI, and was based at the Karoo Botanic Garden. During this period he acquired an extensive knowledge of the genus *Oxalis*.

sections of *Oxalis*. The reliability and taxonomic significance of this character is, however, rather questionable.

These four sections are palynologically very similar and homogeneous, with micro-reticulate, finely reticulate or reticulate pollen of the subtypes C1; C2; C3; C4; C7; C8 and C9 found in most of the taxa. There is no detectable pattern in the distribution of these pollen types within or between the four sections and their subsections (the high occurrence of pollen subtype C2 in section *Oppositae* being the only exception). It could be reasoned that the delimitation of the seven separate pollen types listed here bear very little taxonomic significance, at least at the sectional or subsectional level. This will be discussed in more detail in section 7.4. What is important, however, is that, with only two exceptions, no other pollen type was recorded among these taxa. Palynology therefore contributes little to the demarcation of sections within this group, but supports the separation of these four sections from the rest of the genus.

O. pulchella var. *beneprotecta* [81] and *O. furcillata* var. *caulescence* [103] are the only two taxa that deviate palynologically. In both cases the typical variety has pollen of the subtype C2, while the varieties mentioned here have pollen of the subtype C10. This is peculiar for two reasons: firstly it seems strange to find two such different pollen types in two varieties of the same species and secondly the occurrence of pollen subtype C10 in this group of sections is incongruent with the general trend.

Further investigation revealed that Knuth (1930) originally described *O. pulchella* var. *beneprotecta* as a separate species. Schreiber (1967) states that *O. beneprotecta* deserves recognition as a separate species quite unrelated to *O. pulchella s.l.* Pollen morphology supports this view, and suggests that the sectional placement of *O. beneprotecta* be reconsidered.

Salter (1944) questions the affinity of *O. furcillata* with the other members of the section *Foveolatae*. Although most morphological features support its taxonomic position, *O. furcillata* is the only exendospermous species included in this section and its leaves never become punctate. Palynologically var. *furcillata* is similar to the members of this section, while var. *caulescence* is more problematic. Its pollen is quite different to that of the typical variety and incongruent with the pollen of other members of the section *Foveolatae*. When Salter newly described this variety, he did question its taxonomic affinities. He suggested that var. *caulescence* might belong in section *Angustatae* subsection *Sessilifoliatae*, implying the inclusion of two varieties of the same species in different sections. Although section

Angustatae subsection *Sessilifoliatae* is palynologically diverse, the C10 pollen of var. *caulescence* show now affinity with the pollen types it currently includes. The distribution of C10 pollen within *Oxalis* suggests that var. *caulescence* might be better placed in section *Campanulatae*, groups within section *Latifoliolatae*, section *Crassulae* or near individual species within section *Angustatae* subsection *Multifoliatae*. The true affinities of this taxon need to be resolved through additional taxonomic studies.

SECTION *SAGITTATAE*: Taxa 104—114

Salter (1944) considered section *Sagittatae* as a distinct natural taxon, easily distinguished in the living state by characters of the gynoecium and androecium. The stamens and styles are very slender. The short and medium organs, whether stamens or styles, spread widely on release from the corolla tube, while the longest organs remain erect. The section is further characterised by sagittate anthers.

The integrity of this group is supported by pollen characters. With the exception of *O. minuta* var. *callosa* and *O. fibrosa*, all the included taxa display pollen type A, a type not yet recorded anywhere else in the genus. The anomalous presence of pollen subtype C7 in *O. minuta* var. *callosa* is fairly easily explained. Salter (1944) based his description on a single, incomplete specimen and acknowledges the doubtful placement of the taxon as a variety of *O. minuta*. He noticed differences in flowering time and concluded that var. *minuta* probably represents a new species, perhaps belonging to quite a different section. As pollen subtype C7 is a fairly common type found in numerous sections, it is hard to anticipate the true affinities of this taxon through palynology alone.

Morphologically *O. fibrosa* agrees well with the taxa in section *Sagittatae* and yet it has an unique pollen type (pollen type B), never encountered anywhere else in the genus. Bayer (pers. comm.) states that *O. fibrosa* is the only species in the section with a Karoo Biome distribution, while the others are all essentially confined to the Fynbos Biome. *O. fibrosa* can therefore be seen as an unique ecological variant within the section. Although pollen types A and B are quite distinctly dissimilar, it is possible to regard pollen type B as an evolutionary derivative of pollen type A (see section 7.5.6.1).

SECTION *CAMPANULATAE*: Taxa 115—120

Section *Campanulatae* seems to be a natural taxon characterised by a widely campanulate corolla tube. All the constituent taxa are aquatic or marsh plants (Salter 1944). Ornduff (1973) raised *O. disticha* var. *alba* to species status as *O. dines*, but retained it in this section.

Palynologically the section is very homogeneous with five of the six included taxa displaying pollen subtype C10, while the fifth has pollen of the subtype C11. Figure 5.4 indicates that pollen subtypes C10 and C11 are very similar, the only distinction being differences in reticulum size. These two subtypes often co-occur in what Salter calls "groups of related taxa" in unnatural, poorly defined sections (e.g. within section *Latifoliolatae*). The relation between these two pollen types will be discussed in more detail in section 7.4.

SECTION *LATIFOLIOLATAE*: Taxa 121—144

Salter (1944) describes this section as an entirely artificial taxon containing various small groups of related taxa. These groups are unrelated to one another, with the only delimiting character being the absence of linear or oblong leaves (leaves can be rotund, obcordate, oval, elliptical, ovate or obovate). He provides the following key to the section, attempting to group vaguely similar taxa together:

Hairs pluricellular
  Leaflets rotund, emarginate .... Taxa 121—124
  Leaflets conspicuously incised at apex .... Taxa 125—127
Hairs not pluricellular
  Leaflets obcordate or incised at the apex
    Hairs glandular-pilose .... Taxa 128—129
    Hairs simple .... Taxon 130
  Leaflets rotund, oval or obovate but not deeply incised at the apex
    Leaflets rotund, broader than long .... Taxa 131—137
    Leaflets oval, elliptical, ovate or obovate, longer than broad ...... Taxa 138—144

The artificial nature of this taxon is clearly reflected in the distribution of pollen types within the section. It contains the subtypes C1, C8, C10 and C11 of pollen type C and subtypes D1 and D2 of pollen type D. The co-occurrence of pollen types C and D in the same natural section seems most unlikely, as these two pollen types differ considerably.

When the pollen morphology of the proposed groups of related taxa within the section is compared, however, interesting patterns emerge. The first group [121—124] all have finely reticulate pollen of the subtype C10. The next group [125—127] have micro-reticulate or reticulate pollen of the subtypes C1 and C8. These two subtypes were previously mentioned to be rather similar and will be discussed in more detail in section 7.4. The next group of taxa [131—137] have either pollen subtype C10 or C11, also two pollen types postulated to be rather similar (section 7.4). The last group of taxa [138—144] are bound by the occurrence of pollen type D, a type also occurring in clusters of species in the subsections *Sessilifoliatae* and *Linearis* of the section *Angustatae*.

Oliver (1993) referred the newly described *O. oculifera* [302] to section *Latifoliolatae.* Morphologically and palynologically it correlates best with the group of taxa [131—137].

In conclusion it seems that, although there are so many pollen types present in this section, their distribution corresponds closely with the "groups of related taxa" proposed by Salter (1944). Palynology implicates the need for a critical re-evaluation of the sectional boundaries.

SECTION *CRASSULAE*: Taxa 145—153

Section *Crassulae* is defined as a somewhat succulent group of stemless plants which readily fall apart in the dried state. Bayer (pers. comm.) doubts the integrity thereof, maintaining that the taxa share very few field characters. He regards *O. fabaefolia*, *O. pulvinata* and *O. flava* as conspecific and questions the inclusion of *O. cathara* and *O. namaquana* in this section.

Evidence from palynology supports Bayer's views. Six of the included eight species have finely reticulate pollen of the subtype C10, while *O. cathara* and *O. namaquana* have pollen of the subtypes C7 and C1 respectively. These latter two pollen types are similar to each other, but quite different to pollen subtype C10. This suggests that these two species might be better placed somewhere else in the genus. As pollen subtypes C1 and C7 are fairly common and widespread within *Oxalis*, no real suggestions can be made regarding their true affinities.

SECTION *ANGUSTATAE*
SUBSECTION *PARDALIS*: Taxa 154—170

This subsection, as defined by Salter (1944), includes 11 species and 10 varieties. Salter regards it as a distinct, natural taxon in which many of the species closely resemble one another. Diagnostic characters include an unique bulb structure and linear or linear-cuneate leaflets streaked with short pellucid lines. Similar lines are found on the sepals and in both cases they turn black on drying. Bayer (1992) conducted a comprehensive study of the subsection, including a number of manuscript species such as *O. bombycina* MS, *O. fragrans* MS, *O. heptaphylla* MS and *O. klaasvoogdensis* MS [298—301]. He concluded that the subsection represents a mass continuum, making it very difficult to arrive at a taxonomic rationale which would express the situation adequately. He consequently synonymized the 11 species and four manuscript species under *O. pardalis*, thereby creating an aggregate species (as was done by Salter (1944) in various cases).

Pollen subtypes C1, C3 and C9 were recorded from the subsection. As discussed previously, these subtypes are closely related and could even be viewed as variations of the same basic pollen type. If such a view is taken, palynology could support the idea of lumping this continuum of variation into a single species as proposed by Bayer (1992).

SECTION *ANGUSTATAE*
SUBSECTION *SESSILIFOLIATAE*: Taxa 171—193

Salter (1944) considers subsection *Sessilifoliatae* as not being entirely natural, although he suggests that it does include groups of closely related species. Delimiting characters include the caulescent habit, leafy stems and sub-sessile or squamiform, petioled leaves. The three leaflets are linear, narrowly-cuneate, oblong or cuneate-obovate and the peduncles are usually axillary rather than terminal.

The palynology of this subsection proved complex and palynological trends do not fully agree with the infrasectional affinities proposed by Salter (1944). Both pollen types C and D are represented, including subtypes C1, C7, C8, C9, C15, D1 and D4. Pollen type D was found in all seven the varieties of *O. hirta* [171—177] and in *O. pseudo-hirta* [178], *O. subsessilis* [179] and *O. macra* [186]. Palynologically this group is therefore related to taxa [138—144] in section *Latifoliolatae* and taxa [197—206], [208], [236—242] and [244—250] in section *Angustatae* subsection *Linearis*.

The remainder of the taxa in subsection *Sessilifoliatae* mainly have pollen subtypes C1, C7, C8 and C9. These four types are obviously related (see section 7.4), but since they also occur in numerous other sections of the genus, limited taxonomical significance can be attached to their presence here. What is obvious though, is that this latter group of taxa seem more closely related to one another than to the rest of the subsection, so that the subsection can palynologically effectively be split into two groups.

Bayer (pers. comm.) lumps *O. callimarginata* and *O. urbaniana* from section *Sessilifoliatae* with *O. gonorrhiza* in the section *Linearis*. These three species are palynologically very similar (pollen subtypes C8, C9 and C8), supporting the close affinity proposed by Bayer. Further taxonomic research is needed to verify this intersectional affinity.

The unique pollen subtype C15 was only recorded in *O. giftbergensis*. The monotypic nature of this pollen type makes it difficult to draw definite conclusions from its occurrence, except that it isolates *O. giftbergensis* as being unique in the genus as a whole. Salter (1944) mentions no special morphological features supporting the uniqueness of this species, but mentions similarities with *O. leipoldtii.* Pollen of the latter could unfortunately not be obtained for the present study. A thorough morphological re-examination of *O. giftbergensis* seems necessary.

SECTION *ANGUSTATAE*
SUBSECTION *XANTHOTRICHAE*: Taxa 194—196

Salter (1944) describes this as a small and fairly natural subsection consisting of three species. Diagnostic features include the caulescent habit and the long, uniseriate, pluricellular hairs which often have a yellowish tinge. The three leaflets are oblong, linear or rarely obcordate and the rhizomes are very long.

All three the included species have reticulate pollen of the subtype C10, which makes this section palynologically similar to section *Campanulatae*, groups within section *Latifoliolatae*, section *Crassulae* and individual species within section *Angustatae* subsection *Multifoliatae*.

SECTION *ANGUSTATAE*
SUBSECTION *LINEARIS*: Taxa 197—251

Salter (1944) uses the mostly caulescent habit and the presence of 3 (5—7) narrow, linear, oblong or cuneate leaflets to define section *Angustatae* subsection *Linearis*. He concludes that the included taxa are not necessarily all related, but supplies the following key in an attempt to associate closely related taxa in this heterogeneous assemblage:

Corolla hypercrateriform with a subcylindrical, densely pubescent tube
which is rather longer than the laminae of the petals. Leaflets 3 .... Taxa 197—200
Corolla more or less funnel-shaped
Stem corticate, polished, brown. Leaflets 3, narrowly linear .... Taxa 201—205
Stem not as the above or wanting
Caulescent
Stem normally simple
Capsule exerted beyond the calyx .... Taxa 206—211
Capsule not or scarcely exerted
Longer filaments toothed .... Taxa 212—234
Longer filaments not toothed .... Taxa 235—243
Stem branching. Leaflets 3—5, sometimes cuneate-obovate ....
.... Taxa 244–247
Stem not exerted. Leaflets 3 .... Taxa 249–251

Palynology clearly supports the alleged heterogeneous nature of this subsection, with pollen subtypes C1, C5, C7, C8, C9, C11, C12, C14, D1 and D3 all being represented. The first two [197—200; 201—205] and last three groups of taxa [235—243; 244—247; 249—251] delimited in Salter's key are palynologically uniform and similar. With the exception of *O. levis*, *O. comptonii* and *O. oligophylla*, these 25 taxa all have pollen of the subtype D1 (or D2 in the case of *O. linearis*). The occurrence of pollen subtype C5 in *O. levis* is peculiar, as it is a complex pollen type quite dissimilar to any other in the genus, while *O. levis* is not too dissimilar to the other taxa in its group. Salter mentions that this species has a very limited geographical distribution, which might have some evolutionary significance. The presence of pollen subtype C8 in both *O. comptonii* and *O. oligophylla* is incongruent with the pollen of the species-groups in which they were placed. They would palynologically be better placed in the fourth group of taxa [212–234] within this subsection.

The third group of taxa [206—211] is a palynological jumble, with only six taxa displaying the following five pollen subtypes: C7, C11, C12, C14 and D1. Palynologically *O. campicola* and *O. xantha* (both with pollen subtype D1) are better placed within the group of taxa discussed above. The two varieties of *O. tenuipes* are palynologically similar to each other (C11 & C12), but seem quite out of place in the subsection as a whole. Their true affinities might be sought in section *Campanulatae*, with groups within sections *Latifoliolatae* and *Crassulae*, or with individual species currently placed in section *Angustatae* subsection *Multifoliatae*. *O. phloxidiflora* has monotypic pollen of the subtype C14. Salter (1944) comments on the variable nature of this species, which again might have some phylogenetic significance as it could indicate evolutionary instability.

The fourth group of taxa [212—234] delimited in this subsection is palynologically fairly uniform and constant. Although it includes pollen subtypes C2, C7 and C8, previous discussions have indicated that these three types are closely related and probably represent only one taxonomically significant group.

In summary, palynology suggests a great discordance within subsection *Linearis*, and reveals the need to reconsider the taxonomy of this taxon.

SECTION *ANGUSTATAE*
SUBSECTION *GLANDULOSAE*: Taxa 252—259

Salter (1944) views section *Angustatae* subsection *Glandulosae* as an unnatural subsection which is separated from subsection *Linearis* by features of the indumentum only. It is characterised by the presence of capitate (sometimes pluricellular) hairs, which are often admixed with simple hairs to form a dense indumentum.

With the exception of *O. droseroides*, the taxa in this subsection are palynologically similar to the fourth group in subsection *Linearis*. Pollen subtypes C2, C7 and C8 are commonly found. *O. droseroides* has a distinctly different, monotypic pollen subtype, C13. As in the case of most of the previously mentioned monotypic pollen types, there seems to be no distinctive macro-morphological feature correlating with the unique pollen characters.

SECTION *ANGUSTATAE*
SUBSECTION *MULTIFOLIATAE*: Taxa 260—267

This subsection can be regarded as a dustbin taxon containing an unrelated group of species which simply show no affinity with any other groups. Salter (1944) describes the subsection as artificial, "consisting of multifoliate species which do not appear to be related elsewhere". He continues by discussing the unreliability of the number of leaflets as a taxonomic denominator.

The taxonomic confusion surrounding this subsection is again clearly reflected in its palynology. Pollen subtypes C6, C8, C9, C10 and C11 occur in an almost random order, making it close to impossible to draw any significant conclusions from the results. One interesting features does, however, merit some discussion. Pollen subtype C6 is rather distinct, and was only found in *O. engleriana* and *O. henrici*, both from the subsection *Multifoliatae*. This will be discussed in more detail in section 7.4.

SPECIES NOT ALLOCATED TO A SPECIFIC SECTION:
Taxa 268—271

At the end of his revision, Salter (1944) lists eight species without specific sectional placements. Of these, only *O. monophylla* was included in the present study, as pollen material of the other seven species could not be obtained.

The presence of pollen subtype C8 in *O. monophylla* var. *stenophylla* is hard to explain, as this pollen type is quite different to the subtypes C10 and C11 which were found in the other three varieties of the same species. In fact, Salter stresses the similarity of this variety to the typical one and questions the validity of recognising it as a separate taxon. The subspecific delimitation of *O. monophylla* therefore needs to be re-examined.

7.4 Taxonomic significance of the different pollen types

Plant systematists often do not think of a previous classification as an hypothesis, but as a baseline data set which can be used to generate a hypothesis (La Duke 1987). This truth had to be kept in mind throughout the present study, since Salter (1944) represents the only fundamental work to date on the southern African members of *Oxalis*. Salter's hypothesis was based on years of field experience, coupled with a critical evaluation of numerous morphological characters. In the present study a new hypothesis is proposed. After an in depth study of its palynology, the genus was subdivided into 21 pollen types. Care was taken not to have this hypothesis clouded or influenced by the morphological hypothesis suggested by Salter (1944). In this section, these two hypotheses are compared and the taxonomic conclusions that could be derived are discussed in some detail. Since neither represent concrete truths, any conclusions drawn remain speculative.

- **Pollen type A** is a fairly specialised type found only in section *Sagittatae*. This exclusive occurrence and the taxonomically well-defined state of the section enhance the taxonomic significance of pollen type A at sectional level within the genus.

- **Pollen type B** is a unique, monotypic type found only in *O. fibrosa* (section *Sagittatae*). As mentioned before (section 7.3), it is feasible to consider pollen type B as an evolutionary derivative of pollen type A. These two types are geographically separated, which suggests that pollen type B could have evolved from type A through selective pressures in a new environment. This evolutionary direction is assumed, based on the monotypic nature of pollen type B. Pollen type B seems to be of taxonomic importance at species level.

- **Pollen subtype C1** occurs in isolation in five species from different sections and subsections. It was found in *O. bowiei* and *O. semiloba* (section *Cernuae* subsection *Purpuratae*), *O. stellata* var. *montaguensis* and *O. tragopoda* (section *Cernuae* subsection *Stellatae*) and in *O. psilopoda* (section *Oppositae* subsection *Subintegrae*). At first glance this distribution seems to have no real taxonomic importance. When it is considered that these five taxa are geographically coherent by occurring exclusively in summer rainfall areas, however, the species-level significance of pollen subtype C1 becomes apparent.

- **Pollen subtypes C2, C3, C4** and **C7, C8, C9** are obviously very closely related. They represent two lineages of increase in lumina diameter, in the first case without inter-luminary bacula and in the second with these structures. In the genus *Pelargonium* of the related family Geraniaceae, the presence or absence of intraluminary bacula proved to be of no taxonomic significance (Dreyer *et al.* 1992).

  With the exception of a concentration of pollen subtype C2 in section *Oppositae*, these six pollen types co-occur almost randomly in the first four endospermous sections of *Oxalis*. Pollen types from this group are found elsewhere in the genus as well. Subtypes C2 (2 taxa) and C8 (1 taxon) are present in three taxa in section *Latifoliolatae*. The entire section *Angustatae* subsection *Pardalis* has pollen of the subtypes C2, C3 and sometimes C9. This is taxonomically significant, since Bayer (1992) regards all the taxa included here as synonyms of *O. pardalis* (pollen subtype C2). They are also found in taxa from the second half of section *Angustatae* subsection *Sessilifoliatae* and in a large group in section *Angustatae* subsection *Linearis*. Section *Angustatae* subsection *Glandulosa* almost exclusively displays pollen types from this group. The six pollen types also occur sporadically throughout the genus, mostly as obvious misplacements.

  Due to the co-occurrence of these pollen types in various seemingly natural sections, their taxonomic significance as separate entities is questionable. As a group their distribution, as summarised above, seems to be of taxonomic importance, while their individual taxonomic significance seems to be limited. Huynh (1969a) grouped all of these types (and more) together in her pollen type **A1**. Retaining them as separate types, however, reflects the palynological variation that exists on a sectional, subsectional, specific or even subspecific level.

- **Pollen subtype C5** is a complex, monotypic type which reveals little about the taxonomy of the heterogeneous section *Angustatae* subsection *Linearis* in which it is found. At species level, however, it separates *O. levis* from all the other taxa in the genus. Although this uniqueness is apparently not supported by morphological features, *O. levis* has a limited geographical distribution, which in combination with the palynological complexity, could be indicative of a fairly specialised species.

- **Pollen subtype C6** is only found in *O. engleriana* and *O. henrici*, both from section *Angustatae* subsection *Multifoliatae*. Previous discussions have indicated that such unique pollen types are often monotypic within *Oxalis*. They could indicate ends of evolutionary lines along which the grains have evolved. Here this strange pollen type is found in two species, though, which almost seems incongruent with what was found in the genus thus far. Salter (1944) mentions that *O. henrici* was only known to him in the dried state from type material, and comments on the close affinity with *O. engleriana*. Bayer (pers. comm.) regards these two species as conspecific, a view which is supported by palynology. If this view is taken, pollen subtype C6 is of considerable importance at species level, since it delimits the species *O. engleriana*.

- **Pollen subtypes C10, C11** and **C12** seem to be very closely related. These three types again represent a lineage of increase in lumina diameter and are separated on arbitrarily chosen lumina diameters (Table 5.1). Pollen subtypes C10 and C11 are often found together within various taxonomic groups throughout the genus. Section *Campanulatae* is defined by floral features and appears to represent a fairly natural group. In this section pollen subtype C10 dominates with only one, obviously related, species displaying pollen of the subtype C11. Pollen subtype C10 and a random selection of subtypes C10 and C11 are found in two of the proposed groups of related taxa in section *Latifoliolatae*. With the exception of two seemingly misplaced taxa, pollen subtype C10 is found in all the taxa of section *Crassulae* and section *Angustatae* subsection *Xanthotrichae*. The monotypic pollen subtype C12 is found in the typical variety of *O. tenuipes* (section *Angustatae* subsection *Linearis*), with pollen subtype C11 occurring in the other variety of the same species. This implies a close affinity between these two pollen types. Finally there is a fairly high representation of pollen subtypes C10 and C11 in the complex section *Angustatae* subsection *Multifoliatae*.

Various conclusions can be drawn from this wide, yet clustered, distribution of pollen subtypes C10, C11 (and C12) within *Oxalis*. The exclusive occurrence of pollen type

C10 in two sections suggests that it should perhaps be considered as quite unrelated to pollen subtype C11. The integrity of these two sections is, however, rather questionable. The co-occurrence of the two pollen types in section *Campanulatae*, which, in contrast, is perceived as a fairly natural taxon, supports the view that pollen subtypes C10 and C11 are very closely related, and could perhaps be lumped together. In turn, the occurrence of pollen subtypes C11 and C12 in two varieties of the same species suggests a very close affinity between these two pollen types. Regarding pollen subtypes C10, C11 and C12 as separate but related pollen types appears to be the most meaningful taxonomical approach. In this way palynological variation is shown, while possible taxonomic affinities on a sectional, specific and subspecific level is still reflected. These three pollen types are clearly separated from the other subtypes in pollen type C, and it is suggested that the taxa containing them should be re-evaluated in search of additional characters which may link them taxonomically.

- **Pollen subtypes C13, C14** and **C15** are monotypes found in the species *O. droseroides* (section *Angustatae* subsection *Glandulosa*), *O. phloxidiflora* (section *Angustatae* subsection *Linearis*) and *O. giftbergensis* (section *Angustatae* subsection *Sessilifoliatae*) respectively. There is no reflection of the palynological uniqueness in the morphology of any of these taxa. Due to the monotypic state of the pollen types, no real taxonomic conclusions can be drawn from their occurrences. They do, however, isolate the species as being unique in the genus and could indicate advanced evolutionary states. This is partly due to their monotypic nature and partly to the inherent complexity of each of the three pollen types.

- **Pollen type D** represents the most complex pollen in the genus. It was subdivided into the subtypes D1, D2, D3 and D4 chiefly because of variations in the shape, size and arrangement of the supratectal areolae. Pollen subtype D1 is the most common, with only one occurrence each of pollen subtypes D2 and D3 and two occurrences of pollen subtype D4. The distribution of the subtypes seems to have limited taxonomic significance, as they are spread throughout the genus. Pollen subtype D4 was, however, found in two of the varieties of *O. hirta*, while the other four varieties have pollen of the subtype D1. Here the distinction between subtype D1 and D4 might have some taxonomic implications at the subspecific level.

This limited taxonomic significance questions the value of demarcating subtypes within pollen type D. The subtypes do, nevertheless, reflect the considerable variation found within the pollen type and are therefore retained as four separate, yet closely related, pollen types. Pollen type D as a whole seems to be of great taxonomic significance within *Oxalis*. Clusters of taxa with D-type pollen are found in the sections *Latifoliolatae* and *Angustatae* subsections *Sessilifoliatae* and *Linearis*. The occurrence of such an unique pollen type in such apparently unrelated taxa stresses the need to re-examine the morphology and taxonomy of these groups. One of the objectives of such further investigations should be to establish the extent to which homoplasy may be involved.

It is evident that some of the sections in Salter's classification are palynologically fairly homogeneous. These include sections *Cernuae*, *Oppositae*, *Stictophyllae*, *Foveolatae*, *Sagittatae*, *Campanulatae*, *Crassulae* and *Angustatae* subsection *Xanthotrichae*. In a sense this could be seen as support of Salter's system. In many cases, however, the same pollen types are found in more than one section, which again obscures the proposed sectional boundaries. The sections *Latifoliolatae* and *Angustatae* are palynologically very heterogeneous, although pollen features correspond remarkably well with the proposed groups of related species within section *Latifoliolatae*. In these two sections particularly, palynological data reiterate the need for a new taxonomic classification of *Oxalis*. Bayer (pers. comm.) suggests that Salter's classification is really a very weak basis on which to assess the significance of pollen characters. He stresses the need for a re-assessment of the genus, and acknowledges the contribution palynological data could make towards achieving an improved classification. Establishing such a classification mainly on palynological features, however, would be irresponsible, especially as the angiosperms are notorious for parallelism and convergence. These two phenomena cause similar structures to materialise independently in otherwise unrelated groups and are seen as two major obstacles in the way of satisfactory classifications of higher plants (Stebbins 1971). In combination with results from other study fields, however, palynology can contribute greatly to achieving a more natural classification of the genus *Oxalis*.

7.5 General discussion and evolutionary trends

7.5.1 Diversity

Oxalis is considered one of the most diverse genera in southern Africa. At present 270 infrageneric taxa have already been identified and all indications are that many still await description or discovery (Stirton & Oliver, pers. comm.). Salter (1944) mentions that, although there are a considerable number of fairly clearly defined species, the genus contains many large, aggregate species (species groups) (Stace 1989). These consist of inter-related micro-varieties so numerous and inextricably overlapping that they seem to defy detailed classification as fixed units. This phenomenon is clearly exemplified by the subsection *Pardalis* (Bayer, 1992). Salter (1944) used characters such as the number of leaflets, sessile or petiolate leaflets, petal width, sepal length, plication of bulb tunics, proportion of lamina to tube length, indumentum, size, exertion of the filaments, number of ovules and flower colour to define this subsection. When Bayer (1992) conducted an in depth study of this group, he found all of these characters to be most variable. Ecotypes occurred across the spectrum linked by continuous variants from one population to the next. In the Ceres-Karoo a strong-scented, night-flowering form with white flowers was observed and provisionally named *O. fragrans* MS. Further investigation showed that even this unique population gradually petered into others through intermediate characters of smell and morphology. This continuum of variation eventually caused him to synonymize the 11 species and four manuscript species under the single species, *O. pardalis*. The variation exemplified by this subsection seems to be the rule rather than the exception in *Oxalis*. It is obvious that the genus has undergone severe diversification in southern Africa and in many cases still seem to be actively speciating.

7.5.2 Biogeography

The explosive diversification of *Oxalis* in southern Africa calls for an explanation. Perhaps part of the answer can be found in the geographical distribution of the genus within the subcontinent. More than 90% of the southern African taxa are found in the southern and southwestern parts of the Western Cape Province. This area is included in the very unique and widely discussed Cape Floristic Region (Good 1974).

Bond & Goldblatt (1984) give a detailed account of the Cape flora and the numerous factors that may have contributed to its astounding diversity. The area is very mountainous with several parallel series of steep mountain ranges separated from one another by intermontane valleys. Climatic conditions such as temperature and rainfall vary considerably between the narrow coastal plain, the mountain slopes and the intermontane valleys. The area displays a variety of soil types ranging from coarse-grained, acidic, nutrient poor types on the mountains to heavier, richer soils in the valleys. Soils derived from granites, limestones and calcareous rock are also found locally throughout the area.

The Western Cape region has been subjected to extensive climatic change during the past two million years. According to Sudgen & Meadows (1990) it has experienced dramatic shifts in both temperature and precipitation gradients. During the Last Glacial Maximum (LGM) some 18 000 years ago, the region was much cooler and the precipitation was greater than today. These conditions reduced both fire frequency and intensity, which favoured fire sensitive species. As the area gradually became hotter and drier, vegetation patterns changed, and culminated in the patterns we find today. The distribution of species that flourished during the LGM contracted, resulting in the isolation of peripheral populations.

Linder (1991) conducted an interesting study into the environmental correlates for the species richness of the Cape flora. He found areas of high species richness in the southwestern Cape region to be strongly correlated with high rainfall. In turn, high rainfall is generally correlated with high altitudes and the occurrence of sandstone substrates and Fynbos vegetation. Species richness was found to be weakly correlated to the range of substrates in a given area. This is curious, since edaphic factors have generally been thought to be important in the patterns of diversity in the Cape flora.

The variations in habitat, climate, vegetation and substrate has resulted in a mosaic of different micro-habitats within the Western Cape. These micro-habitats are often separated by small ecological barriers which promote population isolation. This has resulted in a fragile ecology, with numerous taxa displaying restricted distributions.

Bond & Goldblatt (1984) listed the Oxalidaceae as one of the larger families and the genus *Oxalis* as the sixth largest genus in the Cape flora. Disproportionately large genera are often a feature of floras which developed in isolation under conditions of extreme climatic change or ecological stress. Since such conditions have prevailed in the Western Cape since the Oligocene, it is quite feasible how a genus such as *Oxalis* could have thrived within the area. All the southern African taxa are tuberous, which could facilitate survival during unfavourable conditions. Additionally the genus has developed a most successful vegetative reproduction system, while retaining efficient sexual reproduction mechanisms. This must have given *Oxalis* great adaptive advantages under even the most severe climatic changes, which may be one of the reasons why it has diversified to such an extent in the given environment.

7.5.3 Speciation

The climatic gradients along with the dissected and diverse landscape of in the Western Cape increased the number of ecological niches available within the region. Such an environment strongly favours gradual (Stace 1980) or geographical (Grant 1981) speciation. Through regular chance mutation and recombination, the genepool of a given population increases and becomes more variable. Changed interactions between the genepool and the changed environment lead to visible changes in the population through the process of natural selection. According to Stace (1980) the processes of ecotypification and the evolution of geographical races can be considered as early stages in gradual (geographical) speciation. As previously discussed, examples of such geographical races abound in *Oxalis*. Per implication, this supports the view that *Oxalis* is still actively evolving through the process of gradual speciation.

Quantum speciation is another form of speciation which has probably been active in *Oxalis*. It differs from gradual speciation in being more rapid and radical. The semi-isolation of a peripheral population of a given species cuts this population off from the main stream of gene flow of the population as a whole (Grant 1981). This leads to inbreeding in the peripheral population, resulting in drastic genetic and phenotypic modifications. In a varied environment such as is found in the Western Cape, this altered population may be better adapted to its specific micro-habitat, which will cause it to expand and stabilise as a separate, isolated species. The net result of this mode of speciation is a central ancestral species surrounded by geographically isolated daughter species with variant characteristics.

One of the most abrupt modes of speciation and evolution is achieved through changes in the chromosome number of a given taxon. When an individual within a population acquires a different chromosome number, successful crossings with other individuals from that population is impaired, which could result in genetic isolation from the group. The best known example of speciation through changes in chromosome numbers is that of allopolyploidy. This phenomenon involves simultaneous genetic isolation and phenetic differentiation of the new taxon. What is striking about the genetic study of *Oxalis* by Marks (1956), is that 18 of the 27 southern African taxa he studied proved to be polyploid. This very high percentage (66%) supports the view that abrupt speciation through polyploidy has and probably still is affecting speciation in *Oxalis*.

Quantum speciation and speciation through polyploidy may well account for the high number of clearly defined species described in the genus, while gradual (geographic) speciation adequately explains the occurrence of aggregate species.

7.5.4 Reproductive isolation

The final stage of any mode of speciation is completed once reproductive isolation between two populations is achieved. This enables the coexistence of related populations in the same habitat, each of which maintains the integrity of its own gene pool. Through this, related populations can diverge further from each other by evolving different ways of exploiting the same environment.

Grant (1981) discusses a number of ways in which successful reproductive isolation can be achieved. Some of these are summarised in Table 7.1.

Table 7.1 Isolating mechanisms proposed by Grant (1981).

ISOLATING MECHANISMS		
Spatial		Geographical isolation
Environmental		Ecological isolation
Reproductive	External	Temporal isolation
		Mechanical isolation
		Ethological isolation
		Isolation due to autogamy
	Internal	Incompatibility barriers
		Hybrid inviability
		Hybrid sterility
		Hybrid breakdown

The reproductive biology of *Oxalis* is still understudied, which complicates the evaluation of possible means in which the genus could have established isolating barriers. The wide diversity of ecologically unique micro-habitats that exist within the Western Cape offer an explanation of how the genus could have attained spatial and environmental isolation. It is also known that *Oxalis* is essentially winter flowering, but that the exact flowering times of different species vary. This explains how temporal isolation, certainly between individual species, could have been established. Pollination syndromes and the tristylic nature of the southern African *Oxalis* taxa are likely to have affected the other external isolating mechanisms. This will be discussed in more detail in section 7.5.5. Almost nothing is known about the breeding systems of southern African *Oxalis* species, which makes it impossible to comment on the influence of internal modes of reproductive isolation on their speciation.

7.5.5 Pollination

An understanding of the evolution of angiosperms is often closely related to an understanding of the their pollination mechanisms and the evolution thereof (Crepet 1979). Within *Oxalis* insects were identified as pollinators in studies of the American *O. alpina* (Rose) Knuth (Weller 1981) and *O. suksdorfii* Trel. (Ornduff 1964). In the first species solitary bees and dipterans were most prominent, while flies, bees and small beetles were found pollinating the second species. Pollination studies of southern African *Oxalis* species are limited. The most comprehensive account available is that of Crouch (1989), who studied the pollinators of *O. obliquifolia* in KwaZulu-Natal. He identified blister beetles, thrips and butterflies as active pollinators. The different stylar forms were not preferentially visited, although butterflies were never seen visiting midstylar forms of the species. In a pollination study of the introduced weed *O. corniculata*, Crouch (1988) found thrips and springtails to be the main pollinators.

Thrips were also observed visiting flowers of *O. oculifera* (Oliver 1993). Although no actual pollination study has been undertaken for any of the other southern African taxa, indications are that they are mostly insect pollinated. This assumption is based on the following facts and observations:

- All the southern African members of *Oxalis* are considered tristylous, although all the stylar forms are not equally abundant in all species (Salter 1944). This morphological heteromorphism must have had an important impact on the breeding systems, pollination biology and evolutionary trends within the genus. Tristyly in *Oxalis* is often associated with self-incompatibility or residual self-incompatibility (Ornduff 1974). Weller (1981) states that seed production by heterostylous, self-incompatible species is obligatedly dependent on animal vectors for movement of pollen between different floral morphs in the population. The issue is further complicated by the difference in pollen diameters between the different stylar whorls. It seems obvious that such a complicated scenario calls for a fairly specialised pollination syndrome.

- The manuscript species *O. fragrans* displays a perfect moth pollination syndrome. This night-flowering taxon has white, tubular flowers with a strong, sweet aroma. A single potted plant was monitored, and it was found that the flowers opened at *ca.* 22:00, emitting the strong fragrance on opening. No pollinators were, however, observed in this artificial environment.

- The majority of *Oxalis* flowers are bicoloured, often with a yellow, greenish or white tube and pink, orange, yellow, white or scarlet flowers. In monochromatous taxa the tube is often slightly darker coloured than the rest of the flower. *O. oculifera* is tricoloured with a wine-red tube, a white ring in the throat and violet pink corolla lobes. Such decorative floral displays are often associated with insect pollination syndromes (Macoir 1971). Kevan (1978) proposed that contrasting flower colours function as long-distance signals to flying diurnal flies and bees. The tube and throat colour patterns can also act as nectar guides to visiting insects.

- Both the sections *Campanulatae* and *Sagittatae* are characterised by distinct floral features. Flowers found in section *Campanulatae* have a campanulate corolla and the longer filaments are prominently toothed. Section *Sagittatae* has flowers with very slender styles and stamens. The medium organs, whether stamens or styles, spread widely on release from the corolla tube, while the longest organs remain erect. The anthers of all the included taxa are sagittate. Both of these sections are palynologically uniform, and section

Sagittatae is characterised by a unique pollen type not yet found anywhere else in the genus. This sectional floral specialisation is likely to be the result of selection for a specific pollinator or pollination syndrome.

- *Oxalis* pollen displays a tendency towards the formation of supratectal spinules, spines or areolae. Such structures were observed in pollen types A, B, C5, C6, D1, D2, D3 and D4. The evolutionary implications of this feature will be discussed in more detail in section 7.5.6. What is relevant here is that spinescent pollen is often associated with insect pollination. According to Stebbins (1974) the spiny character of the exine promotes the aggregation of grains into clumps, which can then be transported with relative ease by pollen vectors. Vaissiere & Vincent (1994) found that spinate pollen in cotton (*Gossypium hirsitum* L.) readily got caught in the haircoat of their bee vectors and that the length of the spines directly affected the efficiency of such pollination activities. The fact that spines are present in so many unrelated pollen types within *Oxalis* strongly suggests the involvement of insect pollinators in a diverse number of taxa.

- Hesse (1981) has shown that there is variation in the amount, distribution and consistency of pollenkitt on pollen surfaces in entomophilous and anemophilous species in a wide range of families. Large amounts of pollenkitt is often associated with bird or insect pollination. Most of the *Oxalis* pollen examined showed substantial amounts of pollenkitt, which thus strengthens the possibility of insect pollination.

- *Oxalis* is renowned for the occurrence of different colour forms within the same species (Salter 1944; Bayer 1993). It is possible that such colour variation can have significance in terms of attracting different pollinators. Macoir (1971) warns, however, that some pollinators may visit different colour forms with equal vigour. This was confirmed in the study of pollinator visits to different colour forms of *Pelargonium tricolor* Curt., where colour variation had little effect on the frequency or type of visiting pollinators (McDonald & Van der Walt, 1992).

- Mimicry is another intriguing feature often observed in *Oxalis*. Stirton (pers. comm.) mentions *Oxalis* flowers mimicking a wide range of families, including the Iridaceae, Liliaceae and Mesembryanthemaceae. Floral mimicry seems to be effective in isolating and sustaining plant populations sharing the same micro-habitats (Macoir 1971). Through mimicry one species imitates the floral syndrome of another, often unrelated, species in response to pollinator requirements. Manning & Goldblatt (1995) have shown how this can be beneficial to both the pollinator and the plants involved. In short mimicry sustains pollinator interest in an area by enlarging the functional size of the plant population. In turn the probability of successful pollination of the mimicking species is greatly enhanced.

It is clear that *Oxalis* has developed numerous ways in which to facilitate insect pollination. Most of these methods correlate directly or indirectly to the mosaic of micro-habitats that exist in the southern African centre of diversity for the genus. As ecotypic or peripheral populations of a given population radiate into new micro-habitats, they are likely to encounter new pollinators and new pollination syndromes. Amongst others, mimicry offers an excellent method of dealing with these new reproductive pressures. Individuals that mimic taxa with successful pollination syndromes in this new environment the most effectively, will be favoured by natural selection. Similar arguments can be used to explain the effectiveness of strategies such as floral colour variations, altered floral structures, the formation of more spinescent pollen grains or even the development of a moth pollination syndrome. Bond & Goldblatt (1984) state that under conditions such as those found in the Cape Flora, the relative importance of bees and selective pollinators increases, which in turn promotes diversity. Grant & Grant (1965) adds that adaptive radiation for pollination by different vectors has in some instances been responsible for the differentiation of subspecies within species, species within genera and even genera within families.

7.5.6 Evolution

Preceding discussions emphasised the great morphological variation in the southern African members of *Oxalis*. It was concluded that *Oxalis* is an evolutionary unstable genus, which in places still seems to be actively evolving. It is, nevertheless, known that morphological features are rather susceptible to environmentally induced changes. In contrast, palynological features are known to be much more conservative and stable in an evolutionary sense. According to Kuprianova (1969) pollen is more resilient against environmentally induced changes because of its involvement in the reproductive system of the plant. Yet 21 different pollen types/subtypes were identified within *Oxalis*. In this section possible palynological evolutionary trends within the genus are discussed under two separate headings: 7.5.6.1 Evolution of pollen types and 7.5.6.2 Phylogenetic implications.

7.5.6.1 Evolution of pollen types

Detailed palynological studies of fossils, gymnosperms and primitive angiosperms have revealed much about the evolutionary trends within palynology. The topic has been widely discussed in the literature and numerous suggestions regarding the evolutionary sequences of tectum and apertures development have been proposed. Studies by Wodehouse (1935), Van Campo (1967 & 1976), Muller (1970), Doyle (1977), Walker & Doyle (1975), Heslop-

Harrison (1976), Punt (1976, 1978), Walker (1976) and Muller (1979), amongst others, are consequential in this regard. Some of the more widely accepted and relevant evolutionary trends are summarised below:

- Monosulcate pollen is believed to represent the ancestral angiosperm type, with tricolpate pollen the ancestral type for dicotyledons (Walker & Doyle 1975).
- From these ancestral types, the following patterns are suggested for the a) number, b) position and c) type of apertures:

  a) zono-aperturate → panto-aperturate
  b) tri-aperturate → poly-aperturate
  c) colpate → colporate → porate
- Atectate pollen is regarded as the most primitive angiosperm type. From there, the following developmental sequence is proposed:

  atectate → tectate-imperforate → tectate-perforate → semitectate
- Many groups display an evolutionary tendency towards an increase in the complexity of pollen wall structure (Van Campo 1967 & 1976; Muller 1970; Ferguson & Skvarla 1982).
- Muller (1970) proposes an evolutionary progression of exine structure from:
  - columella-derived structures (mostly with reticulate architecture) to
  - tectal structures (mostly spinose or verrucose supratectal structures) to
  - combined structures such as are found in the spinose exines of the Compositae.

  Walker (1976), however, warns that sculpturing represents a more or less reversible character which should be interpreted in terms of the individual correlations observed within a given taxon.
- Presence or absence of an endexine and footlayer and their relative thickness are phylogenetically significant, but more data is necessary before generalisations of major evolutionary trends can be made about exine stratification (Walker & Doyle 1975).
- According to Walker & Doyle (1975) primitive angiosperm pollen falls in the large grain size class (55—99 µm). From these large grains, two developmental lines have been traced: one towards even bigger to gigantic grains and the other towards smaller and minute grains. Muller (1979) cautions, however, that pollen size constitutes an extremely variable character which is influenced by diverse factors such as flower size, soil type and level of ploidy.

In her assessment of oxalidaceous pollen, Huynh (1969a & b) proposed various possible evolutionary trends within *Oxalis*. Reference to pollen types mentioned here follows the classification as proposed in the present study. The most significant of these evolutionary trends is her hypothesis of gradual tectum destruction which proposes that from an ancestral reticulate type (pollen type C) there has been a progressive loss of the tectum. Pollen types A and D are seen as transitional stages in this process, which culminated in a complete loss of the tectum in pollen type B. Results of the present study, however, contradicted this theory (see section 7.2).

Another major evolutionary trend proposed in Huynh's work is the gradual simplification of the apertural structure. She proposes an evolutionary progression from a colporate state in the American taxa to a more advanced colpate state in the southern African taxa. This contradicts the generally prevailing view that colporate pollen is more advanced than colpate pollen. Additional evolutionary tendencies proposed in her work include:

- A gradual increase in the average lumina diameter within pollen type C. Coupled with this is a gradual reinforcement of the thickness of the walls and the exine, and a transition from the simplicolumellate to the pluricolumellate state.

- An increase in the number of apertures from tri-aperturate, via a tetra-aperturate, to the most advanced panto-aperturate state.

- An increase in the dimension of pollen grains within the Oxalidaceae. The "more primitive" genera (*Averrhoa* & *Sarcotheca*) have the smallest grains, whereas the allegedly most advanced genus *Oxalis* has the largest grains.

The present study suggests a whole new range of possible evolutionary trends. Tricolpate, reticulate grains are assumed to be the most primitive pollen type for the southern African members of the genus. The reason for this assumption is threefold:
a) it represents the most common and widespread pollen types in the group
b) it is in accordance with the general trends within the angiosperms (as discussed above)
c) this type of pollen represents the most primitive state in the neighbouring family Geraniaceae (Verhoeven *et al.* 1990). The latter view is also congruent with that of Huynh (1969b).

From this ancestral tricolpate, reticulate state, evolutionary lines have migrated in different directions, resulting in three distinctly different new pollen types and 15 variations on the basic reticulate pattern. A possible hypothesis of how this palynological diversity could have evolved is set forward in Figure 7.1. This is based on the following observations and assumptions:

- From the ancestral tricolpate state there seems to be a gradual increase in the complexity of the wall structure. This is both noticeable within pollen type C and in the three derived pollen types (A, B & D).

- There is a general tendency towards the formation of supratectal structures (spinules, spines or areolae) within all the main pollen types of the genus. Formation of these supratectal structures is here interpreted as a special form of complication of the exine. In previous discussions on pollination (section 7.5.5), spine formation was correlated with pollination syndromes. This confirms the views of Crepet (1979) who states that understanding the evolution of pollination syndromes forms an integral part in understanding the evolution of angiosperms.

- There is a general trend towards an increase in the number of apertures in the pollen of *Oxalis*. Pollen type C is relatively primitive in this regard, with a limited number of aberrant grains representing the only deviations from the tri-aperturate state. The progressive increase in aperture number is clearly displayed within both pollen types A and D. Derived panto-aperturate grains are the norm in both types, although a few tri- and tetra-aperturate grains are still to be found. Pollen type D is renowned for aberrations affecting the number and arrangement of apertures (see section 5.6). Previous discussions indicated that this could be indicative of an actively evolving, derived state. The more primitive tri-aperturate state still prevails in pollen type B.

- There is a somewhat vague, yet noticeable, trend towards an increase in average grain diameter. Grains of pollen type D are proportionately larger than those of the other pollen types.

- There seems to be a gradual, yet progressive, increase in the average lumina diameter within pollen type C.

- Within pollen type C there is also a progression from the simplicolumellate to the pluricolumellate state. This is sometimes coupled with an increase in the average muri diameter and the formation of muri perforations (pollen subtypes C13, C14 & C15).

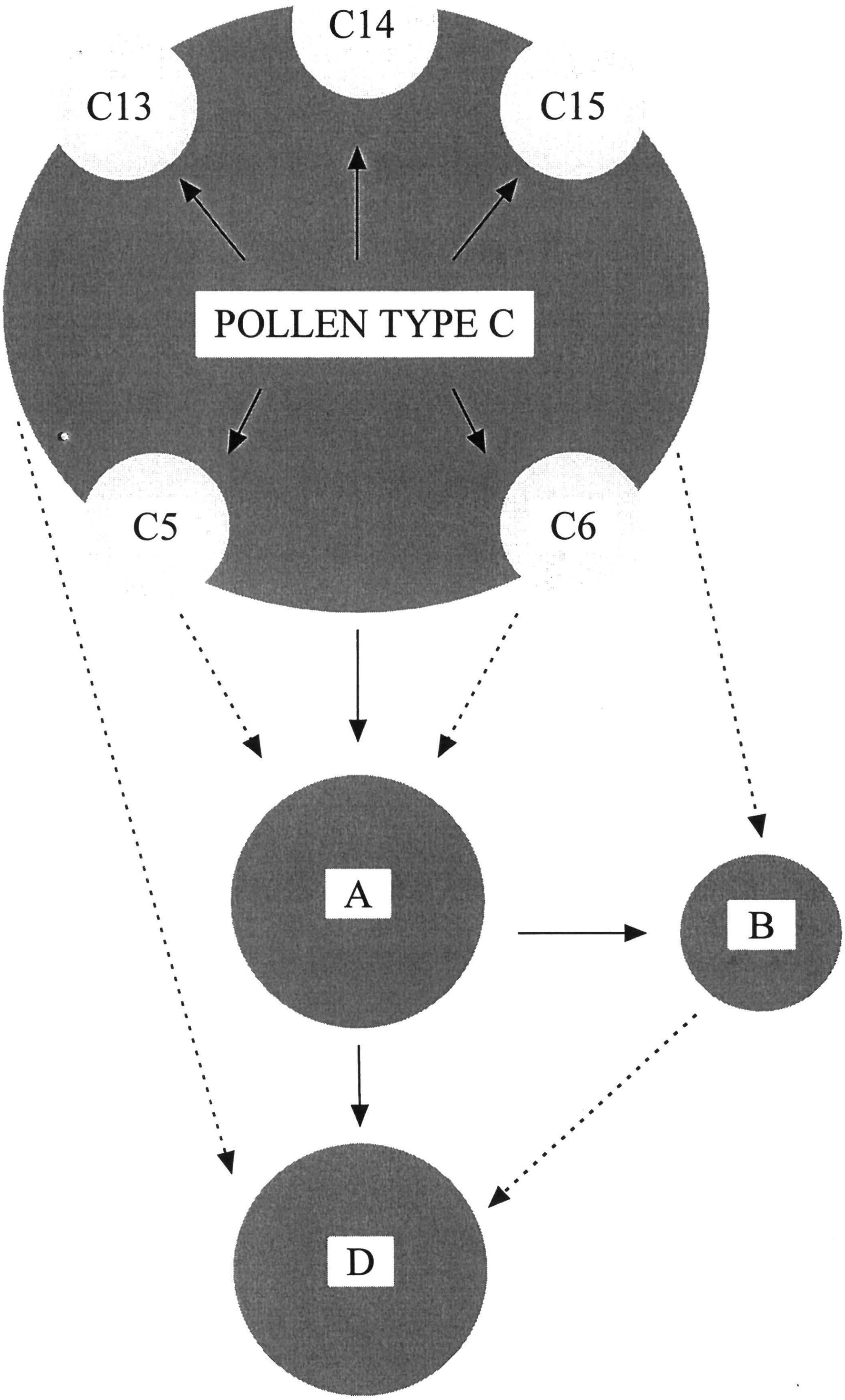

Figure 7.1 Schematic representation of possible evolutionary trends in the southern African members of the genus *Oxalis*. Solid lines represent the most probable evolutionary lines, while broken lines represent feasible alternative paths. Since the evolutionary lines of the other C-types are not evident, they are all included within the widely defined pollen type C.

The monotypic pollen subtypes C5, C6, C13, C14 and C15 are believed to represent relatively advanced types within pollen type C. Their progressed state can partly be ascribed to their monotypic nature, which could suggest independent, isolated evolution under the influence of a specific set of selective pressures. If a gradual increase of complexity in wall structure is accepted as an evolutionary path, then the acquisition of supratectal spinules in both pollen subtypes C5 and C6 contribute to their advanced status. Pollen subtype C5 displays an additional complication of the exine in that the muri are arranged on two different levels. In pollen subtype C6 the average lumina diameter is greatly enlarged. In pollen subtypes C13, C14 and C15 the average lumina diameter has increased, the simplicolumellate state has progressed to a pluricolumellate condition and the muri have increased in relative thickness and become distinctly perforate.

It is feasible that the rugulate-reticulate tectum of pollen type A could have developed from an ancestral reticulate type (type C) through a gradual decrease in the average lumina diameter. The presence of supratectal spinules in pollen type A suggests that such a developmental line could have been derived from pollen subtypes C5 or C6, but this is not necessarily the case. Supratectal structures could quite easily have developed independently in more than on place in the genus. Additionally the columellate layer underlying the tectum of pollen type A is fine and rather similar to that of micro-reticulate grains of the subtype C2. It is therefore also possible that pollen type A could have been derived from spineless micro-reticulate grains within pollen type C.

It is likely that the micro-rugulate-spinate tectum of pollen type B developed from an ancestral type comparable to pollen type A through a reduction in muri dimensions and an increase in the size of the spinules. The co-occurrence of these two pollen types in the fairly natural section *Sagittatae* suggests that they are probably fairly closely related. The monotypic nature of pollen type B and the fact that it occurs in a geographically isolated species, favours the evolutionary direction proposed here. It would, nevertheless, have been possible for pollen type B to develop directly form pollen type C, but this seems unlikely.

Pollen type D represents the most advanced palynological group, with the most complex exine structure and the most prolific modifications in aperture numbers. It also has the largest grains in the genus. The presence (all be it much reduced) of a columellate layer, suggests that it was most probably derived from a reticulate pollen type. The presence of well-developed supratectal structures suggests that it could have been derived from a pollen type in which such structures were already present. But, as mentioned for pollen type A, this need not necessarily have been the case. Establishing the developmental line which culminated in this pollen type is therefore rather difficult. It could have developed from pollen type C, via types A and/or B, or it could have developed directly from pollen type C.

Pollen type D includes a large number of aberrant grains, which inherently bears some evolutionary significance. Both Clarke (1975) and Ferguson (1980) identified a succesiform series as described by Van Campo (1967 & 1976) in the abnormal pollen grains of the groups they studied. According to the succesiform theory, tricolpate grains with a fairly simple structure represent the most primitive state, while pantocolpate grains with a more complex structure, constitute a phylogenetically advanced state. The abnormal grains in *Oxalis* were also found to form succesiform series. In taxa with pollen type D, the most advanced 12-pantocolpate state could have been derived from tricolpate grains in the following ways:

tricolpate→spiralization→12-pantocolpate
tricolpate→tetracolpate→4-aperturate→12-pantocolpate

These series and variations thereof, are found in a very high percentage of pollen type D grains. It is important to remember that, if these complex pollen types can occur accidentally as a result of faulty meiotic divisions in species with primitive pollen, production of complex pollen in itself is not an advanced character (Clarke 1975). The phylogenetic advancement of these series would rather be in their selection as standard rather than abnormal types, a tendency already observed to some extent in pollen type D.

In conclusion the structure of pollen grains must be regarded as a compromise between complex interrelationships including pollination mechanisms and functionality (Muller 1981). This implies that similar pollen structures can develop independently in unrelated taxa merely to improve the functionality of their grains. The problems of relationship, convergence and parallelism must therefore be conceded when studying the patterns of pollen morphological variation (Van Campo 1976).

With this in mind, the evolutionary hypothesis proposed here must be regarded as a speculative view. It was based on the confined results of the present study, a number of generally accepted evolutionary trends in the angiosperms and to some extent the results of the study by Huynh (1969a & b). Additional data on the pollen of the American members of *Oxalis*, related genera and even related families are needed to see these trends in full perspective. Finally, these evolutionary suggestions need to be compared to results from other phylogenetic studies of *Oxalis* to determine their true significance.

7.5.6.2 Phylogenetic implications

To conclude the evolutionary discussion, it is necessary to have a brief look at the phylogenetic implications of the results of the present study on the genus *Oxalis*. A thorough phylogenetic discussion would need reference to:

- the relationships among the southern African species of *Oxalis*
- the relationship between the southern African taxa and their American counterparts
- the relationships between *Oxalis* and the other genera in the Oxalidaceae
- the relationship between the Oxalidaceae and related families in the Geraniales

Results from the present study divides the genus into four palynological units. Although these results need to be validated by additional phylogenetic studies, they supply a basis on which future studies can be evaluated. The extent of occurrence and diversity of pollen type C restricts the phylogenetic deductions that can be made from its distribution within the genus. Taxa with pollen subtypes C1—C4 and C7—C9 are, however, believed to be more closely related to each other than to those with pollen subtypes C10—C12 and visa versa. The five monotypes included in pollen type C are thought to represent phylogenetically relatively advanced states. They also isolate the taxa in which they occur from the rest of the genus. Pollen types A and B are thought to be closely related. They occur in the well-defined section *Sagittatae* which is both palynologically and morphologically isolated within the genus, and phylogenetically probably fairly advanced. Pollen type D represents the most advanced state in *Oxalis*. Taxa with this pollen type occur in various sections throughout the genus. Although it is possible for such a complex pollen type to have arisen independently in these different sections, it seems unlikely. A comprehensive re-examination of the morphology of these taxa is therefore suggested. They are likely to represent the most advanced group within *Oxalis*.

Huynh (1969a & b) found the southern African members of *Oxalis* to be more advanced that their American counterparts, and she considers *Oxalis* to be the most advanced genus in the family. Since the present study was restricted to the southern African members of *Oxalis*, no additional comments can be added.

There is believed to be a strong affinity between the Oxalidaceae and the Geraniaceae within the Geraniales. Verhoeven & Marais (1991) studied the palynology of the Geraniaceae and mentioned the following general trends:

- Tricolpate, reticulate grains represent the basic pollen type in the family.
- In three of the five genera colpate apertures have been replaced by colporate ones.

- A general tectal developmental line from reticulate→reticulate-striate→striate-reticulate→striate is suggested
- There is a limited tendency towards spine formation in the genera *Monsonia* and *Geranium*.
- Randomly scattered intraluminary processes are sometimes observed.

These results reveal some convergent similarities with oxalidaceous pollen in general and the pollen of *Oxalis* in particular. The ancestral pollen types are similar and there is a similar tendency towards complication of the exine structure. Additionally there is a mutual tendency towards spine formation (all be it limited in the Geraniaceae) and intraluminary bacula are recorded from both families. Most modern systems of classification (Takhtajan 1980; Thorne 1980; Dahlgren 1983; Cronquist 1988) regard the Geraniaceae as being more primitive than the Oxalidaceae. If this view is accepted, it supports the reversed notion that colpate apertures represents the advanced state in the Oxalidaceae. A much more in depth study would be needed for further phylogenetic comparisons between these two families.

CHAPTER 8

CONCLUSIONS

8.1 Palynological conclusions

- Structural and sculptural features of the exine proved highly significant in the demarcation of pollen types.
- Four main pollen types were identified within *Oxalis*. They are: rugulate-reticulate (pollen type A), micro-rugulate-reticulate (pollen type B), reticulate (pollen type C), supra-areolate (pollen type D).
- Average pollen grain diameter differs between different stylar whorls in an *Oxalis* flower. Grains from longer stamens are larger than those from shorter stamens.
- Largest pollen grains (81.99 µm) were recorded from *O. hirta* var. *intermedia.*
- Smallest pollen grains (25.26 X 26.08 µm) were recorded from *O. camelopardalis.*
- Average grain diameters of pollen types A, B and C are smaller than those of pollen type D.
- Polar pollen grains are mostly triangularly rounded in polar view and spherical to oblate in equatorial view.
- Apolar pollen grains are generally isodiametrically rounded.
- All the southern African *Oxalis* species have colpate pollen.
- Grains can be tri-, tetra- or pantocolpate. Pollen types B and C are mostly tricolpate, while pollen types A and D are predominantly pantocolpate.
- There is a tendency towards the formation of supratectal structures in *Oxalis* pollen. Such structures were observed in pollen types A, B, C5, C6, D1, D2, D3 and D4.
- The majority of the taxa have reticulate pollen of the type C.
- Fifteen subtypes were identified within pollen type C.
- The most significant characters used in the demarcation of subtypes within pollen type C include: average lumina diameter, presence or absence of bacula, bacula position, presence or absence of supratectal spines, presence or absence of muri perforations.
- Pollen subtypes C13, C14 and C15 are characterised by muri perforations and pluricolumellate muri.

- The sexine structure of supra-areolate pollen (type D) is reminiscent of the crotonoid pollen type found in families such as the Thymelaeaceae and Euphorbiaceae, but it lacks the characteristic underlying ring structure.
- In pollen type D the columellate layer is reduced.
- Four subtypes were identified within pollen type D.
- Variations in the shape, size and arrangement of the areolae could be used to demarcate subtypes within pollen type D.
- Pollen type D (and to a lesser extent type C) is prone to the formation of aberrant grains.
- Seven categories of grain aberrations could be identified within the genus.
- There seems to be no direct link between ploidy level and the formation of aberrant pollen.
- Huynh (1969) recorded the same palynological variation as was found in this study, but interpreted the results quite differently.
- The hypothesis of tectum destruction proposed by Huynh (1969) is contradicted by the detailed SEM and TEM results of the present study.

8.2 Taxonomic conclusions

- Palynology reiterates the need for a new taxonomic classification of *Oxalis* in southern Africa.
- Palynology can contribute substantially towards a better understanding of the taxonomy of the southern African members of *Oxalis*.
- Pollen type A is of taxonomic significance at sectional level within *Oxalis*.
- Pollen type B is of taxonomic significance at species level within *Oxalis*.
- Pollen subtype C1 occurs exclusively in five species from summer rainfall areas and is therefore taxonomically significant at species level within *Oxalis*.
- The demarcation of pollen subtypes C2—C4 and C7—C9 has limited taxonomic significance, while the combined distribution of these six pollen types are taxonomically important.
- Retaining pollen subtypes C2—C4 and C7—C9 as separate entities reflects palynological variation at sectional, subsectional, species and infraspecific levels.

- Pollen subtypes C10, C11 and C12 appear to be closely related, bearing taxonomic significance as a unit.
- Pollen type D is of major taxonomic significance at sectional and subsectional level.
- The subtypes of pollen type D are of limited taxonomic importance.
- Endospermous species have micro-reticulate to reticulate pollen.
- The presence or absence of intraluminary bacula appear to have limited taxonomic significance within *Oxalis*.
- The position of intraluminary bacula within reticulate pollen seems to be of taxonomic importance.
- Palynology contributes little to the demarcation of the sections *Cernuae*, *Oppositae*, *Stictophyllae* and *Foveolatae*, but separates these four sections from the rest of the genus.
- Palynology suggests that *O. pulchella* var. *beneprotecta* deserves recognition as a separate species quite unrelated to *O. pulchella*.
- Palynology suggests that *O. furcillata* var. *caulescens* deserves recognition as a separate species which should perhaps be placed in the section *Sessilifoliatae*.
- Palynology sustains the integrity of section *Sagittatae*.
- Palynology suggests that *O. minuta* var. *callosa* deserves recognition as a separate species quite unrelated to *O. minuta.*
- *O. fibrosa* should be regarded as a geographical variant within section *Sagittatae*.
- Palynology sustains the integrity of section *Campanulatae*.
- Infrasectional distribution of pollen types reflects the artificial nature of section *Latifoliatae.*
- Distribution of pollen types within section *Latifoliatae* corresponds perfectly with the infrasectional "groups of related taxa" proposed by Salter (1944).
- Pollen types of *O. cathara* and *O. namaquana* are incongruent with the pollen of the rest of section *Crassulae*, which questions the taxonomic placement of these two species.
- Palynology does not oppose the suggestion to synonymize all the species included in section *Angustatae* subsection *Pardalis* under the single species *O. pardalis*, as was proposed by Bayer (1992).

- Section *Angustatae* subsection *Sessilifoliatae* is palynologically complex, and the distribution of pollen types do not fully agree with the infrasectional affinities proposed by Salter (1944).
- Monotypic pollen types B, C5, C12, C13, C14 and C15 were found in the taxa *O. fibrosa*, *O. levis*, *O. tenuipes* var. *tenuipes*, *O. droseroides*, *O. phloxidiflora* and *O. giftbergensis* respectively. The monotypic nature of their pollen isolates each of these taxa as being unique within the genus.
- Section *Angustatae* subsection *Xanthotrichae* is palynologically uniform and similar to the sections *Campanulatae*, *Crassulae*, groups within section *Latifoliatae* and individual taxa within section *Angustatae* subsection *Multifoliatae*.
- Palynology reflects the heterogeneous nature of section *Angustatae* subsection *Linearis*, and suggests the need to reconsider the taxonomy of this subsection.
- Palynology questions the infrasectional placement of *O. comptonii* and *O. oligophylla* (section *Angustatae* subsection *Linearis*), as their pollen is incongruent with that of the "group of related taxa" in which they are placed.
- Section *Angustatae* subsection *Glandulosa* is palynologically uniform.
- Palynology confirms the poor taxonomic state of section *Angustatae* subsection *Multifoliatae* and reiterates the need for a revision of this taxon.
- Pollen features support the view that *O. engleriana* and *O. henrici* are conspecific.

8.3 Conclusions regarding pollination

- It is postulated that *Oxalis* is mainly insect pollinated.
- The tristylic nature of *Oxalis* flowers and the differences in pollen diameters of grains from these different stylar whorls are likely to affect pollination syndromes.
- The manuscript species *O. fragrans* displays a moth pollination syndrome.
- Bi- and tricoloured flowers and different colour forms of many *Oxalis* species can probably be associated with insect pollination syndromes.
- The spinescent nature of *Oxalis* pollen could have evolved in response to selective pollinator requirements.
- It is likely that *Oxalis* species mimic diverse families such as the Iridaceae, Liliaceae and Mesembryanthemaceae in response to pollinator requirements.

8.4 Evolutionary conclusions

- Quantum speciation and speciation through polyploidy can account for the large number of clearly delimited species in *Oxalis*.
- Gradual speciation adequately explains the occurrence of aggregate species within *Oxalis*.
- The occurrence of numerous ecotypes and complex aggregate species within *Oxalis* suggests that the genus is still actively evolving.
- Tricolpate, reticulate pollen are assumed to be the most primitive type for southern African members of *Oxalis*.
- There is a tendency towards an increase in the complexity of the pollen wall structure.
- There is a tendency towards the formation of supratectal structures in *Oxalis* pollen.
- There is a general trend towards and increase in the number of apertures in the pollen of *Oxalis*.
- There is a vague tendency towards an increase in the average grain diameter.
- There is a linear increase in the average lumina diameter within pollen of type C.
- Pollen type C is regarded as the most primitive pollen type in *Oxalis*.
- Within pollen type C the monotypic subtypes C5, C6, C13, C14 and C15 are regarded being relatively advanced.
- Monotypic pollen types could indicate an advanced evolutionary state of the taxa in which they are found.
- Pollen types A, B and D are seen as derived forms of an ancestral pollen type C.
- Pollen type B is most probably an evolutionary derivative of pollen type A.
- Pollen type D is most probably an evolutionary derivative of pollen type A.
- Pollen type D is regarded as the most advanced type within *Oxalis*.
- Two succesiform series could be identified in the aberrant grains of pollen type D.
- The evolutionary hypothesis set forward in the present study is seen as a speculative view, which needs to be substantiated by additional phylogenetic studies.

8.5 Suggested further studies

- Although palynology proved highly significant within *Oxalis*, it represents only once source of taxonomic evidence. Evidence from all other features should be integrated to draw real taxonomic conclusions and improve the current classification of the genus.

- Results of the present study call for a verification of the taxonomic placement of a number of taxa. These include:

  - *O. pulchella* var. *beneprotecta*. This variety has pollen of the subtype C10, while the typical variety has C2 pollen. The recognition of var. *beneprotecta* as a separate species and its subsequent sectional placement should be considered.

  - *O. furcillata* var. *caulescence*. This variety has pollen of the subtype C10, while the typical variety has C2 pollen. The recognition of var. *caulescence* as a separate species and its subsequent sectional placement should be considered.

  - *O. minuta* var. *callosa*. This variety has pollen of the subtype C7, while the typical variety and all the other taxa in section *Sagittatae* display pollen type A. The recognition of var. *minuta* as a separate species and its subsequent sectional placement should be considered.

  - *O. cathara* (pollen subtype C1) and *O. namaquana* (pollen subtype C7). These two species are palynologically out of place in section *Crassulae*. According to Bayer (pers. com.) this incompatibility is also reflected in their morphology. Their true affinities should be established.

  - *O. callimarginata* (pollen subtype C9), *O. urbaniana* (pollen subtype C8) and *O. goniorrhiza* (pollen subtype C8). Bayer (pers. com.) believes these three species to be closely related. Although they are currently placed in the section *Angustatae*, the first two belong to the subsection *Sessilifoliatae*, while the third is placed in subsection *Linearis*. Palynologically such an affinity is feasible. These three species need to be studied in more detail to establish their true taxonomic affinities.

  - *O. tenuipes* var. *tenuipes* (pollen subtype C12) and *O. tenuipes* var. *biapiculata* (pollen subtype C12). The pollen types of these two taxa are both incongruent with the 'Group of related taxa" in which they are placed and with the subsection *Linearis* as a whole. Their taxonomic placement should be reconsidered.

  - *O. henrici* and *O. engleriana*. Pollen subtype C6 was only recorded from these two, obviously related species. The possibility to synonymize *O. henrici* under *O. engleriana* must be investigated.

- ♦ The taxonomy of the varieties included in *O. monophylla* must be reconsidered. The presence of pollen subtype C8 in var. *stenophylla* is peculiar, as the other three varieties have either pollen of the subtype C10 (one taxon) or C11 (two taxa).

- Palynology implicates the need for a critical re-evaluation of the integrity of section *Latifoliatae*.

- The integrity of section *Angustatae* subsection *Sessilifoliatae* should be reconsidered. Palynologically the section is effectively split into two seemingly unrelated groups.

- Species with monotypic pollen types need a morphological re-assessment to establish whether their uniqueness is reflected beyond palynology. These include:
    - ♦ *O. levis* (pollen subtype C5)
    - ♦ *O. engleriana* (*O. henrici*?) (pollen subtype C6)
    - ♦ *O. droseroides* (pollen subtype C13)
    - ♦ *O. phloxidiflora* (pollen subtype C14)
    - ♦ *O. giftbergensis* (pollen subtype C15)

- Palynology suggests a great discordance within section *Angustatae* subsection *Linearis*, implying the need for a thorough re-assessment of its taxonomy.

- Palynology suggests a great discordance within section *Angustatae* subsection *Multifoliatae*. This subsection seems to include a random array of unrelated taxa in need of a taxonomic re-evaluation.

- Additional taxonomic synapomorphies linking taxa with pollen subtypes C10, C11 and C12 should be sought.

- Additional material of taxa with pollen subtypes C2—C4 and C7—C9 should be studied to determine the affinity between these pollen types. Such studies could also reveal the full range of palynological variation within individual taxa and the palynological range of aggregate species.

- A thorough re-examination of all the taxa with D-type pollen is proposed. Such studies might reveal additional features linking them taxonomically. One of the objectives of such further studies should also be to establish the extent to which homoplasy may be involved.

- Ontogenetic studies of taxa with pollen types A, B and D might reveal something about their evolutionary development.

- Further synapomorphies among the first four exendospermous sections (*Cernua, Oppositae, Stictophyllae, Foveolatae*) should be sought. Palynologically these sections might be viewed as a unit. Unfortunately the possession of exendospermous vs. endospermous seed is a fairly unreliable character, which cannot be used to substantiate this division.

- The evolutionary hypothesis set forward in the present study should be tested through comparison with phylogenetic data from other study fields.
- Additional atomic force microscope (AFM) studies, measuring the variation within a given pollen type, should be conducted. This might reveal the taxonomic significance of fine sculptural detail (such as the steps in the muri of pollen subtypes C2 and C3) which was detected in the preliminary AFM analysis. Further AFM studies of aggregate species may also contribute to resolving their taxonomy.

CHAPTER 9
SUMMARY

A palynological review of *Oxalis* (Oxalidaceae) in southern Africa

by

Léanne Laurette Dreyer

Promoter: Prof. Dr A.E. van Wyk
Department of Botany, University of Pretoria

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PHILOSOPHIAE DOCTOR

The genus *Oxalis* includes about 800 species, with centres of diversity in both South America and southern Africa. There are an estimated 210 *Oxalis* species within southern Africa, with the highest species diversity found in the Western Cape. Although it is a diverse and interesting genus with marked horticultural potential, the taxonomy of southern African members is badly neglected. The disputable revision by Salter (1944) constitutes the most comprehensive treatment to date. The main objective of the present study was to determine the taxonomic significance of palynology among the southern African members of *Oxalis*. To this end LM, SEM and TEM techniques were employed. Preliminary AFM results were also evaluated.

Oxalis was found to be palynologically diverse, resulting in the identification of four main pollen types (A, B, C & D) and 19 subtypes within the genus. Detailed structural and sculptural characters of the exine proved useful in this regard. Keys to pollen types and subtypes are provided, supplemented by full LM, SEM and TEM descriptions of each type. The palynological classification proposed in the present study was compared to the taxonomic classification proposed by Salter (1944). Palynological groupings were found to be congruent with some of the sections in Salter's system, while palynology reiterated the need for a taxonomic re-assessment of others. The different pollen types proved to be significant at

different levels of the taxonomic hierarchy within the genus. Pollen types A and D are important at sectional and infrasectional levels, while pollen type B is meaningful at the specific level. Pollen type C is diverse, with significance at various levels.

An evolutionary discussion, considering morphological diversity, biogeography, means of speciation and pollination led to a more detailed discussion of the evolution of pollen types. A hypothesis is set forward according to which pollen type C constitutes the ancestral type, with pollen types A, B and D representing derived states. Pollen type D is considered as the most advanced type in the genus. The phylogenetic implications of the results of the present study are also briefly considered.

It is concluded that palynology can greatly assist in the construction of an improved classification of *Oxalis* in southern Africa.

CHAPTER 10
OPSOMMING

’n Palinologiese oorsig van *Oxalis* (Oxalidaceae) in Suider-Afrika

deur

Léanne Laurette Dreyer

Promotor: Prof. Dr. A.E. van Wyk
Departement Plantkunde, Universiteit van Pretoria

Augustus 1996

PHILOSOPHIAE DOCTOR

Die genus *Oxalis* sluit ongeveer 800 spesies in, met diversiteitssentrums in Suid-Amerika sowel as Suider-Afrika. Daar is na raming 210 spesies in Suider-Afrika, met die hoogste spesiediversiteit in die Wes-Kaap. Ten spyte daarvan dat *Oxalis* ’n uiteenlopende en interessante genus is met besliste tuinboukundige potensiaal, is die taksonomie van die Suider-Afrikaanse verteenwoordigers baie verwaarloos. Die betwisbare hersiening deur Salter (1944) is die mees omvattende ondersoek beskikbaar tot op datum. Die hoofdoelstelling van die huidige ondersoek was om die taksonomiese belang van palinologie binne die Suider-Afrikaanse *Oxalis*-taxons te bepaal. LM-, SEM- en TEM-tegnieke is hiervoor gebruik. Voorlopige AFM-resultate is ook ge-evalueer.

Oxalis is palinologies uiteenlopend, en dit het gelei tot die identifikasie van vier hoofstuifmeeltipes (A, B, C, & D) en 19 subtipes binne die genus. Fyner kenmerke van die eksienstruktuur en -skulptuur was betekenisvol vir hierdie afbakening. Sleutels tot die stuifmeeltipes en subtipes, sowel as volle LM-, SEM- en TEM-beskrywings van elke tipe word voorsien. Die palinologiese klassifikasie wat hier voorgestel word, is vergelyk met die klassifikasie van Salter (1944). Daar is gevind dat die stuifmeelgroepe met sommige van die seksies in Salter se klassifikasie ooreenstem, maar dat palinologie die behoefte aan ’n taksonomiese hersiening van ander seksies bevestig. Die verskillende stuifmeeltipes is van

belang op verskillende vlakke binne die taksonomiese hiërargie van die genus. Stuifmeeltipes A en D is van belang op seksie- en infraspesifieke-vlak, terwyl stuifmeeltipe B betekenisvol is op spesievlak. Stuifmeeltipe C is uiteenlopend en is op verskeie vlakke van belang.

'n Evolusionêre bespreking van morfologiese variasie, biogeografie, spesiasie en bestuiwing het gelei tot 'n meer omvattende bespreking van die evolusie van stuifmeeltipes binne die genus. 'n Hipotese word voorgestel waarvolgens stuifmeeltipe C as die voorouerlike tipe beskou word, en stuifmeeltipes A, B en D as afgeleide vorms. Stuifmeeltipe D word as die mees gevorderde tipe binne die genus beskou. Die filogenetiese implikasies van die resultate van hierdie studie is ook vlugtig oorweeg.

Die afleiding is gemaak dat palinologie grootliks kan bydra tot die daarstelling van 'n verbeterde klassifikasie van *Oxalis* in Suider-Afrika.

CHAPTER 11
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CHAPTER 12

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I would like to thank my parents for their help, love and support in every way possible.

CHAPTER 13

CURRICULUM VITAE

Léanne Laurette Dreyer was born in Pretoria on 2 January 1967. At the age of two her family moved to the Western Cape, where she spent the next 23 years of her life. She matriculated from Durbanville High School in 1984 and registered at the University of Stellenbosch at the beginning of the following year. In 1987 she obtained a B.Sc. degree majoring in Botany and Genetics. This was followed by a B.Sc. (Honours) degree in 1988 and a M.Sc. (Taxonomy) degree in 1990, both awarded cum laude. These degrees were obtained for studies on the genus *Pelargonium* (Geraniaceae). During the three years of post-graduate study, she was employed by the University of Stellenbosch as a student assistant.

In 1991 she took up a position as Scientific Officer at the National Botanic Institute (Pretoria), where her duties included curation, identification and database management of numerous plant families. During this time she became interested in the Oxalidaceae, and scientific research in this family commenced. She spent the period August 1993 to July 1994 at the Royal Botanic Garden (Kew), where she acted as South African botanical liaison officer. In February 1995 she was promoted to the position of Scientist within the NBI.

Her research in the Geraniaceae and Oxalidaceae has resulted in 10 presentations at congresses and eight publications in national and international journals.

APPENDIX

ATOMIC FORCE MICROSCOPY AND NUMERICAL ANALYSIS: PROVISIONAL RESULTS

Atomic Force Microscopy (AFM) is a promising new technique by which the surface properties of materials can be studied at the atomic to micron level. The operation of these microscopes are schematically illustrated in Figure 1. Basically the sample surface is probed with a sharp tip, a couple of microns long and often less than 100Å in diameter. The tip is located at the free end of a 100—200 μm long cantilever. Forces between the tip and the sample surface cause the cantilever to bend or deflect. Although various forces are at play, interatomic Van der Waals forces are the most significant. A detector measures these deflections as the tip is scanned over the sample. The measured cantilever deflections allow a computer to generate a map of the surface topography. There are two modes of scanning: contact mode in which the AFM tip physically makes contact with the sample and non-contact mode in which a tip-to-sample distance of 50—100Å is maintained. Non-contact mode proved more successful in the analysis of pollen material.

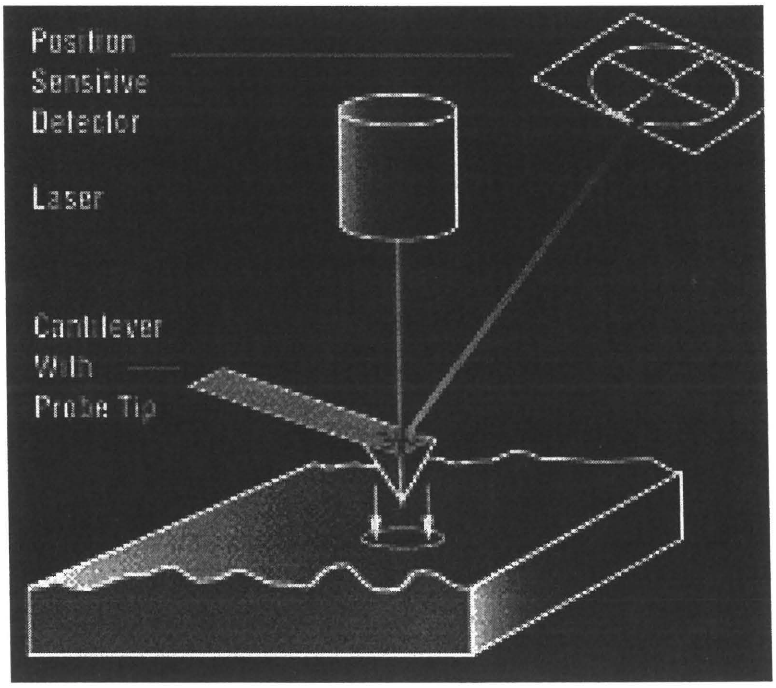

Figure 1. Schematic presentation explaining the operation of an AFM (courtesy Digital Instruments, Santa Barbara, CA).

Additional to the results presented in the present study, preliminary AFM analyses of all the proposed pollen types have been undertaken by Prof. Demanet[1] and his team at the University of the Transkei. These results proved to be very promising and merit further study. To enable comparison of the different techniques, they only investigated material of which LM, SEM and TEM results were obtained in the present study. Three dimensional images of the AFM analyses are supplied in Figures 2—8. In addition to the visual comparison of AFM and SEM/TEM results, a numerical analysis was undertaken using the computer software package Statistica. To this end, 12 SEM/TEM characters used in the present study were selected, coded (Table 1) and plotted in a tree cluster diagram (Figure 9). No weighting was placed on any of the characters. Similarly ten useful AFM characters were identified and measurements were taken. Up to 16 measurements per character of each pollen type were tabulated and subjected to discriminant function analysis (Table 2). Post-hoc analyses showed a success rate of 99% in the grouping of the pollen types based on the deducted functions. The Mahalanobis distance between group centroids was then calculated and used to construct a tree cluster diagram of this data (Figures 10—14). Although additional AFM analyses are needed to substantiate these results, the two trees are remarkably similar.

It is unlikely that AFM analyses could ever replace conventional SEM and TEM techniques, but it could be very useful as an supplementary study method. Advantages of the AFM include:

- The ability to obtain very accurate measurements of surface areas
- The ability to obtain very accurate measurements of the dimensions of structures
- The ability to record fine sculptural detail not always visible on SEM micrographs.
- The relative ease with which a lot of data can be obtained in a very limited time.
- The relatively uncomplicated sample preparation

There are, however, problems which should be kept in mind when conducting an AFM study:

- The range of movement is limited due to the constricted range of the scanner. Measurements within very deep lumina are less accurate than those on the outer surface of the grain. The AFM tends to round the edges of lumina, making them appear rounder and shallower than they really are.
- It is sometimes difficult to determine which part of a pollen grain is being scanned. This is dangerous, as AFM results obtained in the apocolpial region could differ significantly from those taken in a mesocolpial area of the same grain.
- Measurements taken from an oblique AFM scan could be distorted and inaccurate.

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[1] Prof. C.H. Demanet, Department of Physics, University of the Transkei, Private Bag X1, Umtata, 5100, South Africa.

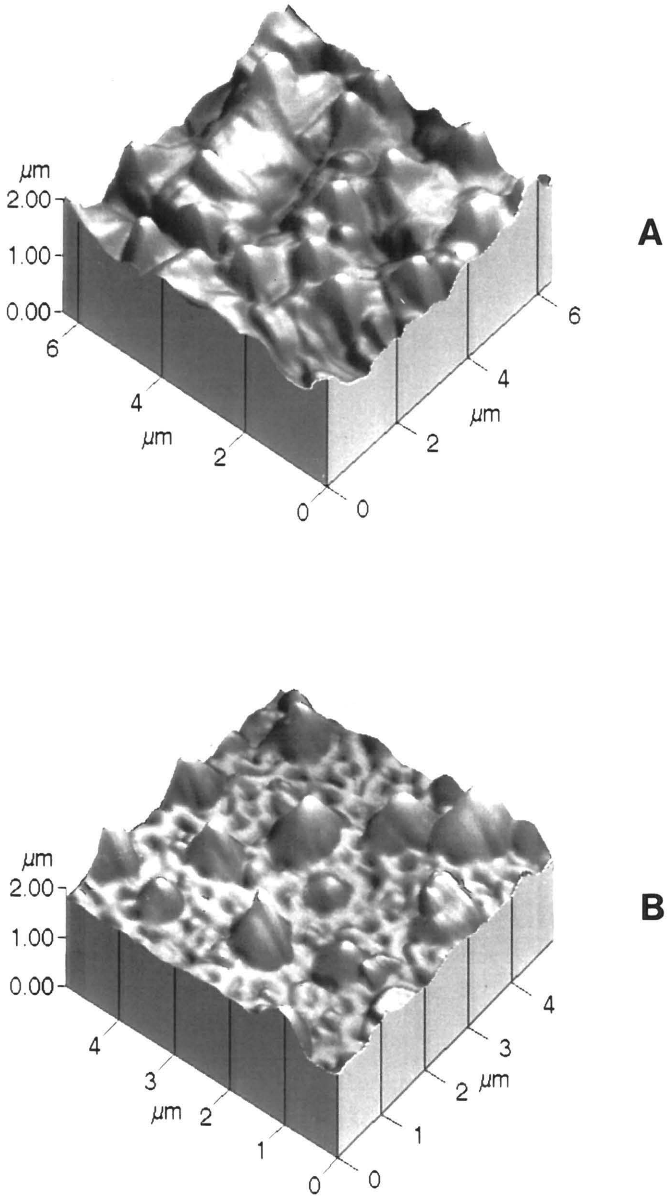

Figure 2 A, B. Three dimensional AFM images of *Oxalis* pollen. (A) *O. eckloniana* var. *sonderi* [114.1], pollen type A. (B) *O. fibrosa* [104.2], pollen type B.

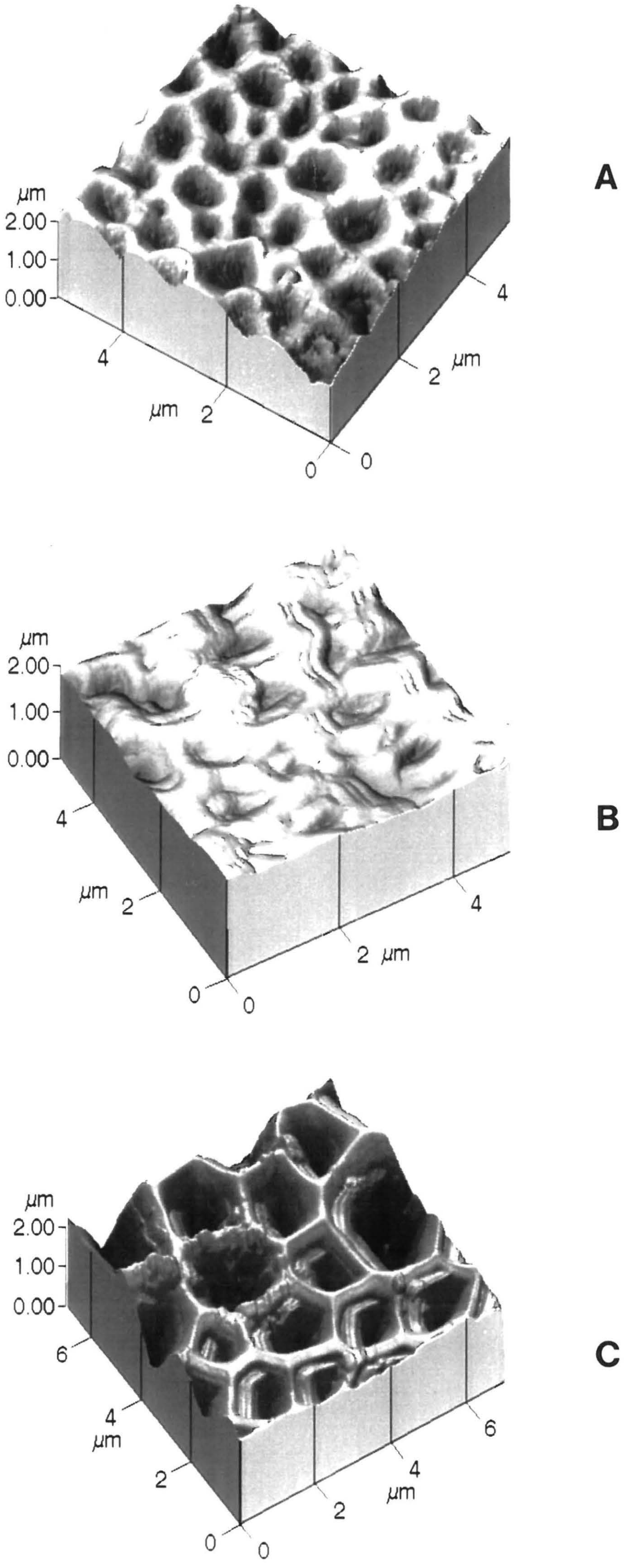

Figure 3 A—C. Three dimensional AFM images of *Oxalis* pollen. (A) *O. davyana* [25.1], pollen subtype C1. (B) *O. stellata* var. *montaguensis* [21.1], pollen subtype C2. (C) *O. obtusa* var. *obtusa* [41.1], pollen subtype C3.

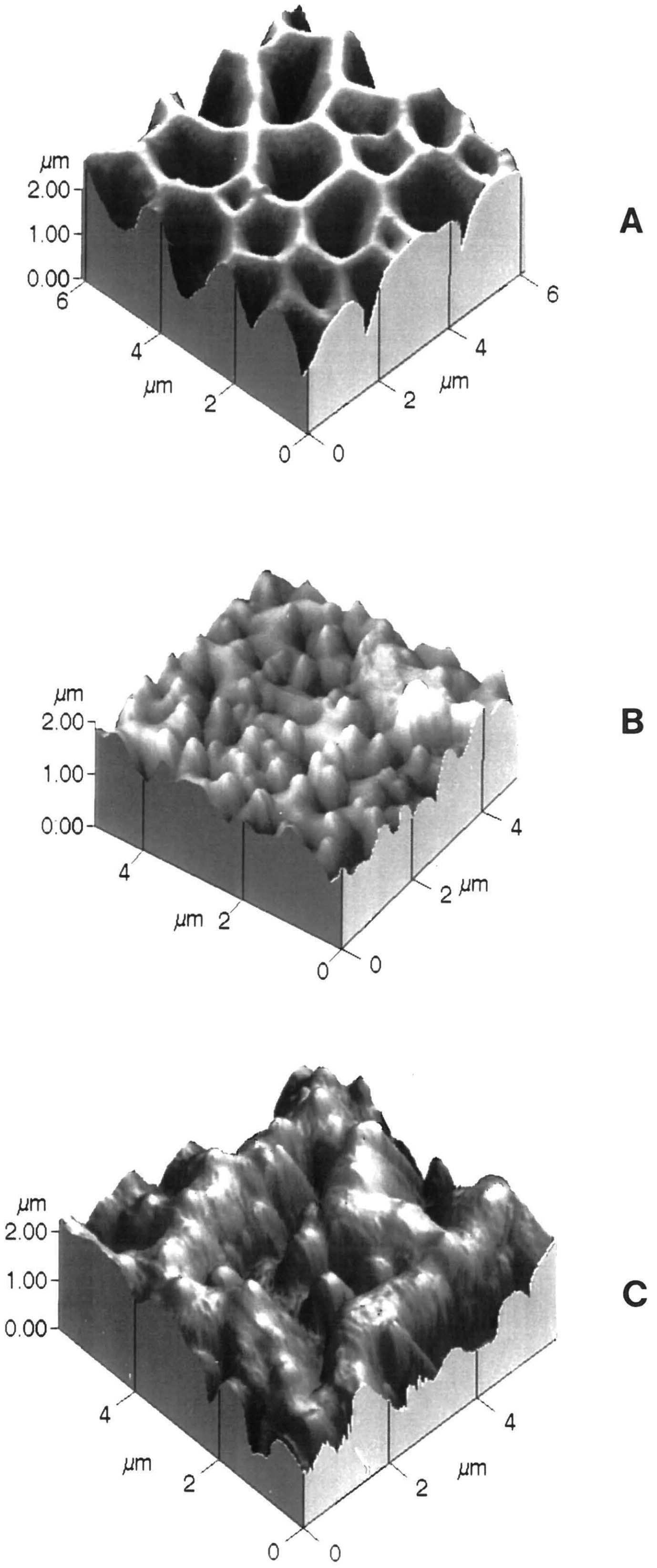

Figure 4 A—C. Three dimensional AFM images of *Oxalis* pollen. (A) *O. inaequalis* [91.1], pollen subtype C4. (B) *O. levis* [235.1], pollen subtype C5. (C) *O. henrici* [261.1], pollen subtype C6.

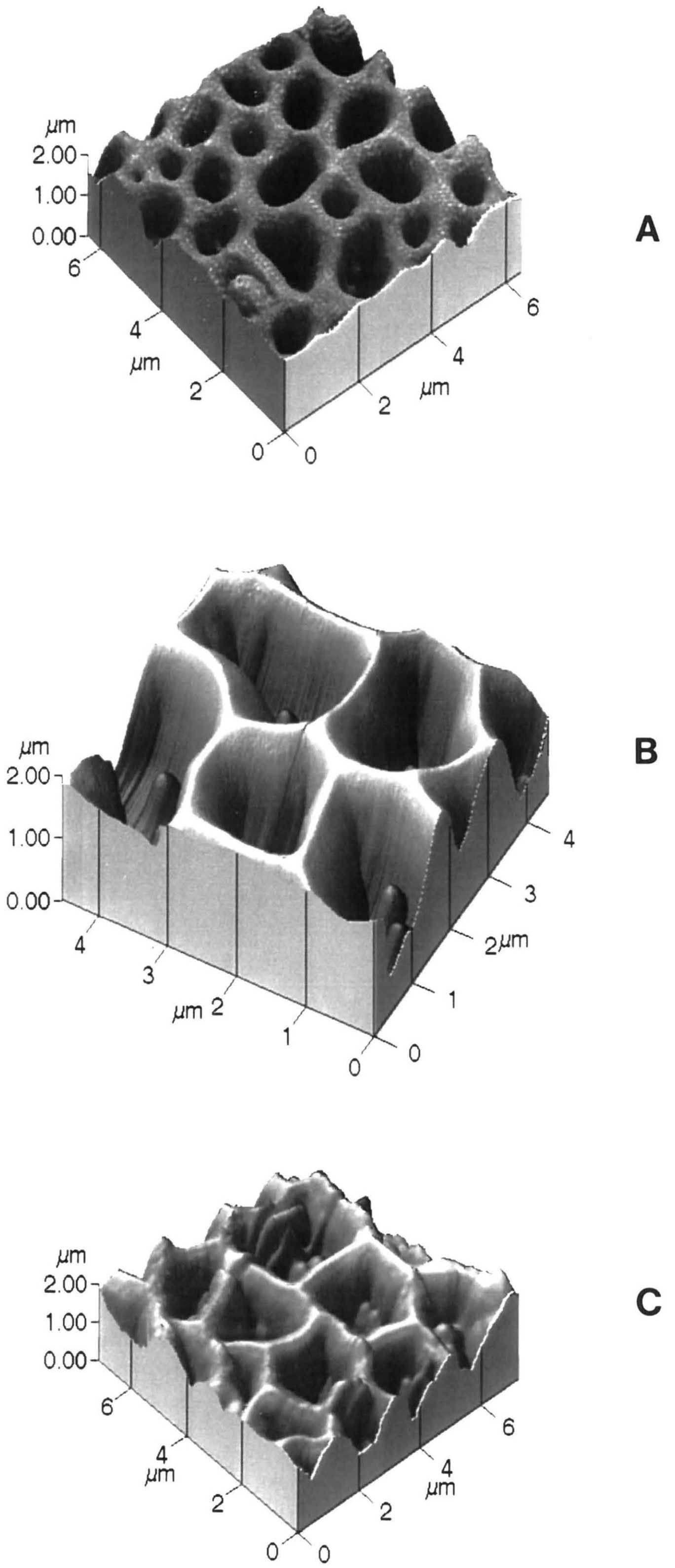

Figure 5 A—C. Three dimensional AFM images of *Oxalis* pollen. (A) *O. suteroides* var. *latituba* [256.1], pollen subtype C7. (B) *O. campylorrhiza* [127.1], pollen subtype C8. (C) *O. deserticola* [253.1], pollen subtype C9.

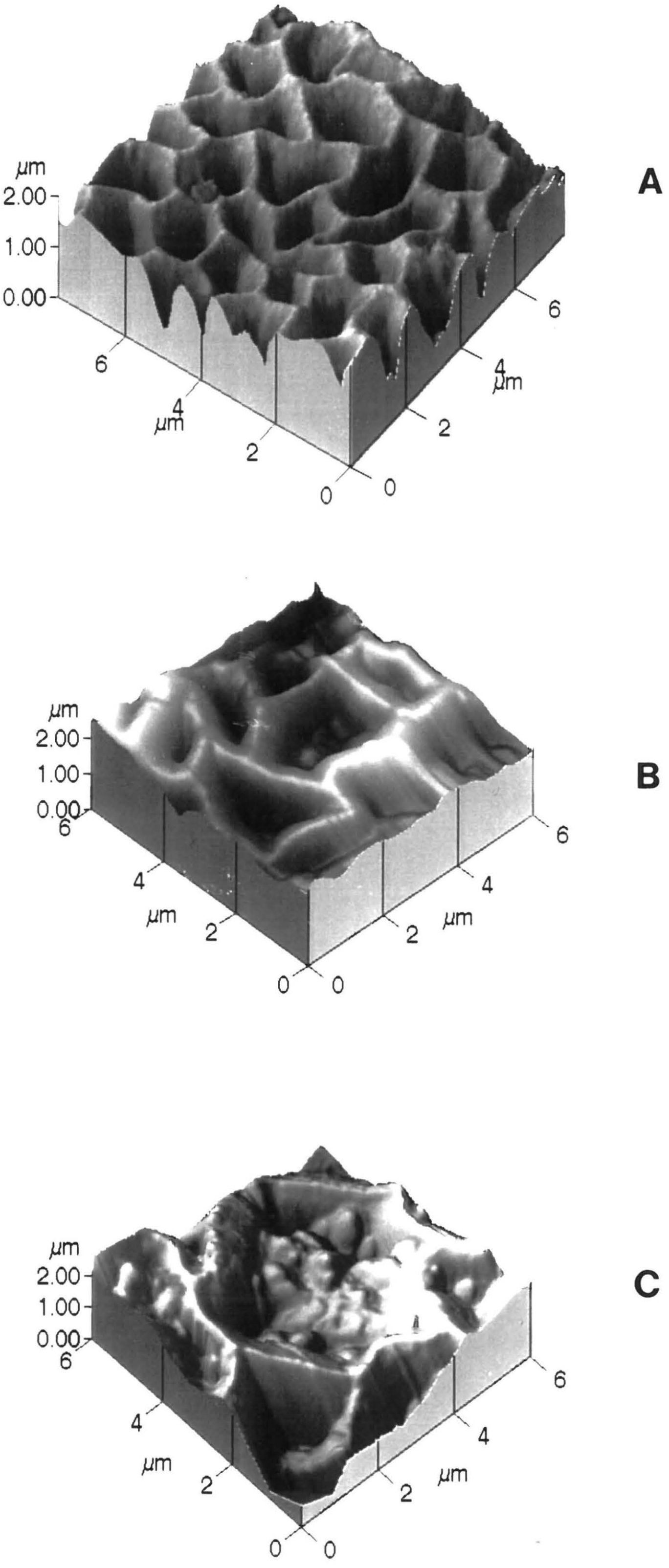

Figure 6 A—C. Three dimensional AFM images of *Oxalis* pollen. (A) *O. fabaefolia* [145.1], pollen subtype C10. (B) *O. sonderiana* var. *alba* [132.1], pollen subtype C11. (C) *O. tenuipes* var. *tenuipes* [209.1], pollen subtype C12.

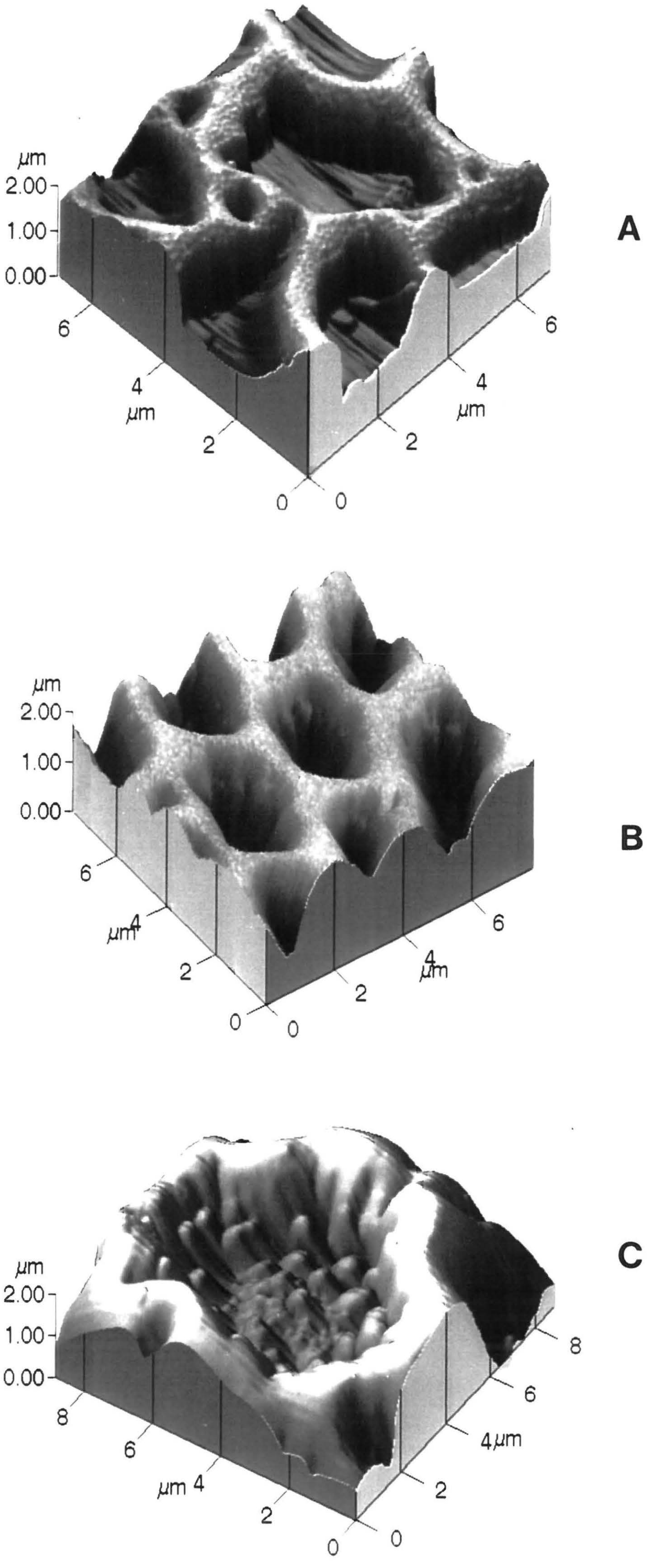

Figure 7 A—C. Three dimensional AFM images of *Oxalis* pollen. (A) *O. droseroides* [254.1], pollen subtype C13. (B) *O. phloxidiflora* [211.1], pollen subtype C14. (C) *O. giftbergensis* [185.1], pollen subtype C15.

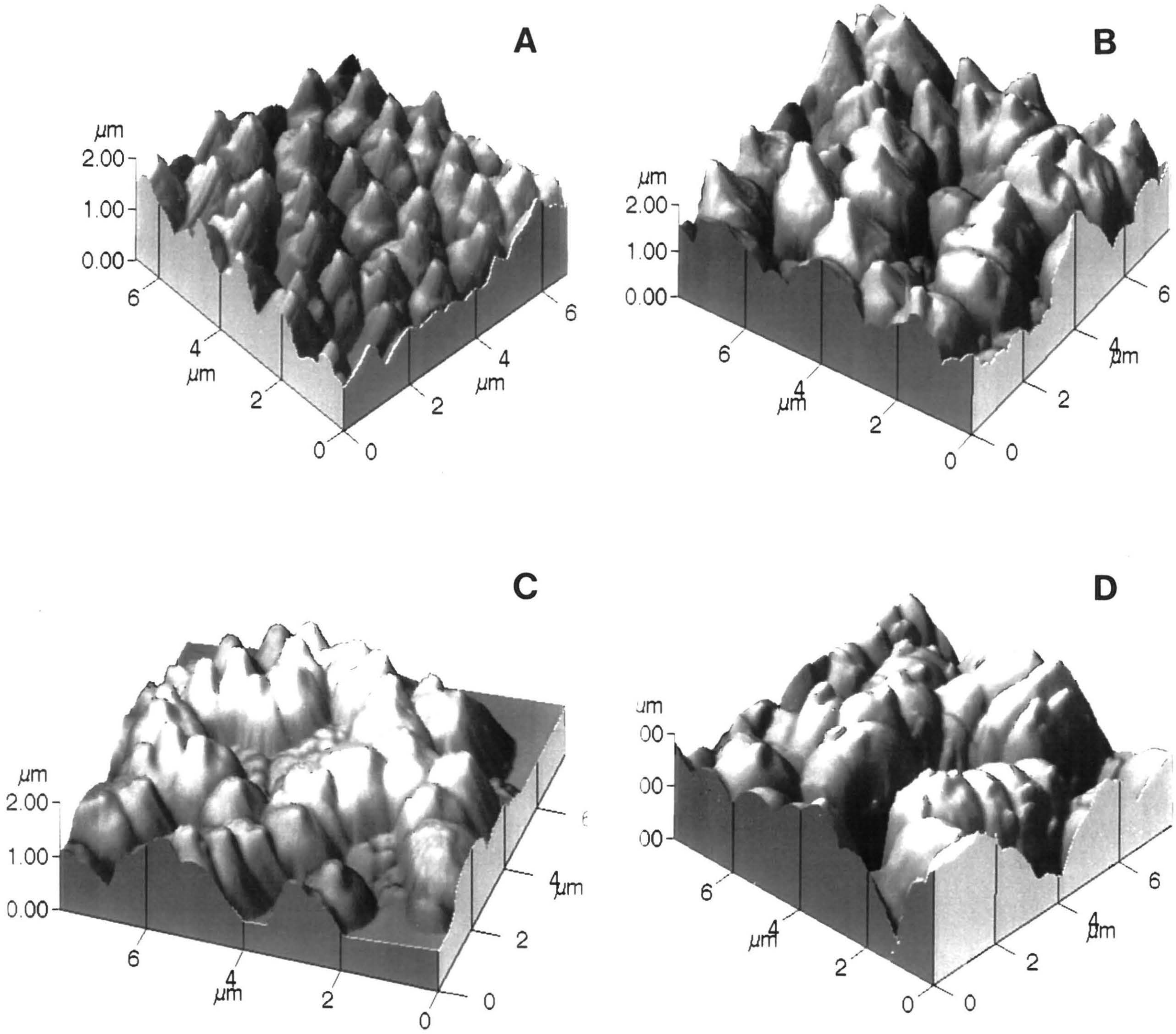

Figure 8 A—D. Three dimensional AFM images of *Oxalis* pollen. (A) *O. tenella* [138.1], pollen subtype D1. (B) *O. petiolulata* [141.1], pollen subtype D2. (C) *O. linearis* [198.1], pollen subtype D3. (D) *O. hirta* var. *intermedia* [174.1], pollen subtype D4.

Table 1 Data set of characters used to construct a tree diagram based on SEM/TEM results. See end of table for an explanation of symbols.

PT	SS	LT	LD	B	T	A	AR	AS	AD	BP	MP	MC
A	spinule	angular	—	present	tectate	pantocolpate	absent	—	—	scattered	absent	simple
B	spine	angular	—	present	tectate	tricolpate	absent	—	—	scattered	absent	simple
C1	—	round	1.00	absent	semitectate	tricolpate	absent	—	—	—	absent	simple
C2	—	oblong	1.00	absent	semitectate	tricolpate	absent	—	—	—	absent	simple
C3	—	round	1.50	absent	semitectate	tricolpate	absent	—	—	—	absent	simple
C4	—	angular	1.00	absent	semitectate	tricolpate	absent	—	—	—	absent	simple
C5	spinule	angular	2.50	absent	semitectate	tricolpate	absent	—	—	—	absent	simple
C6	spinule	angular	2.83	present	semitectate	tricolpate	absent	—	—	scattered	absent	simple
C7	—	oblong	1.00	present	semitectate	tricolpate	absent	—	—	scattered	absent	simple
C8	—	angular	1.50	present	semitectate	tricolpate	absent	—	—	scattered	absent	simple
C9	—	angular	2.50	present	semitectate	tricolpate	absent	—	—	scattered	absent	simple
C10	—	angular	1.50	present	semitectate	tricolpate	absent	—	—	along muri	absent	complex
C11	—	angular	2.50	present	semitectate	tricolpate	absent	—	—	along muri	absent	complex
C12	—	angular	3.50	present	semitectate	tricolpate	absent	—	—	along muri	absent	complex
C13	—	angular	2.50	present	semitectate	tricolpate	absent	—	—	along muri	present	complex
C14	—	angular	3.50	present	semitectate	tricolpate	absent	—	—	along muri	present	complex
C15	—	angular	5.00	present	semitectate	tricolpate	absent	—	—	along muri	present	complex
D1	areola	—	—	—	tectate	pantocolpate	present	club-shaped	2.00	—	absent	reduced
D2	areola	—	—	—	tectate	tricolpate	present	angular	1.80	—	absent	reduced
D3	areola	—	—	—	tectate	tricolpate	present	rounded	0.89	—	absent	reduced
D4	areola	—	—	—	tectate	pantocolpate	present	rectangular	2.27	—	absent	reduced

PT = Pollen type; SS = Nature of supratectal structures; LT = Lumina type; LD = Lumina diameter; B= Bacules present of absent; T = Nature of the tectum; A = Number of apertures; A = Presence of absence of areolae; AS = Areola structure; AR = Areola diameter; BP = Bacula position; MP = Presence or absence of muri perforations; MC = Complexity of the muri

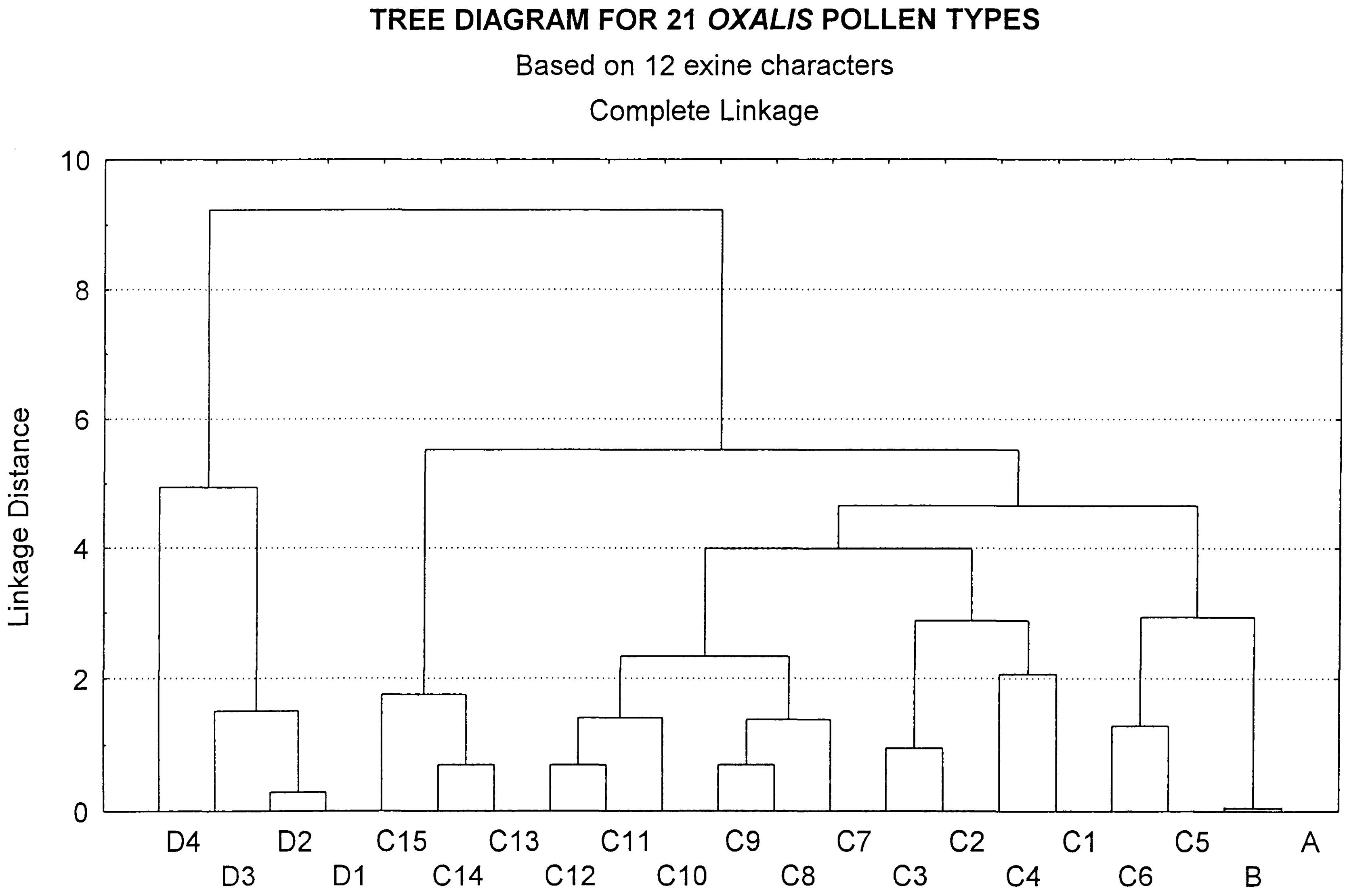

Figure 9 Tree diagram for 21 *Oxalis* pollen types based on SEM/TEM results obtained in the present study.

Table 2 Summary of the discriminant function data set of 10 pollen characters studied in the AFM analysis. See end of table for an explanation of characters. Characters are listed in deminishing order of their contribution to the separation between sentroids of pollen types.

STAT. DISCRIM. ANALYSIS	Discriminant Function Analysis Summary (trial.sta) Step 10, N of vars in model: 10; Grouping: GRP (21 grps) Wilks' Lambda: .00000 approx. F (200,993)=278.00 p<0.0000					
N=138	Wilks' Lambda	Partial Lambda	F-remove 20,108	p-level	Toler.	1-Toler. (R-Sqr.)
BACPOS	.000000	.000003	1633572.	0.000000	.894457	.105543
AREOLA	.000000	.000403	13393.	0.000000	.863045	.136955
WMURI	.000000	.078832	63.	0.000000	.877444	.122556
SUPRAH	.000000	.140834	33.	0.000000	.910285	.089715
HMURI	.000000	.140682	33.	0.000000	.855183	.144817
SUPRADIA	.000000	.312793	12.	.000000	.954952	.045048
NEWAREA	.000000	.425720	7.	.000000	.869901	.130099
BACDIA	.000000	.604793	4.	.000012	.955665	.044335
NIPPLE	.000000	.619031	3.	.000030	.925778	.074222
ROUNDNES	.000000	.619103	3.	.000031	.944690	.055310

BACPOS = Position of bacula; AREOLA = Presence or absence of areola; WMURI = Muri width; SUPAH = Height of supratectal structures; HMURI = Muri height; SUPRADIA = Radius of supratectal structures; NEWAREA = Cumulative area of intraluminary spaces; BACDIA = Bacula diameter; NIPPLE = Height of spine on areola; ROUNDNESS = Quantified lumina shape

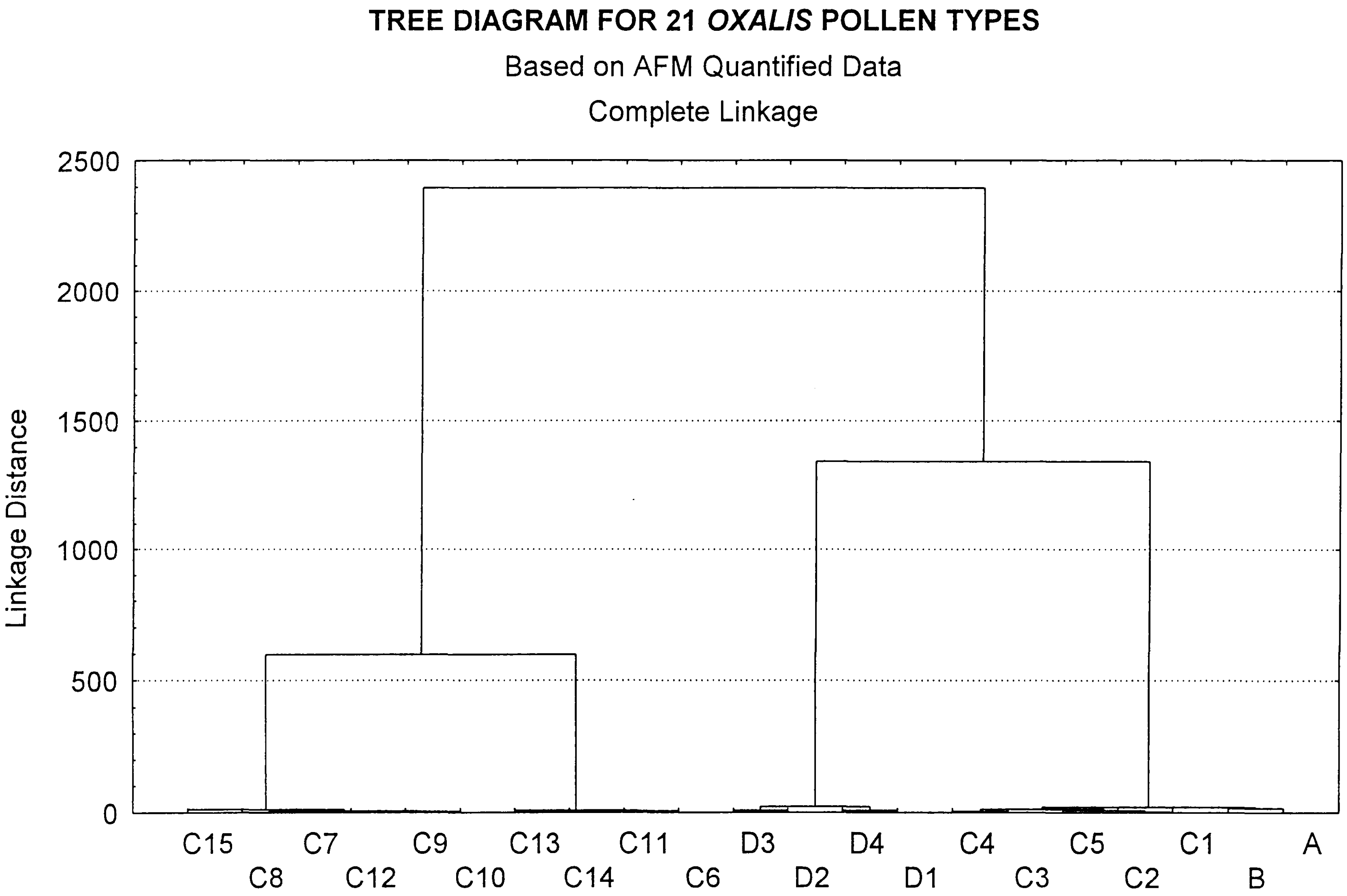

Figure 10 Tree diagram for 21 *Oxalis* pollen types based on quantified AFM data. See Figures 11—14 for details of the main clusters.

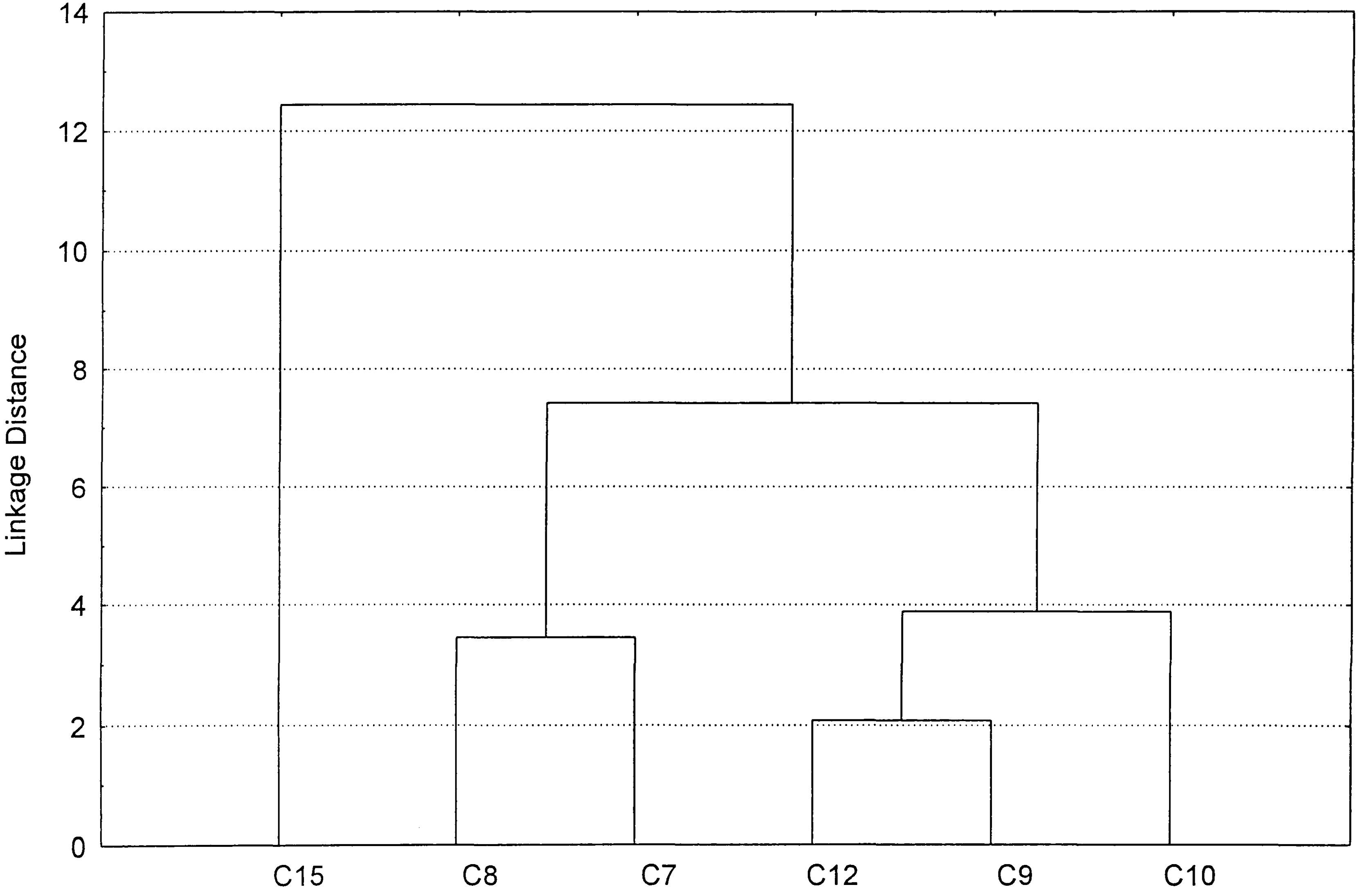

Figure 11 Detailed tree diagram of the first main cluster (pollen subtypes C15, C8, C7, C12, C9 & C10) of the tree depicted in Figure 10.

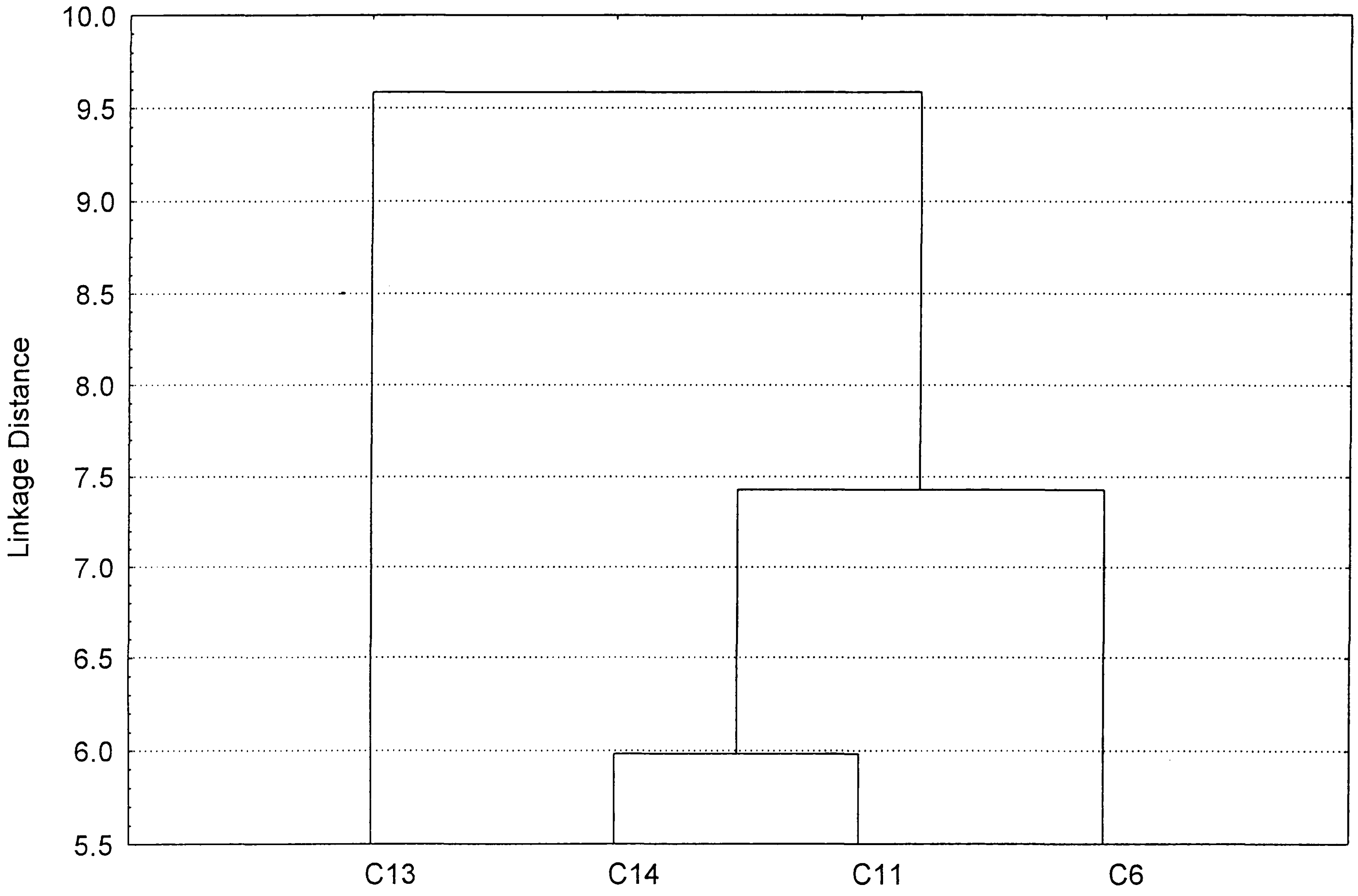

Figure 12 Detailed tree diagram of the second main cluster (pollen subtypes C13, C14, C11 & C6) of the tree depicted in Figure 10.

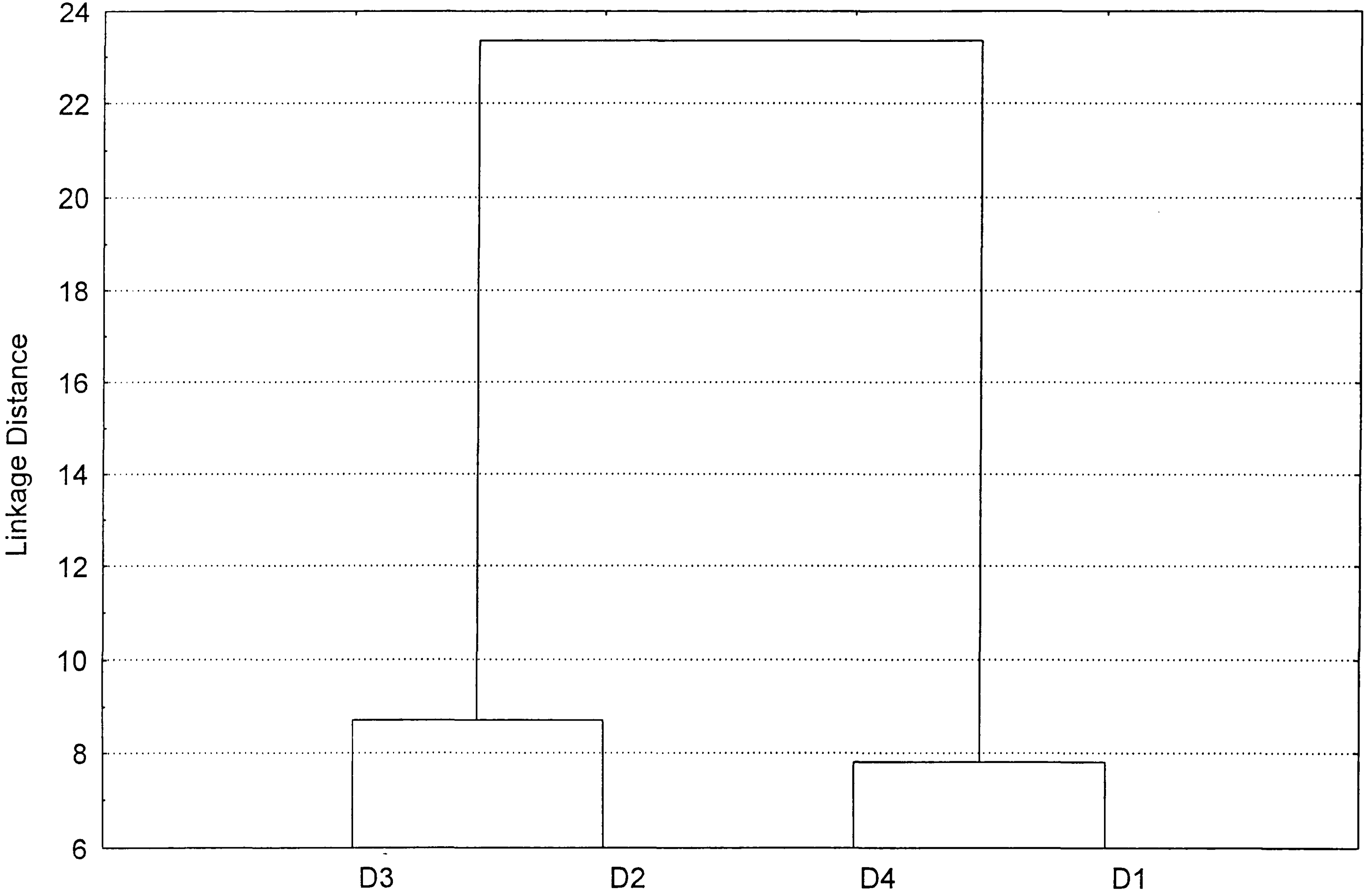

Figure 13 Detailed tree diagram of the third main cluster (pollen subtypes D1, D2, D3 & D4)) of the tree depicted in Figure 10.

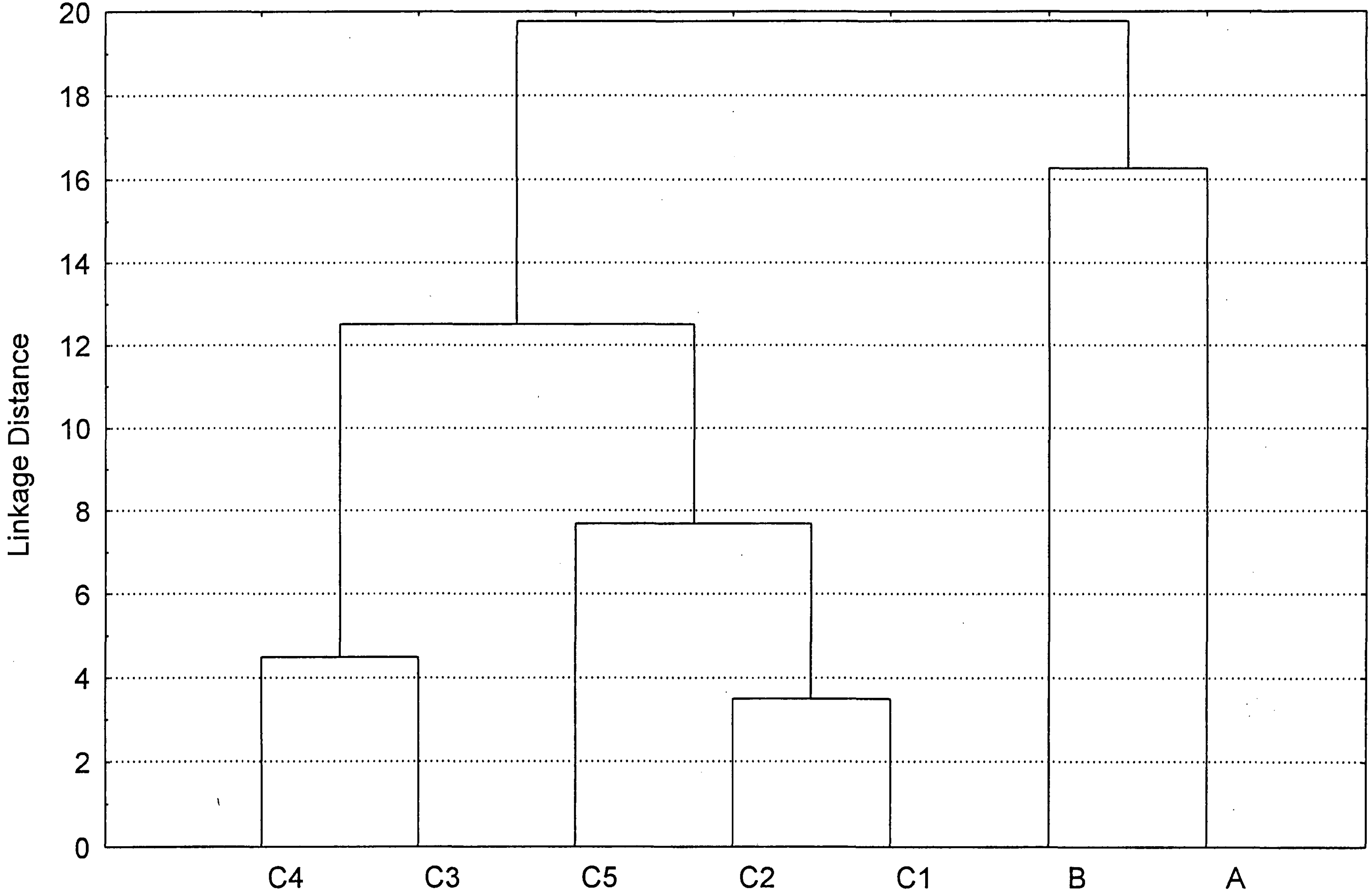

Figure 14 Detailed tree diagram of the fourth main cluster (pollen subtypes C4, C3, C5, C2, C1, A & B) of the tree depicted in Figure 10.