SINGH, YASHICA

CONTRIBUTIONS TO THE SYSTEMATICS OF THE GENUS *ZANTEDESCHIA* SPRENG (ARACEAE)

MSc UP 1996

CONTRIBUTIONS
TO THE
SYSTEMATICS
OF THE
GENUS *ZANTEDESCHIA* SPRENG. (ARACEAE)

by

YASHICA SINGH

Submitted in partial fulfilment
of the requirements for the degree of
MAGISTER SCIENTIAE
in the
Faculty of Biological & Agricultural Science
Department of Botany
UNIVERSITY OF PRETORIA
PRETORIA

Supervisor : Prof. Dr. A.E. van Wyk
Co-Supervisor : Prof. Dr. H. Baijnath (UDW)

July 1996

There is no monotony in flowers,
they are ever unfolding new charms,
developing new forms
and revealing new features
of interest and beauty
to those who love them.

John Wright, c. 1890

ABSTRACT

Singh, Y. Contributions to the systematics of the genus *Zantedeschia* Spreng. (Araceae). Department of Botany, University of Pretoria. Unpublished thesis, 169 pages, 19 tables and 75 figures. July 1996. Keywords: anatomy, descriptions, key, morphology, phytogeography, pollination biology, taxonomy.

Zantedeschia, a genus of eight species and two subspecies, is endemic to Africa, south of the equator. The genus is popular among plant lovers and horticulturalists world-wide, largely through a multitude of hybrids cultivated as garden and pot plants, and marketed as cut flowers. In this study the taxonomic usefulness of morphology, anatomy, pollination biology and phytogeography is surveyed. Variation in tuber form, lamina shape, spathe shape and colour, staminodes and berry colour were found to be particularly important in separating species. Anatomy, on the other hand, provided few attributes for species differentiation. Post pollination changes are distinct in *Z. aethiopica*. Patterns of distribution also proved to be useful in confirming the identity of taxa. Based on morphology and distribution pattern, *Z. albomaculata* subsp. *valida* is raised to species level as *Z. valida*. Finally, a taxonomic treatment for the *Flora of southern Africa* is included.

Yashica Singh, Natal Herbarium, National Botanical Institute, Botanic Gardens Road, DURBAN, 4001.

TABLE OF CONTENTS

Chapter 2 Economic importance

Chapter 3 Nomenclatural history

Chapter 4 Vegetative morphology

Leaves

Chapter 5 Vegetative anatomy

Internal anatomy

Chapter 6 Morphology of floral and fruiting structures

Floral structures

Fruiting structures

Taxonomic implications

Chapter 7 Pollination biology

Floral reward/deceit mimicry

Chapter 8 Phytogeography

Geographical distribution

Chapter 9 Discussion

APPENDICES
Publications emanating from this study

INDEX TO SPECIES NAMES

Accepted names are in **bold**; synonyms are in *italics*

CHAPTER 1

INTRODUCTION

The monocot family Araceae Juss., commonly referred to as aroids, is a large family of the order Arales Lindley. It comprises more than 2000 species (Bogner 1987; Mabberley 1987; Heywood 1993) grouped in 107 genera, and these in turn are arranged in nine subfamilies (Bogner & Nicolson 1991).

The Araceae is distributed world-wide with more than 90% being tropical. There are only a few temperate species that tend to inhabit shady places under trees or shrubs. Most aroids are perennial herbs growing on the forest floor, or subshrubby climbers on forest trees. Rarely are they free floating aquatics, e.g. *Pistia stratiotes* L. Generally, aroids favour warm and humid conditions, with only a few species adapted to arid conditions. During the dry season, these plants may survive as dormant rhizomes as in *Stylochaeton* Lepr. or tubers as in *Zantedeschia* Spreng.

Aroids display great diversity in their morphology [see detailed discussion by Bogner (1987)]. Despite this morphological diversity, the family forms a distinctive and coherent group, easily recognised by its inconspicuous flowers crowded on an unbranched finger-like stalk, called a spadix. The spadix is either subtended by, or sometimes enclosed within, a prominent bract-like structure, the spathe, which is often brightly coloured.

In southern Africa, the family is poorly represented by five varied genera (Singh *et al.* 1995, Appendix 1). These are listed in Table 1.1. Subfamily Philodendroideae comprises

Table 1.1 Summary of southern African Araceae

Genus	Number of species		Subfamily	Tribe
	Total	southern Africa		
Amorphophallus Blume ex Decne.	90	1	Aroideae	Thomsonieae
Gonatopus Hook.f. ex Engl.	5	2	Lasioideae	Zamioculcadeae
Stylochaeton Lepr.	15	1	Aroideae	Stylochaetoneae
Zamioculcas Schott	1	1	Lasioideae	Zamioculcadeae
Zantedeschia Spreng.	8	8	Philodendroideae	Zantedeschieae

18 genera of which *Zantedeschia* and the two monotypic genera *Anubias* Schott and *Typhonodorum* Schott occur in Africa. *Zantedeschia*, although a relatively small genus of 8 species and 2 subspecies, is the largest genus among the southern African aroids. Species recognised in the present study are listed, together with their synonyms, in Table 1.2.

Zantedeschia is still popularly, though confusingly, known as Arum Lilies or Calla Lilies; both *Arum* L. and *Calla* L. being distinct genera in the Araceae. The reason for the analogue *Arum* is the similarity in the leaves, and that of *Calla* is that *Zantedeschia* was initially classified as *Calla* by Linnaeus. As currently defined, *Arum* and *Calla* are restricted to the Northern Hemisphere. The popularity of *Zantedeschia* as a cut flower, pot plant and garden ornamental has reached its peak in present times and a multitude of hybrids and cultivars are available. The export of these plants constitutes a significant part of the horticultural revenue in some countries, notably New Zealand and the United States of America. A short account on the horticultural value of *Zantedeschia* together with other uses of the genus is presented in Chapter 2.

Table 1.2 Members of *Zantedeschia* recognised in this study and their synonyms

Species	Synonyms
Z. aethiopica (L.) Spreng.	*Arodes aethiopicum* (L.) Kuntze *Aroides aethiopicum* (L.) Heist. ex Fabric. *Arum aethiopicum* Herm. *Arum africanum* Herm. *Calla aethiopica* L. *Colocasia aethiopica* (L.) Link *Otosma aethiopica* (L.) Rafin. *Richardia africana* Kunth *Zantedeschia aethiopica* var. *minor* Engl. *Z. aethiopica* var. *umganiensis* Leicht. & Engl.
Z. albomaculata (Hook.) Baill. subsp. *albomaculata*	*Aroides albomaculatum* (Hook.) Kuntze *Arodes hastatum* (Hook.) Kuntze *A. angustilobum* (Schott) Kuntze *Calla oculata* Lindl. *Richardia albomaculata* Hook. *R. hastata* Hook. *R. angustiloba* Schott *R. melanoleuca* Hook. *R. melanoleuca* var. *tropicalis* N.E.Br. *Z. angustiloba* (Schott) Engl. *Z. chloroleuca* Engl. & Gilg. *Z. hastata* (Hook.) Engl. *Z. melanoleuca* (Hook.f.) Engl. *Z. melanoleuca* var. *tropicalis* (N.E.Br.) N.E.Br. ex Engl. *Z. oculata* (Lindl.) Engl. *Z. tropicalis* (N.E.Br.) Letty
Z. albomaculata subsp. *macrocarpa* (Engl.) Letty	*Richardia macrocarpa* (Engl.) Watson *R. angustiloba* sensu N.E.Br. *Z. melanoleuca* var. *concolor* Burtt Davy *Z. macrocarpa* Engl. *Z. oculata* sensu Burtt Davy *Z. angustiloba* sensu Traub
Z. elliotiana (Watson) Engl.	*Calla elliotiana* Watson *Richardia elliotiana* Watson
Z. jucunda Letty	
Z. odorata P.L. Perry	
Z. pentlandii (Watson) Wittm.	*Calla pentlandii* Whyte ex Watson *Richardia pentlandii* Watson *R. Sprengeri* Comes
Z. rehmannii Engl.	*Richardia Lehmannii* Watson *R. rehmannii* (Engl.) N.E.Br.
Z. valida (Letty) Y. Singh	*Z. albomaculata* subsp. *valida* Letty

A survey on the nomenclatural history indicates that the generic name of this aroid has changed several times. The changes in name have been outlined in tabular form in Chapter 3. The basis for the name changes is also briefly explained.

Although, the genus *Zantedeschia* has captured the attention of plant breeders world-wide, it has received little attention from systematists since Cythna Letty's revision in 1973. Letty provided a comprehensive description of six species and three subspecies based exclusively on gross morphology. It is not the intention of this study to repeat these descriptions. Rather, this investigation contributes mainly to the vegetative anatomy of the genus, with the aim of providing additional characters of potential taxonomic value and in so doing, supplements that which is known about gross morphology. By no means, however, is the morphology of the group ignored in this study. The morphology of the vegetative and, reproductive and fruiting structures is presented in Chapters 4 and 6 respectively, with emphasis on those characters of taxonomic significance. It is hoped that these contributions will reflect the range of infrageneric diversity.

Members of the Araceae display a range of strategies to attract pollinators and effect pollination. Features such as spathe colour, presence of a dark-coloured blotch at the base of the spathe interior, provision of food or shelter, production of odour and of heat, may serve to attract insects. In some members such as *Arum*, the pollination system has become specialised to trap the insect within the spathe until pollination is achieved (Richards 1986). In addition to the specialised attraction mechanisms, modes of floral behaviour seem to have a direct influence on pollination biology. For instance, observations on *Z. aethiopica* have revealed that self-pollination is prevented by marked protogyny. The floral biology of *Z. aethiopica* and the other species is addressed in Chapter 7.

In numerous instances, vegetative anatomy has been a powerful tool in separating taxa at species level (Metcalfe & Chalk 1950; Ayensu 1970). The anatomy of *Zantedeschia* has hitherto not been described in detail. Chapter 5 represents the first illustrated account on this aspect, with an assessment of its value to infrageneric relationships. Furthermore, since differences in vegetative anatomy form an essential component in resolving discrepancies in relationships between genera (Nicolson 1960), this data on *Zantedeschia* may be of relevance to the intergeneric classification of the group.

Zantedeschia is confined to southern Africa, including Angola, Malawi, Tanzania, Zimbabwe and Zambia. The patterns of distribution range from species spread throughout the region to those known only from single, restricted localities. The value of distribution patterns in species delimitation is assessed in Chapter 8.

Materials and methods used in this study are detailed in the relevant chapters, namely Chapters 4, 5, 6, 7 and 8. Under Discussion (Chapter 9), the findings of this study are critically elaborated upon in relation to the knowledge that already exists, and to its value in the taxonomy and phylogeny of the genus *Zantedeschia*. The attributes displayed by *Zantedeschia* are discussed in relation to the character states selected by Grayum (1990) for the family.

The relevant conclusions emerging from the discussion are summarised in Chapter 10. In Chapter 11, a key to species based on vegetative and floral characters as well as on distribution pattern, is presented in the taxonomic treatment of the genus for the *Flora of Southern Africa*. Finally, publications emanating from this study are included under Appendices 1—5.

CHAPTER 2

ECONOMIC IMPORTANCE

2.1 Introduction

Zantedeschia is valued principally as an ornamental and to a lesser degree as a source of food and medicine. Cultivars of *Zantedeschia* are sold as handsome ornamentals which generate a high revenue on the international cut-flower market. Its value as a floricultural crop is discussed in greater detail below (2.2). Although the tubers and unspotted leaves of *Z. aethiopica* and *Z. albomaculata* are edible, these arums, unlike other aroids such as *Colocasia antiquorum* Schott var. *esculenta* Schott and *Xanthosoma sagittifolium* (L.) Schott, are not yet cultivated commercially, either for their starchy tubers or leaves. The leaves and petioles of *Z. aethiopica* in particular, are used as a vegetable by the Black and Indian communities in South Africa. Possible reasons for its limited use as a subsistence crop are elaborated upon in this chapter (2.3). Not surprisingly, this striking genus has some uses in folk-medicine. In this study the validity of medicinal claims were not investigated; rather the uses reported by several authors have been summarised (2.4).

2.2 Horticulture

Although native to southern Africa (especially South Africa), *Zantedeschia* has become well known to florists and plant lovers in most parts of the world, particularly America, Europe, Japan, the Netherlands and New Zealand. Foliage and spathe colours vary considerably, depending on the species and cultivar. It is this rich foliage, which is often white spotted, and the colourful ornamental spathes that have drawn the attention of plant breeders world-wide.

Over 40 years ago, Traub (1948) in his Preface to Plant Life 4, predicted "There is now an active group of Aroid Lily hybridisers in America and Australia, and the future development of this group as a garden and pot plant is very promising". Traub's forecast of the horticultural value of this crop is proving to be well-founded. Currently, *Zantedeschia* species and their hybrids are being promoted as cut flowers, pot plants and garden plants throughout the world.

Extensive breeding efforts have led to the establishment of numerous hybrids of varying spathe colours and sizes (see brochure from New Zealand Calla Council, p. 14). New Zealand and the United States are world leaders in the production and marketing of *Zantedeschia* hybrids. Both countries benefit tremendously from the revenue generated from the sale of these plants. Dr K.A. Funnell (pers. comm.) of Massey University in New Zealand, communicated during 1992, "New Zealand exported over NZ$ 3 million (7 million rands) worth of flowers last season and NZ$ 2 million (4.75 million rands) worth of tubers. Over the last five years the export revenue generated from *Zantedeschia* has been growing at 60% per annum". According to Muller's (1993) report, in the 1992/93 season (October to April), New Zealand exported arums to 27 countries. The five major markets (accounting for 95% of the exports), in decreasing order of quantities imported, are Japan, Germany, Switzerland, The Netherlands and the USA. The high volume of export of these plants has resulted in a rapid growing industry in New Zealand. Apart from striving for high revenue from the export of *Zantedeschia*, much horticultural research is being undertaken by Funnell and co-workers at Massey University, Palmerston North, New Zealand.

Zantedeschia has been grown as a commercial crop in the United States for well over 140 years (Butterfield 1948). Tom Lukens (pers. comm.) of Golden State Bulb Growers indicated the financial value of callas, as these plants are commonly known in the USA, to California. In 1993 the production and marketing of callas as cut flowers, container and garden plants amounted to US$ 3.5 million (12.81 million rands). About a third of this production was exported; between 60% to 70% to The Netherlands and the remainder to the Pacific Rim. In The Netherlands it appears that callas are mainly used as cut flowers, whereas in North America, the primary market is for container plants and secondarily for the home garden. About US$ 5 million (18 million rands) were generated from sale of tubers.

Research conducted over the last decade, focused mainly on determining environmental conditions suitable for the production of the crop. In a recent publication, Corr (1993) reviewed the research of the past, present and future of *Zantedeschia* in the USA. He reported that horticultural research on the genus is currently being conducted at four institutions in the USA, namely Cornell University (New York), University of Georgia (Athens), North Carolina State University and the US Department of Agriculture (Agriculture Research Service).

The percentage sale value of some cut flowers in the former Transvaal, extracted from the annual report (1 March 1993 to 28 February 1994) of Multiflora, the marketing organisation for cut flowers, were as follows: Carnations (14.6), Chrysanthemums (16.0), Roses (13.35), Gladiolus (4.0), Freesias (1.5), Arums (0.00024). Sale of arums is relatively lower than most other cut flowers. In fact, the sale value is negligible when compared with carnations, roses and chrysanthemums.

Currently, there is an informal trade of *Z. aethiopica* cut-flowers at ten for a rand, by street vendors in the Cape. These flowers are sold together with flowers of *Watsonia* Mill. With South Africa's political transformation, all citizens will be able to appreciate the ornamental value of cut flowers and garden plants in the foreseeable future. Such casual sales by vendors may well turn into golden opportunities for money making.

Statistics on the sale of South African cut flowers to overseas countries are extremely difficult to obtain. Two possibilities exist in this regard. Firstly, it is probable that overseas countries applied sanctions to South Africa's cut flower industry and therefore did not support it in the past. Alternatively, large exports to overseas were kept secret, due to fear of sanctions being imposed. There is no doubt that with the changing socio-political climate in South Africa, the cut flower industry is bound to flourish internationally.

The fact that many millions of dollars are being spent on research pertaining to the production of *Zantedeschia* as a commercial crop, confirms its worthiness as an aesthetic ornamental. This project identifies all authentic species and highlights the variation among plants within natural populations. Such variation will be of particular interest to plant breeders who are always eager to introduce new genetic forms or species into their breeding programmes.

2.3 Food

Tubers and unspotted leaves of *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata* are known to be edible (Letty 1962; Fox & Young 1982); this may well be the case for the genus as a whole. The leaves of *Z. aethiopica* in particular, are cooked as a pot herb by the Black and Indian communities in South Africa. Blacks boil the leaves before braising them in oil with onions and chillies. The cooked herb is then eaten with mealie meal porridge. Alternatively, mealie meal is added to the boiling herbs and cooked until converted into a thick paste. The herb adds flavour to the plainer porridge. Indians braise the cut leaves with onions and chillies. Tamarind (*Tamarindus indica* L.) is soaked in water and the juice is then added to the herb. Both boiling and tamarind tend to effectively break down the raphides of calcium oxalate in the leaves. If not properly cooked, the herb causes a burning sensation in the mouth and throat. This is due to the raphides which cause minute lesions in the mouth (Hegnauer 1987).. The needle-like raphides are present as bundles in all organs of the plant and are common in the family. These crystals render the plant unfit for food in the raw state.

Despite its edibility, leaves of *Z. aethiopica* are not a regular dietary constituent of man. Rather, it appears that other herbs such as *Amaranthus* spp. and *Bidens* spp. are preferred by the Blacks. *Z. aethiopica* is used mainly when other herbs are not available (so-called famine food). Fox & Young (1982) reported that leaves of *Z. albomaculata* subsp. *albomaculata* are utilised as a vegetable. They also state that the leaves appear to be less palatable and less wholesome than those of *Z. aethiopica.* Spotted leaves and leaves of the yellow-flowered species are apparently not utilised for food. The reason for this is still unknown. It may be attributed to superstition, non-palatability or to the presence of irritating raphides. The presence of raphides may be of relevance to anti-herbivory. Furthermore, the presence of spots may discourage animals and insects. There is no published data on the functional role of raphides or spots in this family.

Although a good source of starch, tubers of *Zantedeschia* are not frequently used as food. The tubers of *Z. aethiopica* and *Z. albomaculata* are reported to be eaten by certain Blacks in southern Africa (Letty 1962). Consumption of the raw tuber causes irritation of the mouth. Gelfand *et al.* (1985) list *Z. albomaculata* subsp. *albomaculata* as a poison plant, noting that if a portion of the tuber is chewed, it causes a stinging sensation and swelling of the tongue and throat which lasts for about four hours. This may explain why *Zantedeschia* has not been cultivated as a food crop as is *Colocasia antiquorum* var. *esculenta* (madumbe, taro) and *Xanthosoma sagittifolium* (cocoyams). However, in the early days the tubers of *Z. aethiopica* were boiled and fed to pigs (Jackson 1986). Hence, the allusion to the vernacular name “pig-lily”.

Although *Zantedeschia* has not yet been developed as a commercial food crop, the edible species are worth noting as an inexpensive food source. Since *Z. aethiopica* grows in marshy ground along rivers or streams and in vleis, it lends itself to be grown in areas of low rainfall where water is available by irrigation. Hence there is great potential for adapting the plant to a broader range of habitats. Nothing is known, however, about the nutritional value or digestibility of tubers and leaves of this genus. Better acquaintance with these aspects are necessary in promoting the plant as a commercial crop. Commercialisation of *Zantedeschia* may help to overcome food shortages in the future. Its cultivation as a food source may become substantive, should the cultivation of madumbe and cocoyams become problematic. Until then, *Zantedeschia* remains an underexploited herb with promising economic potential.

2.4 Folk-medicine

Warmed leaves of *Z. aethiopica* are applied to sores, boils and insect bites by the Xhosa and Whites in South Africa (Watt & Breyer-Brandwijk 1962). It is reported to have a soothing effect. The same preparation is applied to parts of the body affected by gout and rheumatism. A decoction of *Z. albomaculata* subsp. *albomaculata* is used by Zulu women to prevent repeated miscarriages and giving birth to small, weak babies. *Z. albomaculata* subsp. *albomaculata* is used as a "last resort" remedy where the patient either dies or recovers when the incinerated tubers are rubbed into incisions on his back (Guillarmod 1971).

Although the leaves of *Zantedeschia* were widely used medicinally in the past, these practices have diminished in recent times. Further chemical and pharmaceutical research is required to substantiate its medicinal claims. Despite, the advance in modern medicines, people still rely on herbal remedies. Although at present, *Zantedeschia* plays a limited role in traditional medicine, it may hold considerable promise as a home-remedy for self-medication in the future.

ÜBER NEUSEELAND

Neuseeland ist ein wunderschönes Land auf der südlichen Erdhalbkugel, ungefähr 2000 km südöstlich Australiens. Das Land besteht aus zwei Hauptinseln - der Nord- und der Südinsel sowie zahllosen kleineren Inseln. Das Land ist ungefähr so groß wie Großbritannien, aber es gibt nur 3,2 Millionen Einwohner - viel Platz für jedermann!

Aufgrund seiner großartigen schneebedeckten Bergketten auf beiden Inseln, seiner großen Gebiete mit saftigen grünen Weiden, seiner kristallklaren Seen und Flüsse und seiner frischen, gesunden Luft wird Neuseeland oft als die Schweiz des Südpazifiks bezeichnet.

Ausfuhren von Hauptagrarprodukten wie Fleisch, Milchprodukten, Fisch, Obst und Gemüse tragen zu einem großen Teil zur Wirtschaft des Landes bei und haben Neuseeland zu einem ausgezeichneten Ruf unter den anspruchsvollen Einfuhrländern der Welt als leistungsfähige Erzeuger und Verarbeiter von Lebensmitteln verholfen.

Neuseeland ist ein Vielvölkerstaat. Ungefähr 10% der Bevölkerung besteht aus den eingeborenen Maoris und die übrige Bevölkerung besteht aus Europäern, Polynesiern, Asiaten und Indern. Egal welcher kulturellen Herkunft - Neuseeländer sind bekannt für ihren Einfallsreichtum, ihre Leistungsbereitschaft und ihre Integrität.

DIE NEUSEELÄNDISCHE CALLA GESCHICHTE

Die Calla ist der gebräuchliche Name für die Gattung Zantedeschia, die zur Familie der Araceae gehört. Sie kommt aus dem Süden Afrikas und wurde Anfang des neunzehnten Jahrhunderts nach Europa gebracht. Die Gattung wurde nach Professor Zantedeschia, einem bekannten italienischen Botaniker, benannt. Ausgedehnte Züchtungen, die in Neuseeland vorgenommen wurden, brachten Hybriden in einer großen Anzahl verschiedener Farben hervor, für die im Ausland als Schnittblumen, Topfpflanzen oder Zierpflanzen in Gewächshäusern Nachfrage besteht.

Callas wachsen am besten in Gebieten mit gemäßigtem Klima bei Temperaturen von 16 - 22°C.

Das gemäßigte neuseeländische Klima ist bestens für die Kultivierung der Calla geeignet und außerdem bieten die meisten neuseeländischen Böden ausgezeichnete Voraussetzungen für die empfindliche Calla-Pflanze, da sie leicht entwässern und doch die Feuchtigkeit halten.

Von Oktober bis Mai steht die Pflanze in Blüte, wenn die Nachfrage auf der nördlichen Erdhalbkugel am größten ist.

In vielen der größten Blumenmärkte sind Callas sehr in Mode gekommen und werden als neuartige Blumen bei besonderen Gelegenheiten wie Parties, Hochzeiten und im geschäftlichen Rahmen verwendet. Die Calla ist bei Blumenarrangeuren und Floristen für hochwertige und elegante Blumenarrangements sehr beliebt.

1991 haben Züchter, Versandhäuser und Exporteure den New Zealand Calla Council Inc. (Neuseeländischer Calla Verein e.V.) gegründet, eine brancheneigene Organisation, die das Ziel hat, die Entwicklung und Expansion der Callablumen- und Knollenindustrie durch Entwicklung von Zielmärkten, Koordination von Forschung und Entwicklung und durch erstklassiges Management zu fördern.

TM

NEUSEELÄNDISCHE
CALLAS - FÜR DIE GROSSEN
BLUMENKÜNSTLER DER
WELT GEZÜCHTET.

NEW ZEALAND
CALLA council
Pyes Pa Road, RD3
Tauranga, New Zealand,
Phone/Fax 64-7-543-3077

YOUR DISTRIBUTOR

German

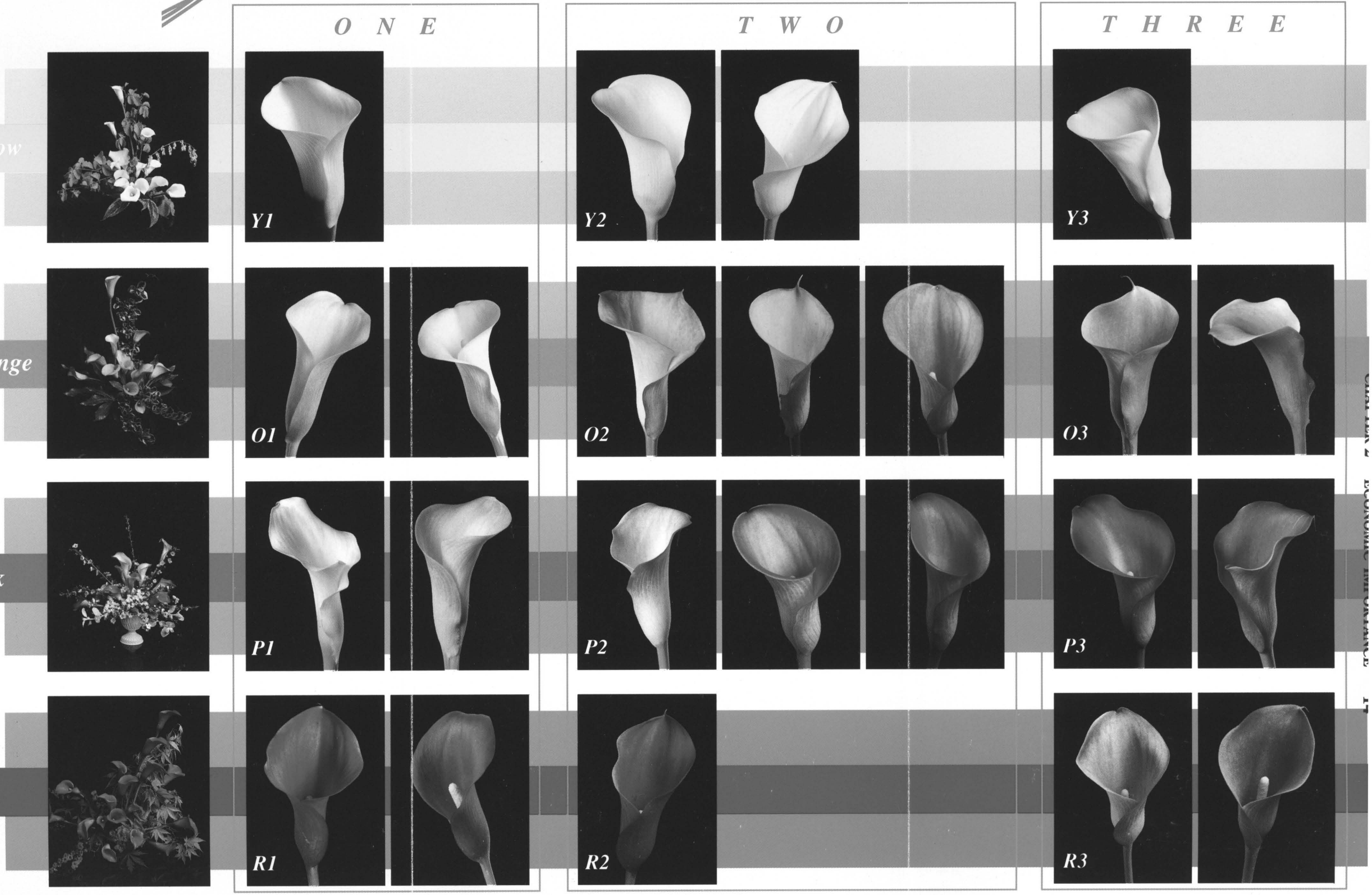
TM

NEW ZEALAND
CALLA council

COLOUR GUIDE 1993

NEW ZEALAND CALLA council
COLOUR GUIDE 1993

Pyes Pa Road, RD3
Tauranga, New Zealand,
Phone/Fax 64-7-543-3077



NEW ZEALAND CALLAS - Grown for the world's great floral artists

CHAPTER 3

NOMENCLATURAL HISTORY

3.1 Introduction

Botanical nomenclature is that part of taxonomy which deals with the assigning of the correct names to a taxon. Nomenclatural procedure is one of the few aspects of taxonomy which gives rise to much argument and misunderstanding among users of plant names and even nomenclaturalists (Stace 1980). The nomenclatural history of *Zantedeschia* is a principal example of such controversy.

This chapter traces the heterogeneous descriptions and names used in reference to *Zantedeschia* from the Pre-Linnaean Era to Post Linnaean times. A bibliography citing literature relevant to the nomenclatural history of the genus is given at the end of this Chapter.

3.2 Pre-Linnaean era

In the pre-Linnaean era, plants were referred to by a descriptive phrase, the wording of which largely depended on the author, and which was mostly different for the same species. The phrases used in reference to *Zantedeschia*, *Z. aethiopica* in particular, are summarised in Table 3.1.

3.3 Generic names

Table 3.2 outlines the generic names and epithets used for members of the genus *Zantedeschia* by authors in the Linnaean and post-Linnaean times. Only selected references from the post-Linnaean era are discussed further.

Table 3.1 Summary of pre-Linnaean history of *Zantedeschia* (1687–1737)

Year	Author	Publication	Phrase name/Illustration
1687	Paul Hermann	Horti Academici Lugduno-Batavi Catalogus: 60	First reference made to *Z. aethiopica*. "Arum aethiopicum flore albo odorato, moschum redolente"
1697	Commelin	Horti Medici Amstelodamensis Rariorum Plantarum Historia: 95 Plate 50	First known illustration of *Z. aethiopica*. Description in Latin and French.
1705	Paul Hermann	Paradisus Batavus: 74	"Arum africum, flore albo odorato" was used to describe *Z. aethiopica*.
1720	Anonymous	Book of wild facsimile paintings	A good picture of *Z. aethiopica*. Annotated by Johannes Burman in 1755.
1737	Linnaeus	Hortus Cliffortianus	Quotes earlier literature references in his description of *Z. aethiopica* which he placed in the genus *Calla*.

Linnaeus (1737) places what is presently known as *Z. aethiopica*, in the genus *Calla*, an aroid genus now considered to be restricted to the temperate regions of the Northern Hemisphere. Linnaeus described the species *Calla aethiopica* L. and *C. palustris* L. in his Species Plantarum (1753). The word "Aethiopia" denotes Africa, hence the specific name *aethiopica*. Fabricius (1763) separated *Calla* into two genera: *Calla* and *Aroides* Heister, placing *C. aethiopica* in *Aroides* as *A. aethiopicum* Heister ex Fabricius. Link (1795) referred to *Z. aethiopica* as *Colocasia aethiopica* Link. Kunth (1818) established the genus *Richardia* to accommodate Linnaeus' *Calla aethiopica*, hence the name *Richardia africana* Kunth. The name *Richardia* was already used by Linnaeus for a genus in the Rubiaceae, which Kunth changed to *Richardsonia* Kunth. In 1826, Sprengel created the genus *Zantedeschia* with *Z. aethiopica* as the sole member.

d taxonomic treatments of *Zantedeschia*
era. A particular colour signifies the same taxon.

AROIDES	*COLOCASIA*	*RICHARDIA*	*ZANTEDESCHIA*											
aethiopicum														
	C aethiopica													
		R. africana												
			Z. aethiopica											
		R. africana												
		R africana												
		R albomaculata												
		R. africana												
		R hastata												
		R angustiloba												
		R melanoleuca												
		R. africana												
			Z aethiopica											
					Z rehmannii							*Z macrocarpa*		
		R africana *R. rehmannii* ***R hastata*** ***R albomaculata*** ***R. angustiloba*** ***R melanoleuca***												
		R. sprengeri												
			Z aethopica	***Z elliotiana***	*Z rehmannii*	***Z melanoleuca***	***Z oculata***		***Z albomaculata***	***Z angustiloba***		*Z macrocarpa*		
				Z elliotiana		***Z melanoleuca***	***Z oculata***							*Z sprengeri*
			Z aethiopica	***Z elliotiana***	*Z rehmannii*	***Z melanoleuca***		***Z hastata***	***Z albomaculata***	***Z angustiloba***				*Z sprengeri*
			Z aethiopica	***Z elliotiana***	*Z rehmannii*	***Z melanoleuca***		***Z hastata***	***Z albo-maculata***	*Z angustiloba*	***Z tropicalis***			
			Z aethiopica	***Z elliotiana***	*Z rehmannii*				***Z albomaculata*** subsp. ***albomaculata***			*Z albomaculata* subsp. *macrocarpa*	***Z albomaculata*** subsp. ***valida***	
			Z aethiopica	***Z elliotiana***	*Z rehmannii*				***Z albomaculata*** subsp. ***albomaculata***			*Z albomaculata* subsp. *macrocarpa*	***Z valida***	

Rafinesque (1837) stated, "*Calla aethiopica* is a peculiar genus, which I call *Otosma*" Endlicher (1837) reverted to the generic name *Richardia*. At this stage six distinct generic names were suggested for a single species.

Between the period 1837 and 1880, five other species of *Zantedeschia* were described, four within the genus *Richardia* and one within *Calla*. Baillon (1880) realised the confusion in the nomenclature of the genus. He pointed out that the name *Richardia* established by Kunth was a later homonym since Linnaeus had already used the name for a plant in the Rubiaceae, which Kunth changed to *Richardsonia* Kunth. Baillon concluded that *Calla aethiopica* and *Richardia africana* refer to the same taxon, to be called *Z. aethiopica* as proposed by Sprengel in 1826.

Despite Baillon's explanation of the nomenclatural confusion, Bentham & Hooker (1883) upheld *Richardia* with *Zantedeschia* as a synonym. Otto Kuntze (1891) reverted to the generic name *Aroides* which he changed to *Arodes* for grammatical reasons. He published the following combinations: *A. aethiopicum* (L.) Kuntze, *A. albomaculatum* (Hook.) Kuntze, *A angustilobum* (Schott) Kuntze, *A. hastatum* (Hook) Kuntze and *A. melanoleuca* (Hook. f.) Kuntze. Eventually, in 1915, Engler reinstated the name *Zantedeschia* for this group of aroids, a decision subsequently followed by all workers on the group.

The nomenclatural history of *Zantedeschia* clearly exhibits the nightmare faced by botanists in assigning a generic name to this group of aroids. Their confusion may be attributed to the lack of published information and knowledge of plants in the wild.

The generic names *Arodes*, *Aroides* and *Richardsonia* are not legitimate under the *International code of botanical nomenclature* (Greuter *et al.* 1988). *Richardia* is a genus of 15 species in the Rubiaceae as assigned by Linnaeus. *Arum*, *Calla* and *Colocasia* are genera in the Araceae. A comparison of floral characters in Table 3.3 demonstrates the relationship of *Zantedeschia* with these aroid genera.

Table 3.3 Comparison of distribution and select floral characters of *Arum*, *Calla*, *Colocasia* and *Zantedeschia*

	Arum	*Calla*	*Colocasia*	*Zantedeschia*
Subfamily	Aroideae	Calloideae	Colocasioideae	Philodendroideae
Number of species	25	1	6	7
Distribution	Eurasia	Canada, United States, Eurasia	Tropical Asia	southern Africa, Angola, Malawi, Zambia, Zimbabwe, Tanzania
Spathe	constricted	constricted	constricted	not constricted
Spadix	appendix present	appendix absent	appendix present (aborted in *C.esculenta*)	appendix absent
Flowers	unisexual	bisexual	unisexual	unisexual
Ovules	orthotropous	anatropous	orthotropous	anatropous

3.4 Major taxonomic revisions

Major taxonomic revisions of *Zantedeschia* are indicated by an asterisk in Table 3.2. The first revision was by Engler (1915), who recognised eight species. He considers *Z. pentlandii* to be a synonym of *Z. angustiloba* (Schott) Engl. The revision by Traub (1948) was along the same lines as Engler and eight species were recognised. Traub's treatment differed from Engler's in that *Z. oculata* was regarded as a synonym of *Z. hastata*. *Z. macrocarpa* was grouped with *Z. angustiloba* as suggested by Brown (1902) and *Z. sprengeri* was recognised as a distinct species. Letty (1973) provided a comprehensive revision of the genus, in which she included a key to six species and three subspecies, based on vegetative and floral characters, and a detailed morphological description of each species. Unlike Engler (1915) and Traub (1948), Letty had a sound knowledge of most of the taxa in the wild, hence she was able to eliminate much of the earlier taxonomic confusion. In the present study, six species and two subspecies recognised by Letty (1973), as well as a new species described by Perry (1989) are upheld. The subspecies *Z. albomaculata* subsp. *valida* Letty is raised to species level as *Z. valida* (Letty) Y.Singh (Singh *et al.* Appendix 5), thus bringing the number of taxa currently recognised in *Zantedeschia* to eight species and two subspecies (Table 1.2, p. 3).

3.5 Bibliography

BENTHAM, G. & HOOKER, J.D. 1883. *Genera Plantarum.* 3: 982. London.

BAILLON, H.E. 1880. *Bulletin mansuel de la Société linneenne de Paris.* 1: 254. London.

BROWN, N.E. 1900. Aroideae. *Flora Capensis* VII: 32–39. London.

BURTT DAVY, J. 1924. New or noteworthy South African Plants–VI. *Kew Bulletin.* 223–235.

COMES, 1902. *Richardia Sprengeri* Comes. *Atti Inst. Incorazz.*, Napoli ser. 5, vol. 3:

COMMELIN, J. 1697. *Horti Medici Amstelodamensis Rariorum Plantarum Historia.* 95pp. Plate 50. Amsterdam.

ENDLICHER, S.L. 1837. *Genera Plantarum.* 238pp. Wein.

ENGLER, H.G.A. 1879. DC., *Monographiae phanerogamarum.* 2: 327. Paris.

ENGLER, H.G.A. 1883. *Botanische Jahrbücher für Systematik.* 4: 63. Leipzig.

ENGLER, H.G.A. 1915. *Das Pflanzenreich* IV, 23Dc.: 61–69. Leipzig.

— & PRANTL, K.A.E. 1889. *Die natürlichen Pflanzenfamilien* 2, 3: 136. Leipzig.

FABRICIUS, P.C. 1763. *Enumeratio methodica plantarum.* ed.2,2: 42pp. Helmstedt.

HERMANN, P. 1687. *Horti academici lugduno-Batavi catalogus*: 60pp. Leiden.

HERMANN, P. 1705. *Paradisus Batavus.* 74pp. Leiden.

HOOKER, W.J. 1859. *Curtis's Botanical Magazine.* t. 5140. London.

HOOKER, W.J. 1860. *Curtis's Botanical Magazine* t. 5176. London.

HOOKER, J.D. 1869. *Curtis's Botanical Magazine* t. 5765. London.

KUNTZE, C.E.O. 1891. *Revisio Genera Plantarum*. 2: 739–40. London.

KUNTH, 1818. *Memoires du Museum nationale d' histoire naturelle*. 4:443. Paris.

KUNTH, C.S. 1841. *Enumeratio plantarum* 3:58. Stuttgart, Tübingen.

LETTY, C. 1962. *Wild flowers of the Transvaal*. Hortors Ltd, Johannesburg.

LETTY, C. 1973. The genus *Zantedeschia*. *Bothalia* 11: 5–26. Pretoria.

LINDLEY, J. 1859. *Gardener's Chronicle* 40: 788. London.

LINK, J.H.F. 1795. *Dissertationes Botanicae Schwerin*. 77. Sverin.

LINK, J.H.F. 1829. *Handbuch* 1:267. Berlin.

LINNAEUS, C. 1737. *Hortus Cliffortianus*. Amsterdam.

LINNAEUS, C. 1753. *Species Plantarum*.ed.1. 968pp. Stockholm.

PERRY, P.L. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447–451. Pretoria.

RAFINESQUE, S.C.S. 1837. *New Flora and botany of North America* 2: 90. Philadelphia.

SCHOTT, H.W. 1856. *Synopsis Aroideanum*. 131. Wein.

SCHOTT, H.W. 1858. *Genera aroideanum*. t. 62. Wein.

SCHOTT, H.W. 1860. *Prodromus Systematis Aroideanum*. 324. Wein.

SCHOTT, H.W. 1865. *Journal of Botany* 3: 35. London.

SPRENGEL, K.P.J. 1826. *Systema vegetabilium*. 3: 765. Gottingen.

TRAUB, H.P. 1948. The genus *Zantedeschia*. *Plant Life* 4: 9–32. California.

WATSON, W. 1892. *Gardener's Chronicle* 12: 123. London.

CHAPTER 4

VEGETATIVE MORPHOLOGY

4.1 Introduction

Morphological data provides the basic criteria for plant identification, classification and relationships (Radford 1986). Since morphological characters are easily observable, they feature prominently in taxonomic keys. There is a tendency to use floral morphology more regularly than vegetative characters. Stace (1980) pointed out that dependence on floral characters is remarkable when one considers that for most of the time, the majority of angiosperms are in the vegetative state. Taxonomists have no alternative in this regard, since very often differences in vegetative characters among taxa are so slight that they are hardly noticeable. In such instances, greater relevance is placed on floral characters. Despite this, there are species in some genera of monocotyledons that possess a striking similarity in their floral features. Nevertheless, whenever possible, keys should be based on a combination of vegetative and floral attributes.

Members of the family Araceae show considerable variation in their gross morphology (Bogner 1987). There is diversity in growth forms, vegetative and floral structures. These differences are often taxonomically significant for recognising subfamilies, genera and species. In this study, differences in vegetative and floral morphology have been investigated for all natural taxa of the genus *Zantedeschia*. Vegetative characters such as leaf shape proved to be important in demarcating species. Reproductive structures, for instance the presence of staminodes amongst ovaries, also provide characters of diagnostic value. In this chapter, vegetative features of the genus are discussed and their value in demarcating infrageneric taxa is assessed. Floral morphological characters will be discussed in Chapter 6.

4.2 Materials and methods

The study was based on observations of plants in the field and in cultivation. Plants from several populations throughout South Africa were examined in the field, kept in cultivation as well as pressed for herbarium records. Examination of earlier herbarium collections (NH, PRE, ROML, SRGH, SWZ) supplemented observations made on living material.

4.3 Growth form

Members of the genus are terrestrial perennial herbs that survive as tubers during unfavourable conditions. During the favourable growing season, the tubers develop leaves and inflorescences. Thus plants are deciduous in habit. However, *Z. aethiopica* has the potential to remain evergreen in areas where there is sufficient moisture throughout the year. In the winter rainfall region of the Cape, this species produces leaves and flowers in mid-winter (June/July) and spring (August/September). In the summer rainfall area, *Z. aethiopica* produces leaves and flowers from spring (August/September) to summer (December/January). Plants of this species may leaf and flower throughout the year, with its growth being more luxuriant during the wet season. The leaves of all other summer rainfall species, despite favourable conditions, were found to die back over the dry season (March-August). These plants have a definite dormant period during winter. *Z. odorata*, a winter-rainfall species from the Cape, is dormant during summer (October to May).

Letty (1973), perhaps unaware that plants of *Z. aethiopica* are deciduous under conditions of extreme drought, used the evergreen habit of this species as a major diagnostic character in a key to the species. Furthermore, she identified "evergreen" as one of the attributes for placing *Z. aethiopica* in an informal section of its own. During this study, plants of *Z. aethiopica* were found to die back in areas of limited moisture. Hence its evergreen state is not a stable diagnostic character for separating this species. It is nevertheless true that *Z. aethiopica* has the potential to remain evergreen under favourable conditions, unlike any of the other members of the genus.

4.4 Roots

At the start of the growing season, several long roots radiate from the base of the shoot and are directed downwards thereby anchoring the tuber firmly into the ground. Roots are annual, cylindrical and of two types, feeding and contractile. Feeding roots are usually 2–4 mm in diameter with many fine hairs about 1 mm in diameter. Roots intertwine profusely to form a compact mass which serves to hold moisture. Contractile roots are usually thicker than feeding roots. Towards the end of the growing season, the feeding roots start to wither towards their tips. At this stage the tissue in the contractile roots contract, characterising these roots. Since there is homogeneity in root disposition among all species, root characters are of no infrageneric taxonomic importance.

4.5 Perennating organs

Zantedeschia grows in areas of seasonal rainfall. It is therefore to its advantage to survive as subterranean tubers during the dry season. Based primarily on shape, two types of tubers are recognisable in *Zantedeschia*, namely rhizomatous (Figure 4.1) which may be vertical or horizontal and discoid (compact) (Figure 4.2).

In both types of tubers, there is one main growing point towards the apex of the existing tuber which gives rise to the main shoot. The growing point may be central or polar. In addition, several adventitious buds form on the tuber. These develop vegetative shoots and subsequently form tubers during the growing season. Adventitious tubers may detach from the parent tuber and establish themselves as independent plants. In the rhizomatous type (Figure 4.3) adventitious tubers detach from the parent tuber, thus giving rise to spreading colonies, while in the discoid type (Figure 4.4), adventitious tubers tend to remain attached to the parent tuber, thereby forming compact clumps.

Z. aethiopica and *Z. odorata* have rhizomatous tubers, whereas those of the remaining species are discoid. It is therefore possible to separate these two species from the others on the basis of their rhizomatous tubers.

Although the two types of tubers are distinct, variation in tuber form does occur depending on the physical conditions of the substrate. In such instances difficulty may be experienced in classifying the tuber type. Perry (1989) indicates the tubers of third year seedlings of *Z. aethiopica* and *Z. odorata* to be somewhat discoid in shape. These illustrations were made from plants cultivated from seeds. A parallel study of tubers in plants raised from seeds and those in the wild will indicate to what extent the growth pattern of tubers depends on the physical environment or developmental stage of the plants.

Z. odorata, *Z. pentlandii*, *Z. jucunda* and *Z. valida* are restricted to rocky outcrops. *Z. albomaculata*, *Z. aethiopica* and *Z. rehmannii* though not restricted to these habitats, may also grow on rocky hillsides. In rocky substrates, the tubers are buried in crevices between and below rocks, making it difficult to dig up complete tubers. This may be an ecological adaptation whereby tubers and roots are kept cool during the dry season and, in the rainy season, the plants benefit from water channelled into rock crevices. Burying itself among rocks may also be an adaptation for protection against rodents. Tubers of *Z. pentlandii* were observed to be dug up by porcupines. Species not restricted to rocky areas may also grow in open vleis (wetlands). In the vleis, the grass cover may help in keeping the root system cool. Usually only part of the tuber contained in the root mass remains alive. With time, the older portions rot away from the base upwards.

4.6 Cataphylls

A cataphyll is a reduced leaf that protects the newly emerging leaf (Croat 1991). In the adventitious buds of *Zantedeschia*, two to three cataphylls enclose the newly emerging leaf. The cataphylls develop on opposite sides of the leaf, with the margins of one overlapping those of the other. The outermost cataphyll/s are about one third the length of the inner cataphyll. The inner cataphyll reaches a length of about one third to half that of the petiole. Mature cataphylls in the genus are subulate with an apiculate apex (Figure 4.5). Except for variations in size, cataphylls are fairly uniform and provide no useful characters for species delimitation. In all taxa the cataphylls are green. However, in *Z. albomaculata* subsp. *albomaculata*, *Z. jucunda* and *Z. valida* cataphylls may be striped or mottled with purple towards the base. Croat (1991) found that cataphylls of *Anthurium* Schott do not contribute useful taxonomic characters as do those of *Philodendron* Schott.

When the leaf emerges fully, cataphylls lose their photosynthetic function and dry up. Dry cataphylls trap debris which helps to retain moisture around the tuber (Croat 1991).

4.7 Leaves

4.7.1 Petiole

Petioles are typically equal to or longer than the laminae. *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata* may have petioles up to twice as long as the lamina. The leaf sheath (Figure 4.6) extends up to half the length of the petiole. Very often a second leaf emerges through the sheath. In *Z. aethiopica* and *Z. rehmannii*, petioles are green throughout their length. In the remaining species, petioles are usually mottled with purple or white, particularly towards the base (Figure 4.7). Petioles are glabrous, except in *Z. jucunda* and *Z. albomaculata* subsp. *albomaculata* where trichomes may be present towards the base. However, the occurrence of trichomes is inconsistent in these species. The presence of trichomes on a sterile specimen is nevertheless taxonomically useful, in suggesting that the specimen may either be *Z. jucunda* or *Z. albomaculata* subsp. *albomaculata*.

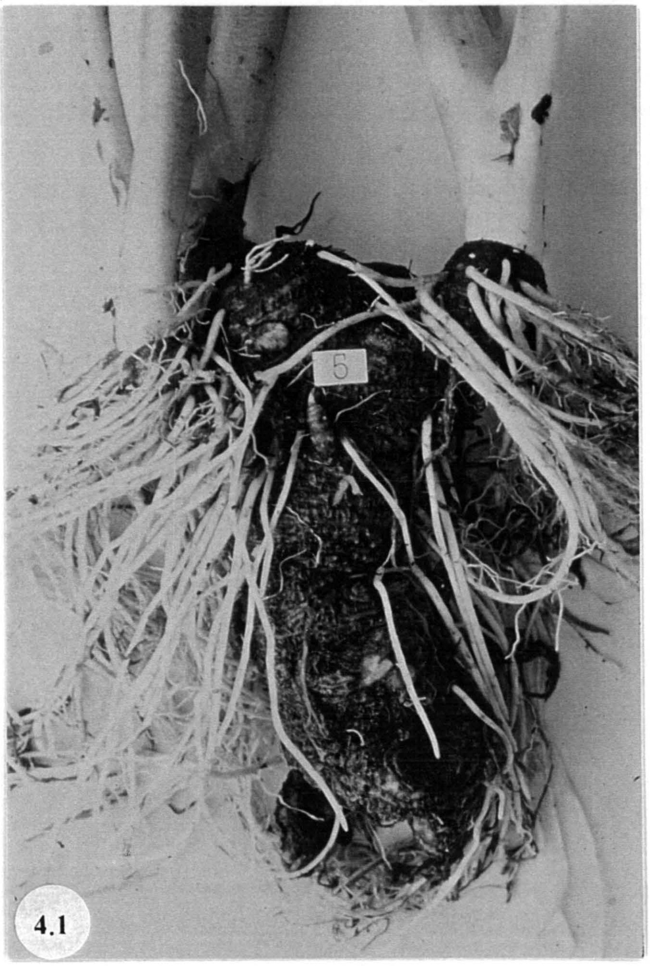
4.7.2 Lamina

Zantedeschia has supervolute vernation which is common in the Araceae. In this type of vernation, one margin of the leaf is rolled inwardly towards the midrib and the other is rolled around the first in-rolled half and the midrib (Figure 4.8).

Leaf shape is quite variable in the genus, ranging from lanceolate through to triangular-hastate to orbicular-cordate (Singh *et al.* 1995, Appendix 2). Leaves of *Z. albomaculata* subsp. *albomaculata* shows considerable plasticity, sometimes displaying characters identical to those of *Z. albomaculata* subsp. *macrocarpa* and *Z. elliotiana*. In such cases, flowering material is necessary for correct identification. Leaves in *Z. aethiopica*, *Z. odorata* and *Z. valida* are similar, and therefore difficult to separate. However, these species can be distinguished from the remaining species on the basis of their ovate-cordate leaves.

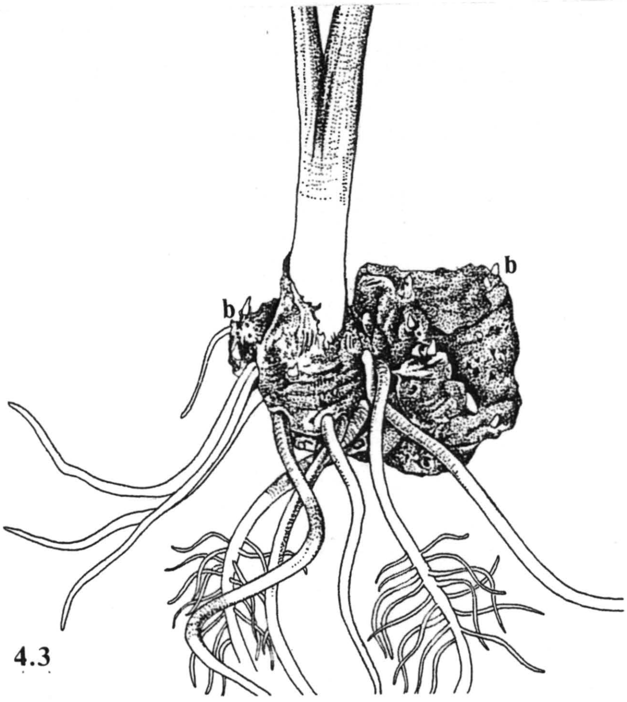
Venation pattern in *Zantedeschia* is pinnate, camptodromous, more specifically eucamptodromous (Hickey 1979). In leaves with hastate bases, the lowest pair of lateral veins are directed backwards into the lobes, while the remaining pairs are directed apically towards the margins of the leaves. In *Z. rehmannii* the leaf base is cuneate and all pairs of lateral veins are directed apically. Despite the wide range of lamina shapes the basic pattern of venation is uniform in all species.

Margins of leaf laminae are markedly undulate. Transparent maculations of irregular shape (mostly elongate) and size are present in some plants. The constancy of maculations vary among species. The presence of maculations on the leaf laminae of *Z. jucunda* and *Z. elliotiana* and its absence in *Z. odorata* is a stable diagnostic character. Although cultivated plants of *Z. aethiopica* are frequently maculate, no plants in the wild were recorded as being maculate. Maculations were found in relatively few plants of *Z. pentlandii*, *Z. albomaculata* subsp. *macrocarpa*, *Z. rehmannii* [Jordaan 2110 (NH), Strey 9390 (NH), Van der Schÿff 5818 (PRU), Van Wyk 7069 (PRU)] and *Z. valida*. In contrast, maculations were rarely lacking in *Z. albomaculata* subsp. *albomaculata*. The irregular presence or absence of maculations in these species is less useful taxonomically.

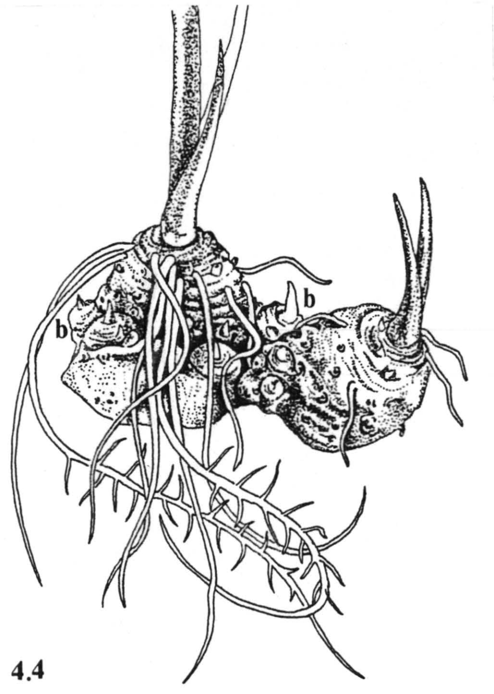


4.1

4.2



4.3



4.4

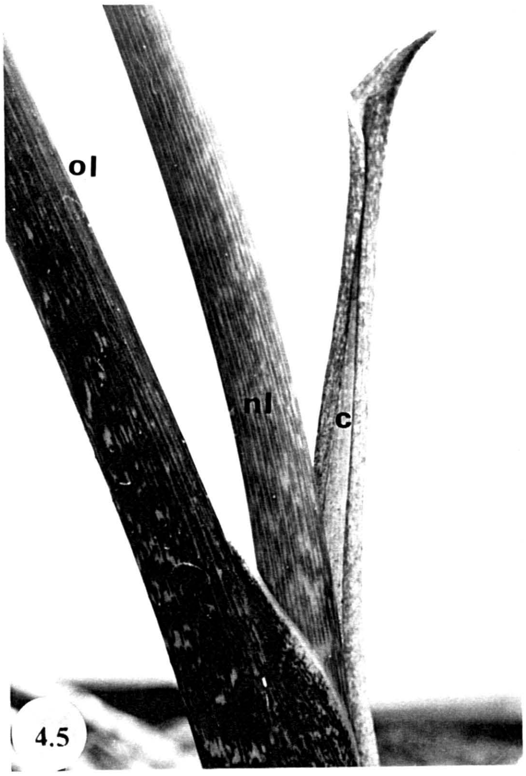
Figures 4.1–4.4 Tuber types in *Zantedeschia*

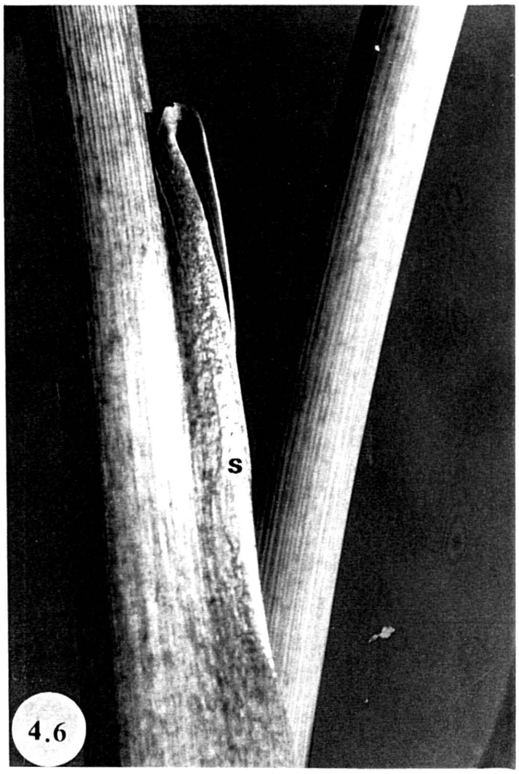
4.1 *Z. aethiopica*, vertical rhizomatous (old plant). Life size

4.2 *Z. valida*, discoid. Life size

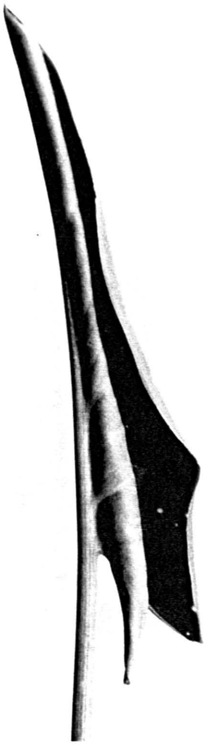
4.3 *Z. odorata*, young tuber showing buds (b) x 0.6

4.4 *Z. albomaculata* subsp. *albomaculata*, showing buds (b) x 0.6


4.5


4.6


4.7


4.8

Figures 4.5–4.8 Leaf characters in *Zantedeschia*

4.5 *Z. albomaculata* subsp. *albomaculata*, cataphyll. Life size
4.6 *Z. aethiopica*, leaf sheath. Life size
4.7 *Z. jucunda*, mottled petiole base x 2
4.8 *Z. pentlandii*, supervolute vernation x 0.5
c = cataphyll; nl = new leaf; ol = old leaf; s = leaf sheath

CHAPTER 5

VEGETATIVE ANATOMY

5.1 Introduction

The application of vegetative anatomy, particularly leaf characters, in improving classifications and identification is evident in numerous publications especially on petaloid monocotyledons (Ancibor 1979, Stern *et al.* 1993, Rudall 1994). Although Engler (1915) emphasised information from vegetative anatomy (laticifers and trichosclereids) in separating subfamilies in the Araceae, no anatomical data of individual genera has yet been published. Until 1994, virtually all anatomical surveys on the vegetative organs of Araceae were broad (Hotta 1971, French & Tomlinson 1981a–d, 1983, French 1987a, b, 1988). With William's (1994) investigation of the leaf anatomy of *Philodendron* Schott (listed in *Kew Taxonomic Literature* 1994) and this study on *Zantedeschia*, some progress is being made towards the understanding of anatomy in the subfamily Philodendroideae. These studies may prove taxonomically useful at suprageneric levels. It is hoped that these detailed surveys would contribute towards the volume on Araceae, in the series *Anatomy of the Monocotyledons* which is being written by staff of the Anatomy Section of the Jodrell Laboratory, Royal Botanic Gardens, Kew, with collaboration from other researchers.

The purpose of this chapter is to detail vegetative anatomical characters of *Zantedeschia* from observations with light (LM) and scanning electron microscopy (SEM). A further objective is to consider the systematic implications of these characters within the genus.

5.2. Material and methods

Root, tuber and leaf samples of all species of *Zantedeschia*, were examined by means of light microscopy. Except for *Z. elliotiana*, which is known only from cultivation, plant parts were collected from the wild. Locality details are recorded in Table 5.1. Plant parts were fixed in formalin-acetic acid-alcohol (FAA) in the ratio of 1:1:18 (Bridson & Forman 1989).

Table 5.1 Locality and voucher specimen details of plants used in anatomical study

Species	Collector's Number	Locality	Leaves of plant	Location of vouchers
Z. aethiopica	36	Kloof, KwaZulu-Natal	maculate	NH
	46	Dullstroom, Mpumalanga ✓	immaculate	NH
	51	Cloudskraal, Western Cape	immaculate	NH, PRU
Z. albomaculata subsp.*albomaculata*	60	Impendle, KwaZulu-Natal	maculate	NH
	82	Fort Nottingham, KwaZulu-Natal	immaculate	NH
subsp. *macrocarpa*	47	Dullstroom, Mpumalanga	immaculate	NH, UDW
Z. elliotiana	44	Dullsroom, Mpumalanga	maculate	NH
Z. jucunda	49	Sekhukhuniland, Mpumalanga	maculate	NH, PRU, UDW
Z. odorata	50	Nieuwoudtville, Western Cape	immaculate	NH, PRU
Z. rehmannii	40	Pretoria, Gauteng	immaculate	NH
Z. pentlandii	42	Dullstroom, Mpumalanga	immaculate	NH, PRU, UDW
Z. valida	58	Elandslaagte, Northern KwaZulu-Natal	immaculate	NH

Root and tuber sections were made at comparable levels in each specimen. Standardised areas equidistant from base to apex of petioles and midribs were selected.

Leaf transverse sections and epidermal scrapes were made midway between the apex and base as illustrated (Figure 5.1).

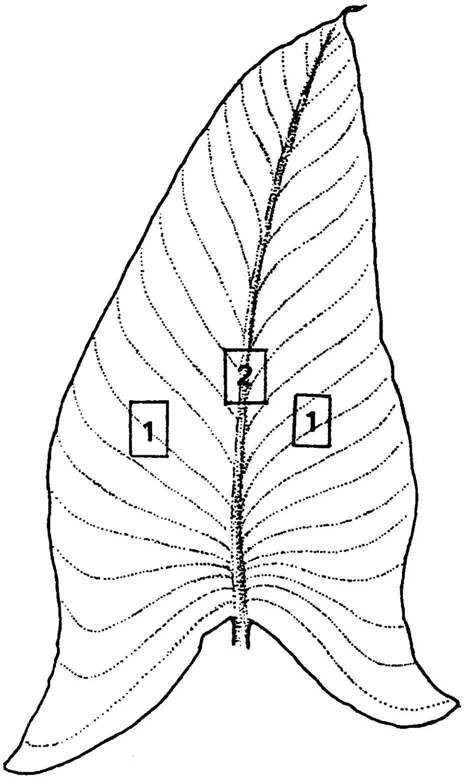


Figure 5.1 Areas of the lamina (1) and midrib (2) used for leaf scrapes (1) and sections (1,2)

Suitable portions of material were passed through an alcohol series, embedded in paraffin wax and sectioned at 14–18µm on a Jung Rotary microtome. Longitudinal (LS) and transverse (TS) sections were stained with safranin and fast green. Epidermal leaf scrapes of ad- and abaxial surfaces of all species were prepared using a razor blade. Scrapes were stained with toluidine blue. Glycol methacrylate embedding technique for LM (Feder & O'Brien 1968) was used for the study of internal leaf structure. In the case of maculate leaves, areas selected included a portion of the maculation. Three micrometer thin sections were cut on a Reichert-Jung OME ultramicrotome. Sections were stained with Periodic acid-Schiff (PAS) reaction and counterstained with toluidine blue (Feder & O'Brien 1968). All stained sections for light microscopy were mounted in Entellan (E. Merck, Art. no. 7961). Sections were photographed using an Olympus Vanox-S photomicroscope.

For SEM, leaf material was dehydrated through an alcohol series, critical point dried, mounted on stubs, sputter-coated with gold, viewed and photographed using a Jeol 840 SEM.

5.3 Description

Since not many anatomical differences were noted, a generic account is given and only differences in particular species are recorded. Information from both LM and SEM have been incorporated in the description. With regard to leaf anatomy, comparisons were made between the ad- and abaxial surfaces, the green areas of maculate leaves and that of immaculate leaves, maculations of various species, and the internal structure of leaves. Since the two subspecies of *Z. albomaculata* were found to be similar to each other, reference to them will be at specific level.

5.3.1 Leaf surface details (Singh *et al.* 1994, Appendix 3)

Green areas (Figures 5.2–5.7)

Cuticular striations present on both surfaces (Figures 5.2–5.3). *Striae* regularly traversing the position of the anticlinal walls (Figure 5.4). *Epidermis* cells 4–6 sided, polygonal in shape (Figure 5.2–5.3). Anticlinal walls continuous, straight; position denoted by shallow depressions (Figures 5.5). *Stomata* paracytic, haphazardly arranged on leaf surface and not in parallel files as in most monocotyledons; longitudinal axis of the pore parallel or obliquely parallel to the veins (Figure 5.6). Guard cell pair outline elliptic to widely elliptic (Table 5.2), surrounded by 2 subsidiary cells (Figure 5.7).

Table 5.2 Guard cell pair outline shapes in *Zantedeschia* species

Species	Guard cell pair outline (l:w) Ad	 Ab
Z. aethiopica	5:3 elliptic	5:4 widely elliptic
Z. albomaculata	3:2 elliptic	2:1 elliptic
Z. elliotiana	2:1 elliptic	5:3 elliptic
Z. jucunda	2:1 elliptic	2:1 elliptic
Z. odorata	5:4 widely elliptic	4:3 widely elliptic
Z. pentlandii	2:1 elliptic	2:1 elliptic
Z. rehmannii	2:1 elliptic	5:2 elliptic
Z. valida	3:2 elliptic	2:1 elliptic

Maculation (Figures 5.8–5.9)

Epidermis cell shape and striae similar on ad- and abaxial surfaces, position of the anticlinal walls similar to those in the green areas. *Stomata* absent.

5.3.2 Internal anatomy

5.3.2.1. Lamina TS (Figures 5.10–5.11).

Outline dorsiventrally flattened, strap-shaped. *Cuticle* thin, following outline of outer walls of epidermis, 2.5 μm thick. *Epidermis* cells in one layer, cells as wide as tall or slightly taller than wide, similar in ad- and abaxial surfaces. Outer periclinal walls 7.5 μm thick. *Prickles* and *Hairs* lacking. *Stomata* superficial. *Guard cells* about one third the size of adjoining subsidiary cells with walls thickened to varying degrees, portions of outer and inner periclinal walls regularly more heavily thickened than poral and epidermal walls, thickening marked at junction of inner and outer periclinal walls with poral wall; outer and inner cuticular lips or ledges present. Outer stomatal lip slightly sunken below surface. *Hypodermis* absent. *Chlorenchyma* in several layers, cells thin-walled, interrupted by well-developed chamber below each stoma, cells towards adaxial surface 2–5-layered, palisade- or mesophyll-like; abaxial region 2–4-layered, with airspaces, generally lobed, rarely palisade-like; both ad- and abaxial layers separated by large circular, laterally elongated or irregularly shaped lacunae formed by single rows of cells. *Vascular bundles* numerous, arranged almost midway; large and medium-sized bundles alternating with smaller ones; phloem poles directed outwards. *Phloem* pole oval or rectangular in outline; sieve tubes narrow, 5–7-sided, companion cells about one third the diameter of sieve tubes, shape irregular. *Xylem* composed of well-developed protoxylem lacunae and 4–8 metaxylem tracheids. *Bundle sheaths* consisting of 2 layers of parenchyma cells; inner sheath composed of distinct cap at phloem pole, cap cells thin-walled with small airspaces; outer sheath of large parenchyma cells. *Sclerenchyma* absent. *Crystals* composed probably of calcium oxalate occurring as: a) bundles of fusiform needle-like raphides in thin-walled idioblasts in chlorenchyma b) druses sometimes present in chlorenchyma, almost spherical in outline c) crystal sand which is widespread. *Secretory cells* absent. *Silica bodies* absent. *Tannin* as amorphous bodies, only in few cells of outer parenchyma sheath, staining maroon with safranin and fast green.

Z. aethiopica

Chlorenchyma lobed, mesophyll-like, with large airspaces, adaxial 3–4 cells wide; abaxial 2–3 cells wide; lacunae irregularly shaped.

Z. albomaculata

Chlorenchyma adaxial palisade-like, compact, 2–3 cells wide; abaxial lobed with airspaces, 2–3 cells wide; lacunae irregularly shaped.

Z. elliotiana

Chlorenchyma adaxial palisade-like, 2–3 cells wide; abaxial slightly lobed, 2–3 cells wide; lacunae irregularly-shaped.

Z. jucunda

Chlorenchyma adaxial palisade-like, 2–3 cells wide, abaxial lobed, 2–3 cells wide; lacunae irregularly shaped.

Z. odorata

Chlorenchyma mesophyll-like, cells almost circular, adaxial 3–5 cells wide with airspaces; abaxial 2–3 cells wide; lacunae almost circular.

Z. pentlandii

Chlorenchyma adaxial palisade-like, 2–5 cells wide; abaxial lobed, 2–3 cells wide; lacunae large, oval, laterally elongated.

Z. rehmannii

Chlorenchyma palisade-like, 2–3 cells wide; lacunae almost circular.

Z. valida

Chlorenchyma adaxial palisade-like, 2–3 cells wide; abaxial slightly lobed, 2–4 cells wide; lacunae almost circular.

Maculation (Figure 5.12)

Cuticle as in green area. *Epidermis* cells square to 1.5 times taller than wide. *Hypodermis* absent. *Stomata* absent. *Chlorenchyma* absent. *Ground mesophyll* 4–6 layers between upper and lower epidermis. *Vascular bundles* absent. *Crystals* absent. *Secretory cells* absent. *Silica bodies* absent. *Tannins* absent.

5.3.2.2 Midrib TS (Figure 5.13)

Outline, dorsiventrally flattened, thickly crescentiform, adaxial surface shallowly concave, abaxial surface convex, slightly wider than thick. *Cuticle* as in lamina. *Epidermis* cells in one layer, cells as wide as tall or slightly taller than wide. *Prickles* and *hairs* lacking. *Stomata* and guard cells as in lamina. *Mesophyll* thin-walled with large lacunae, including a peripheral 2–7-layered chlorenchymatous region demarcated from central lacunose region; adaxial palisade-like, 2–3-layered; abaxial ellipsoid to more or less rounded and isodiametric, 3–7-layered; central ground mesophyll consisting of meshwork of uniseriate parenchyma cells enclosing large air lacunae. *Vascular bundles* ± 20, mainly large with few small or medium-sized, all with xylem facing towards the adaxial surface; occasionally up to 15 small bundles at junction of adaxial chlorenchyma and mesophyll. *Phloem* pole oval in outline, sieve tubes narrow, 5–6-sided; companion cells about one third the size of sieve tubes, shape irregular. *Xylem* composed of 1–3 large canals formed from disintegrated protoxylem elements; metaxylem of 3–5 tracheids next to phloem, with spiral thickening (LS). *Bundle sheaths* consisting of parenchyma cells, inner sheath of distinct cap at phloem pole, composed of large cells with small airspaces; outer sheath of single layer of cells not clearly circumscribed from the ground mesophyll. *Collenchyma* restricted to abaxial region, as triangular girders and strands or rarely as almost continuous band, cells of angular type. *Sclerenchyma* absent. *Crystals* present as raphides and druses in ad- and/or abaxial chlorenchyma and/or in ground mesophyll, crystal sand widespread. *Secretory cells* absent. *Silica bodies* absent. *Tannin* restricted to occasional cells of parenchyma in outer bundle sheath, rarely in xylem.

Z. aethiopica

Vascular bundles comprising about 15 small bundles at junction of adaxial chlorenchyma and ground mesophyll. *Collenchyma* mainly as girders with occasional strands. *Crystals* present as raphides and druses in ground mesophyll. *Tannin* present in xylem cells.

Z. albomaculata

Vascular bundles comprising about 15 small bundles at the junction of adaxial chlorenchyma and ground mesophyll. *Collenchyma* as girders and strands. *Crystals* present as raphides in ad- and abaxial chlorenchyma, druses in abaxial chlorenchyma.

Z. elliotiana

Vascular bundles with small adaxial bundles lacking. *Collenchyma* as girders and strands. *Crystals* present as raphides in ad- and abaxial chlorenchyma.

Z. jucunda

Vascular bundles comprising about 10 small bundles at junction of adaxial chlorenchyma and ground mesophyll. *Collenchyma* as girders and strands. *Crystals* present as raphides in abaxial chlorenchyma, druses in adaxial chlorenchyma.

Z. odorata

Vascular bundles comprising about 10 small bundles at junction of adaxial chlorenchyma and ground mesophyll. *Collenchyma* as almost continuous band subjacent to abaxial epidermis, widest opposite vascular bundles. *Crystals* present as raphides in ad- and abaxial chlorenchyma.

Z. pentlandii

Vascular bundles with small adaxial bundles lacking. *Collenchyma* generally as girders with a few strands. *Crystals* present as raphides in ad- and abaxial chlorenchyma, druses in adaxial chlorenchyma.

Z. rehmannii

Vascular bundles with small adaxial bundles lacking. *Collenchyma* as girders and strands. *Crystals* present as raphides in abaxial chlorenchyma.

Z. valida

Vascular bundles comprising about 12 small bundles at junction of adaxial chlorenchyma and ground mesophyll. *Collenchyma* as girders and strands. *Crystals* present as raphides in ground mesophyll, druses in adaxial chlorenchyma.

5.3.2.3 Petiole TS (Figures 5.14–5.16)

The petiole is very similar to the leaf midrib and differs in the following:

Outline truncated-circular. *Mesophyll* with peripheral cells chlorenchymatous, isodiametric with airspaces, interrupted by strands or girders of collenchyma. *Vascular bundles* with peripheral bundles smaller, followed next by medium-sized and large bundles in central lacunose region. All bundles with xylem directed towards the centre. *Tannin* restricted to occasional cells of parenchyma in outer bundle sheaths, often in xylem.

Table 5.3 Comparison of selected anatomical characters of leaves (lamina, midrib, petiole) of *Zantedeschia* spp.

Taxa	Lamina	Midrib			Petiole	
	crystal type in chlorenchyma	small adaxial bundles	tannin	raphide &/or druses	tannin	crystal type in ground mesophyll
Z. aethiopica	r,s	+	obs, x	gm	obs, x	r, s
Z. albomaculata	r, d, s	+	obs	chl	obs, x	r,s
Z. elliotiana	r,s	–	obs	chl	obs, x	r, s
Z. jucunda	r,d,s	+	obs	chl	obs	r,s
Z. odorata	r,s	+	obs	chl	obs	d,s
Z. pentlandii	r,d,s	–	obs	chl	obs	s
Z. rehmannii	r,s	–	obs	chl	obs, x	r,s
Z. valida	r,d,s	+	obs, x	chl, gm	obs, x	r,s

obs = outer bundle sheath; chl = chlorenchyma; gm = ground mesophyll; d = druse; r = raphide; s = crystal sand; x = xylem; + = present; – = absent

5.3.3 Tuber TS (Figure 5.17)

Epidermis cells obscured by cork layer. *Cork* cells 6–8-layered, cells 25–50 x 12.5–15 µm. *Ground tissue* of uniform, compact parenchyma, square to rectangular, 25–100 x 25–80 µm. *Starch* compound, up to nine grains per cluster, concentrated in inner ground parenchyma. *Vascular bundles* collateral, consists of metaxylem vessels with related parenchyma and phloem cells. *Crystals* present as raphide bundles and druses. *Tannins* present, not associated with vascular bundle.

5.3.4 Roots TS (Figure 5.18)

Outline terete. *Epidermis* cells square to rectangular, 12.5–25 x 7.5–12.5 µm, usually with aseptate root hairs. *Exodermis* cells rectangular, about 30 x 17.5 µm, slightly larger than epidermal cells. *Cortex* cells parenchymatous, 20-layered. *Stele* narrow, endodermal cells rectangular, about 17.5 x 7.5 µm, cell walls slightly thickened, pericycle uniseriate, indistinct. *Xylem* 5–8, metaxylem, circular, 40µm in diameter, with spiral thickening (LS) as in petiole (Figure 5.16). *Phloem* alternating with xylem, 6–9 cells per group, square to rectangular in outline, cells 7.5–12.5 x 5–7.5 µm. *Pith* (2–) 5–8 layers of parenchyma, cells 5–17.5 x 5–17.5 µm. *Tannin* cells few, close to vascular bundles.

5.3.5 Taxonomic notes

The intention of this study was to survey the range of variability of anatomical characters in the genus, to provide a general description for the genus and to highlight attributes of diagnostic value in demarcating species.

Leaf surface

Surface details and ornamentation on both surfaces are rather similar in all the species. In *Z. aethiopica*, the striations on the adaxial surface of the spotted area are more pronounced than those on the abaxial. This difference is of value only in the maculate forms of this species. However, it is known that maculate forms of this species are rare in the wild, and as such this character has limited diagnostic value. In the other species where spots are common, for example *Z. jucunda*, the surface details of the maculate and green areas are similar.

TS Leaf

The internal anatomy of leaves also indicates great similarity in structure in the green areas of both maculate and immaculate leaves of the same species. The maculate areas of the various species are very uniform in their internal leaf anatomy. The complete absence of stomata, chloroplasts and vascular tissue indicates a lack of photosynthetic activity. Minor differences in vascular bundles, collenchyma cells and crystals in the leaves were noted among species (Table 5.3, p. 41).

Stomata

All the species were easily recognisable by being amphistomatic (which might differ in other genera in the subfamily), with the frequency of stomata being similar on both surfaces. The maculate areas of the leaves lack stomata. The stomata are typically surrounded by 2 subsidiary cells. The outline of the guard cell pair was regularly elliptic in all species except *Z. aethiopica* and *Z. odorata*. In *Z. odorata*, the outline of the guard cell pair was found to be widely elliptic. In *Z. aethiopica* stomata on the adaxial surface have elliptic outlines, whereas those on the abaxial surface are widely elliptic.

The outer and inner stomatal ledges are equally developed in all the species. The outer stomatal ledge is said to restrict the front cavity above the pore, and the inner ledge restricts the back cavity which adjoins the substomatal chamber (Fahn 1974).

Petioles

Transverse sections of the petioles of all species show considerable similarity. Their general structure consists of a thin cuticle, a single layer of epidermal cells with stomata, a zone of alternating patches of collenchyma and chlorenchyma, ground parenchyma with large air lacunae and vascular bundles.

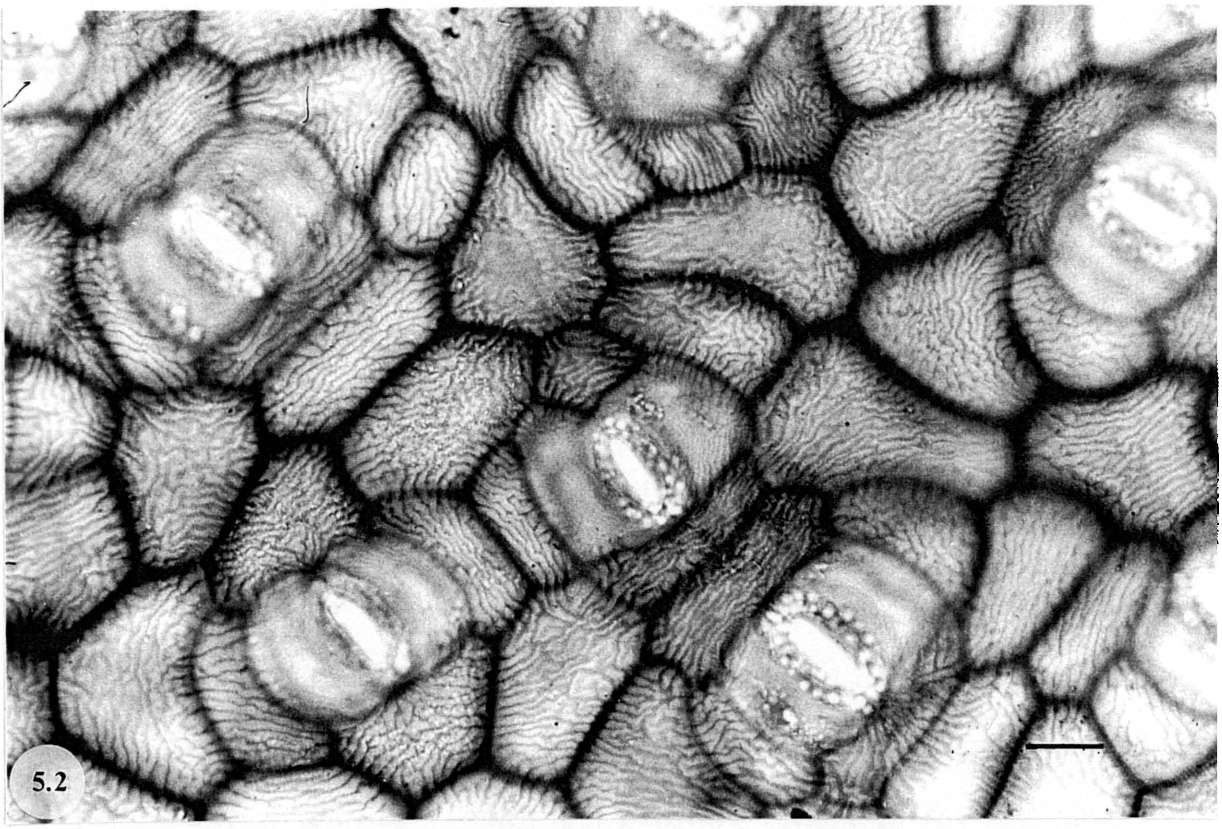
Collenchyma

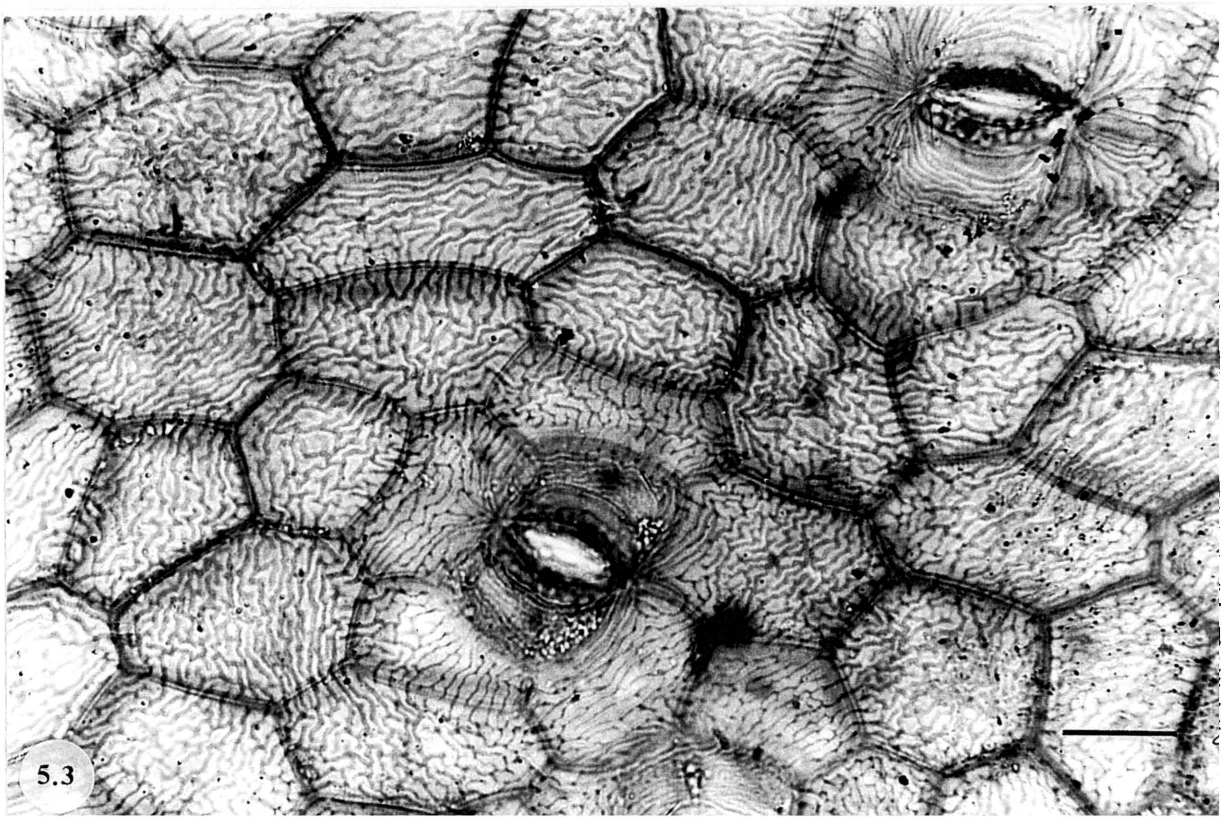
Collenchyma occurs usually as girders and strands and is restricted to the abaxial region in the midrib and petioles. Fahn (1974) considers collenchyma as juvenile supporting tissue which may become sclerified. In *Zantedeschia*, the collenchyma does not become sclerified. In all the species, the thickness of the walls of these cells was found to be similar.

Crystals

Raphides are present in most parts of the plant. Crystal sand was widespread in the petiole, lamina and midrib. In the tubers, raphides and druses were abundant.

Members of *Zantedeschia* are strikingly uniform in their anatomical features of the leaves, thus limiting the taxonomic value of anatomy at the infrageneric level. However, it has already been noted that very little has been published on the anatomy of this family. Characters noted in this study will most probably be useful when comparing the anatomy of related genera.

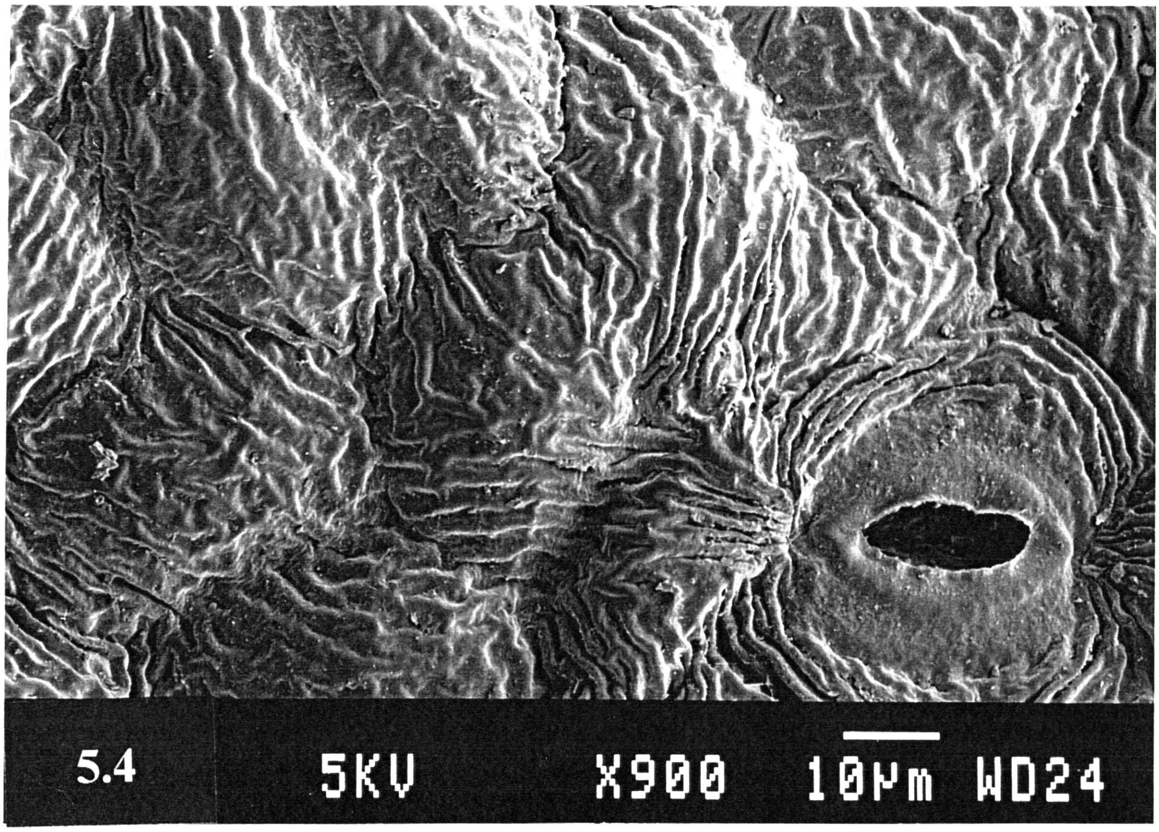


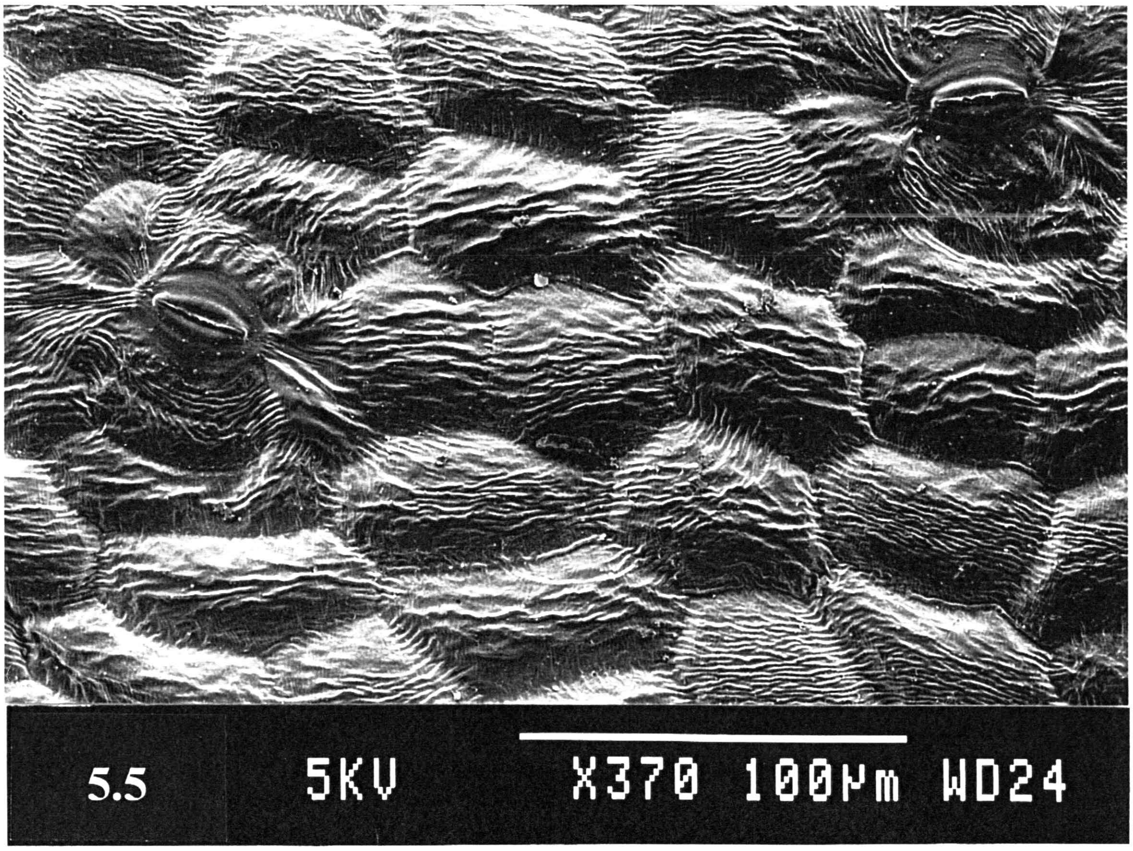


Figures 5.2–5.3 Light micrographs of lamina surface scrapes

5.2 *Z. albomaculata* subsp. *albomaculata*, adaxial epidermis with cuticular striations. Scale bar = 20 µm

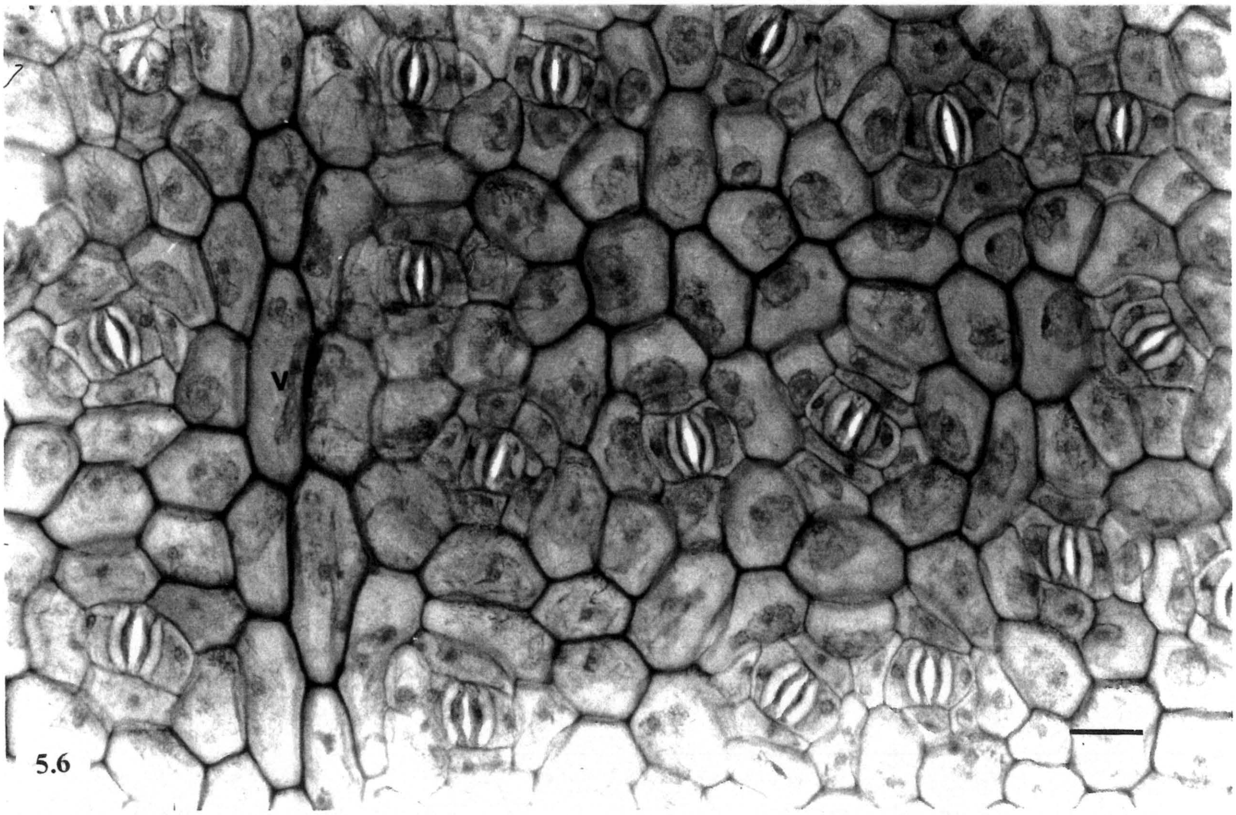
5.3 *Z. pentlandii*, abaxial epidermis with cuticular striations. Scale bar = 30 µm

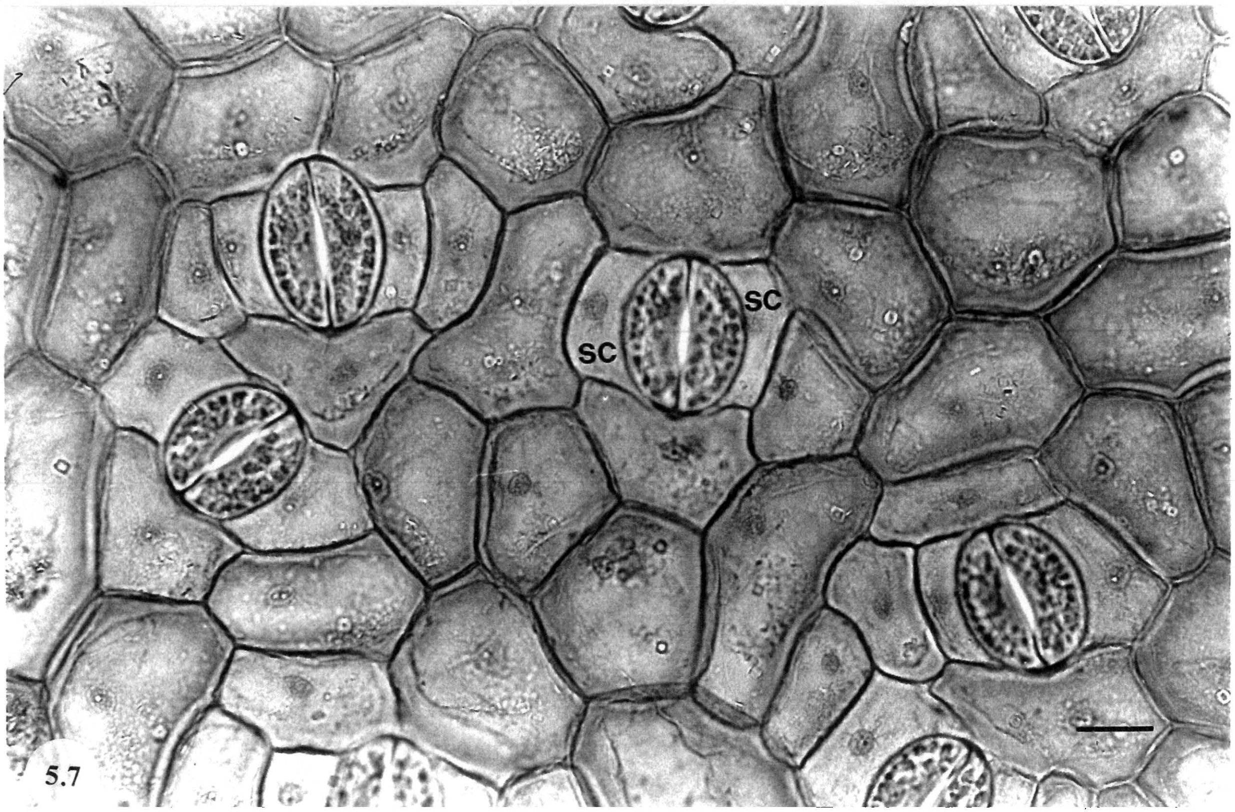




Figures 5.4–5.5 Scanning electron micrographs of lamina

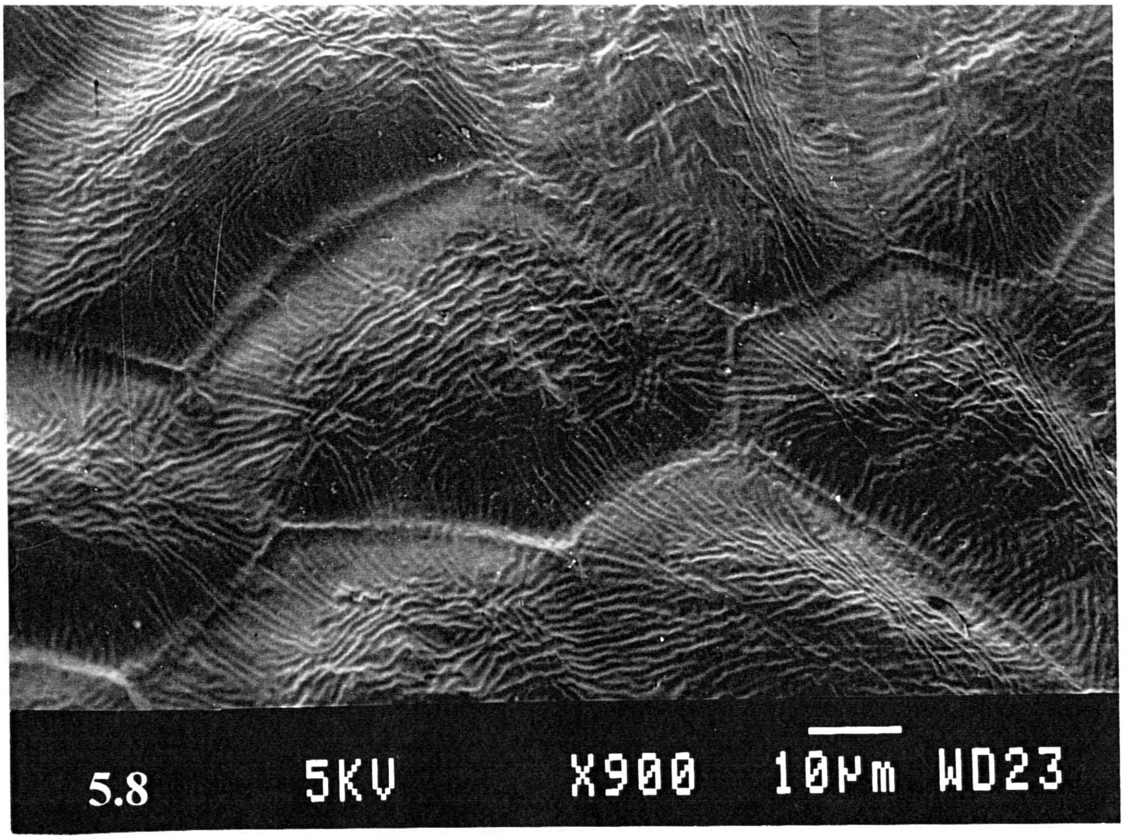
5.4 *Z. odorata*, adaxial surface
5.5 *Z. rehmannii*, abaxial surface

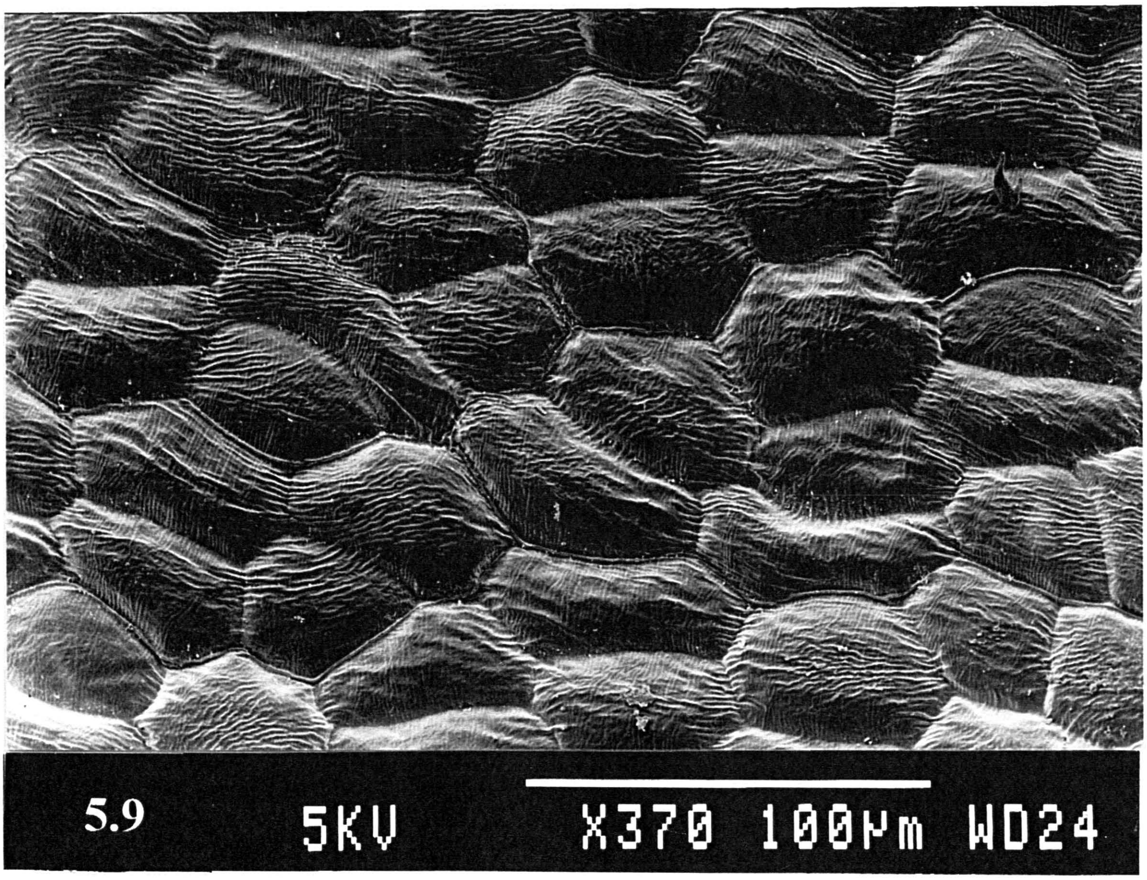

5.6


5.7

Figures 5.6–5.7 Light micrographs of lamina surface scrapes

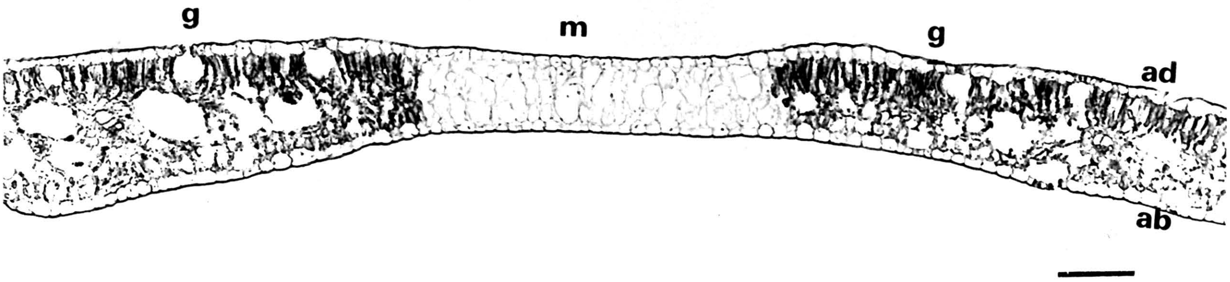
5.6 *Z. rehmannii*, adaxial surface, illustrating vein (v) region and stomatal orientation. Scale bar = 13 μm
5.7 *Z. albomaculata* subsp. *macrocarpa*, abaxial surface, subsidiary cells (sc). Scale bar = 13 μm





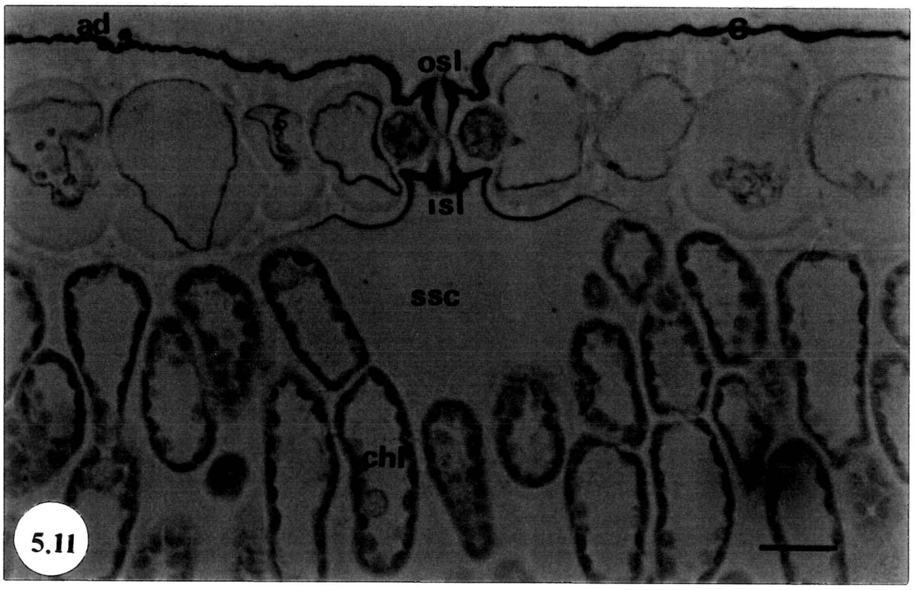
Figures 5.8–5.9 Scanning electron micrographs of maculations

5.8 *Z. elliotiana*, adaxial surface
5.9 *Z. jucunda*, abaxial surface



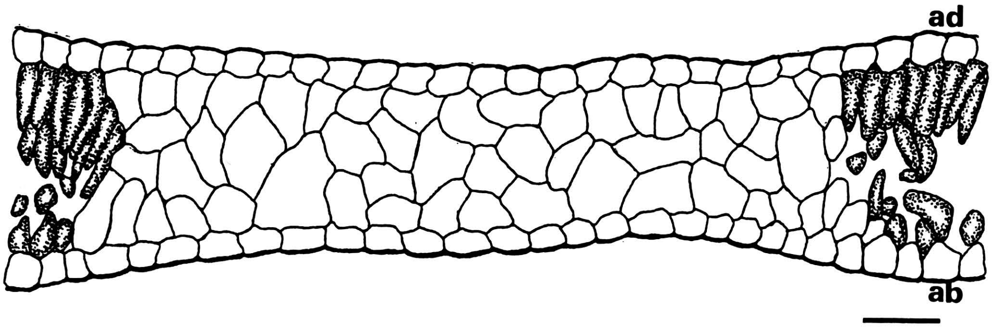
5.10

Figure 5.10 Light micrograph of TS lamina of *Z. albomaculata* subsp. *albomaculata*, outline through green and maculate areas. Scale bar = 220 µm
ab = abaxial surface; ad = adaxial surface; g = green area; m = maculate region



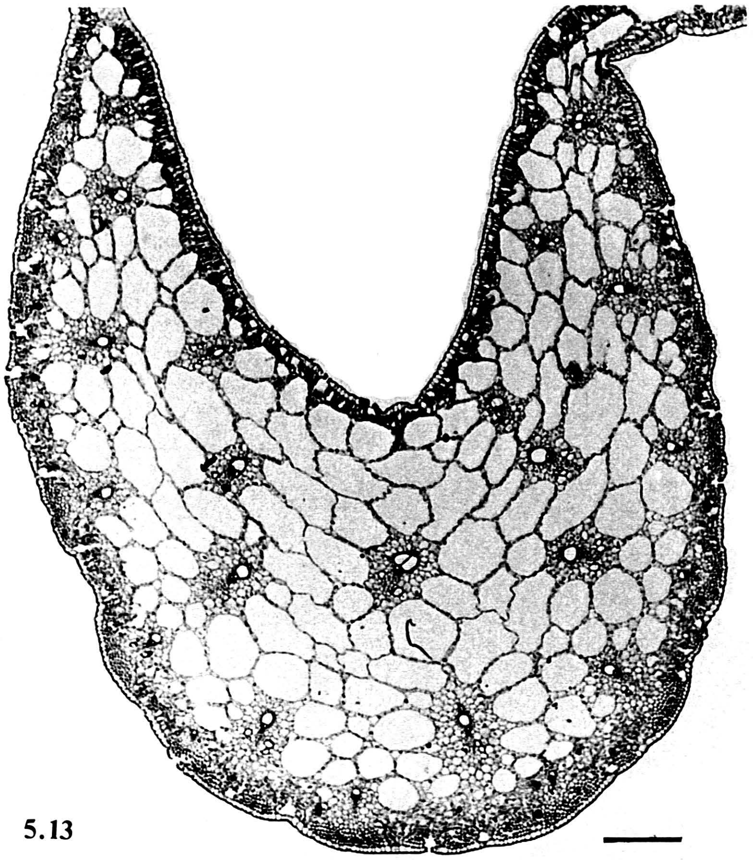
5.11

Figure 5.11 Light micrograph of TS green area of lamina of *Z. elliotiana*, stomatal complex. Scale bar = 45 µm
ad = adaxial; c = cuticle; chl = chlorenchyma; isl = inner stomatal lip; osl = outer stomatal lip; ssc = substomatal cavity



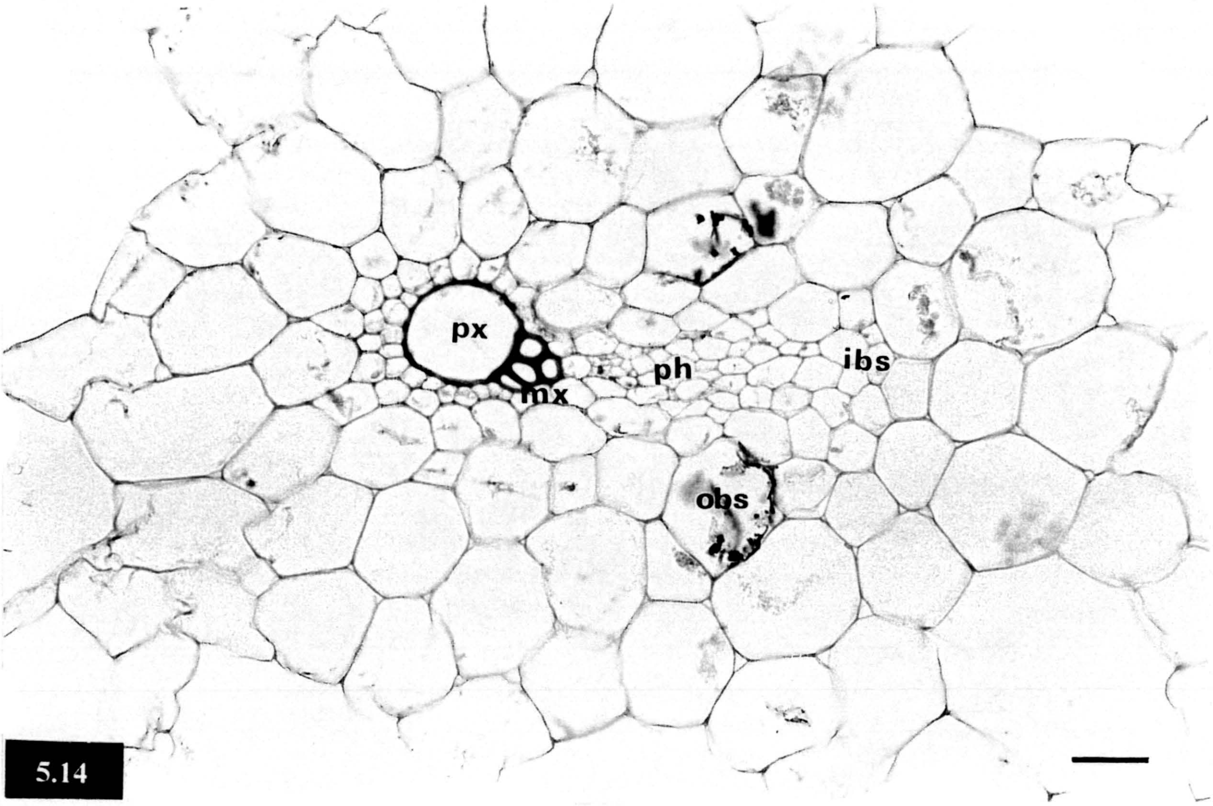
5.12

Figure 5.12 TS lamina of *Z. jucunda*, cells in maculation. Scale bar = 88 µm
ab = abaxial; ad = adaxial



5.13

Figure 5.13 Light micrograph of TS midrib of *Z. albomaculata* subsp. *macrocarpa*, outline, cells in midrib. Scale bar = 400 µm



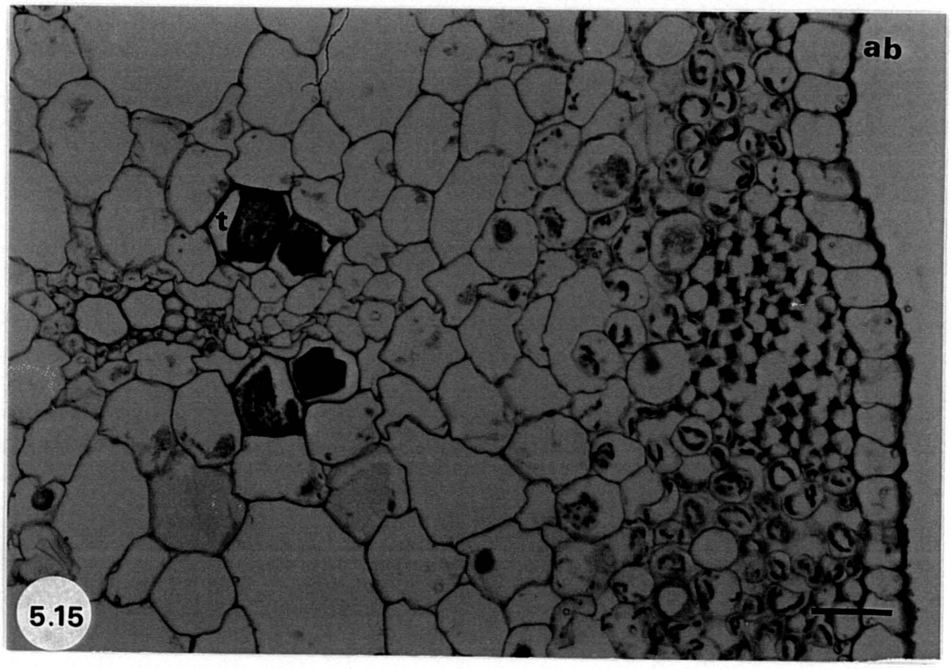


Figure 5.14–5.15 Light micrographs of TS petiole

5.14 *Z. rehmannii*, detail of vascular bundle. Scale bar = 30 µm

5.15 *Z. pentlandii*, tannin cells in outer bundle sheath. Scale bar = 90 µm

ab = abaxial; ibs = inner bundle sheath; obs = outer bundle sheath; mx = metaxylem;
ph = phloem; px = protoxylem; t = tannin

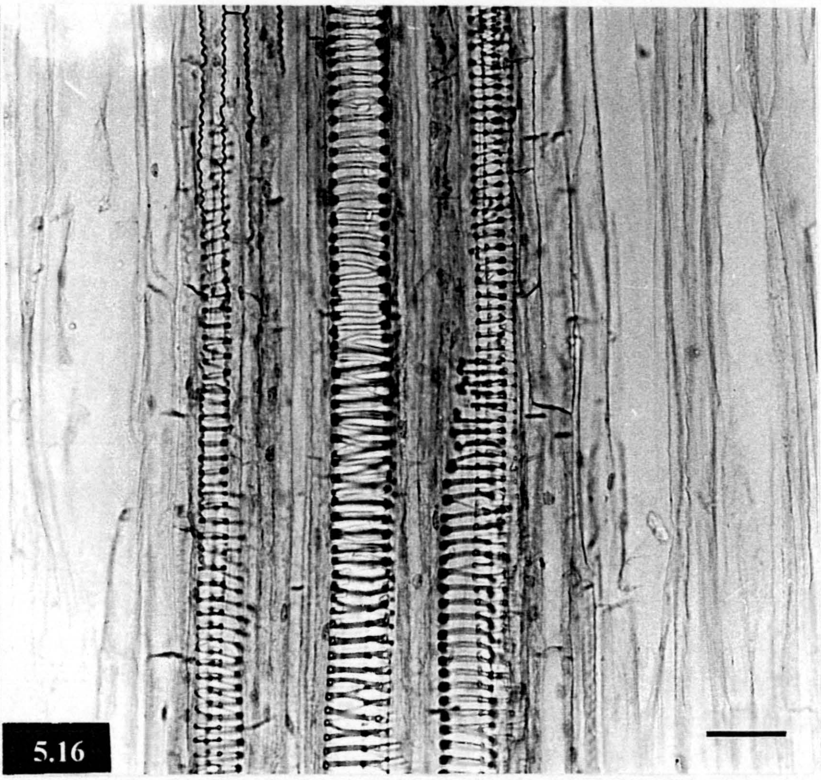


Figure 5.16 Light micrograph of LS petiole of *Z. pentlandii*, illustrating spiral thickening in xylem. Scale bar = 16 µm

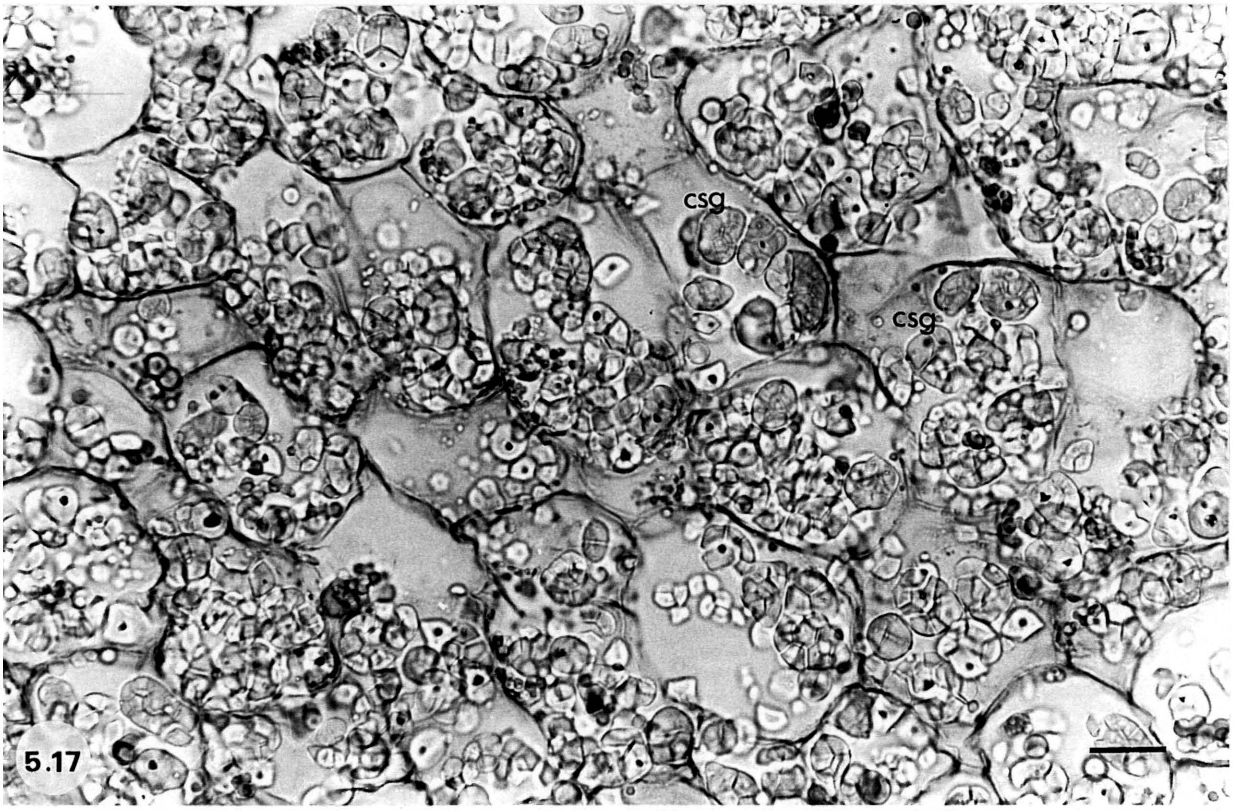


Figure 5.17 Light micrograph of TS tuber of *Z. odorata*, compound starch grains (csg). Scale bar = 35 µm

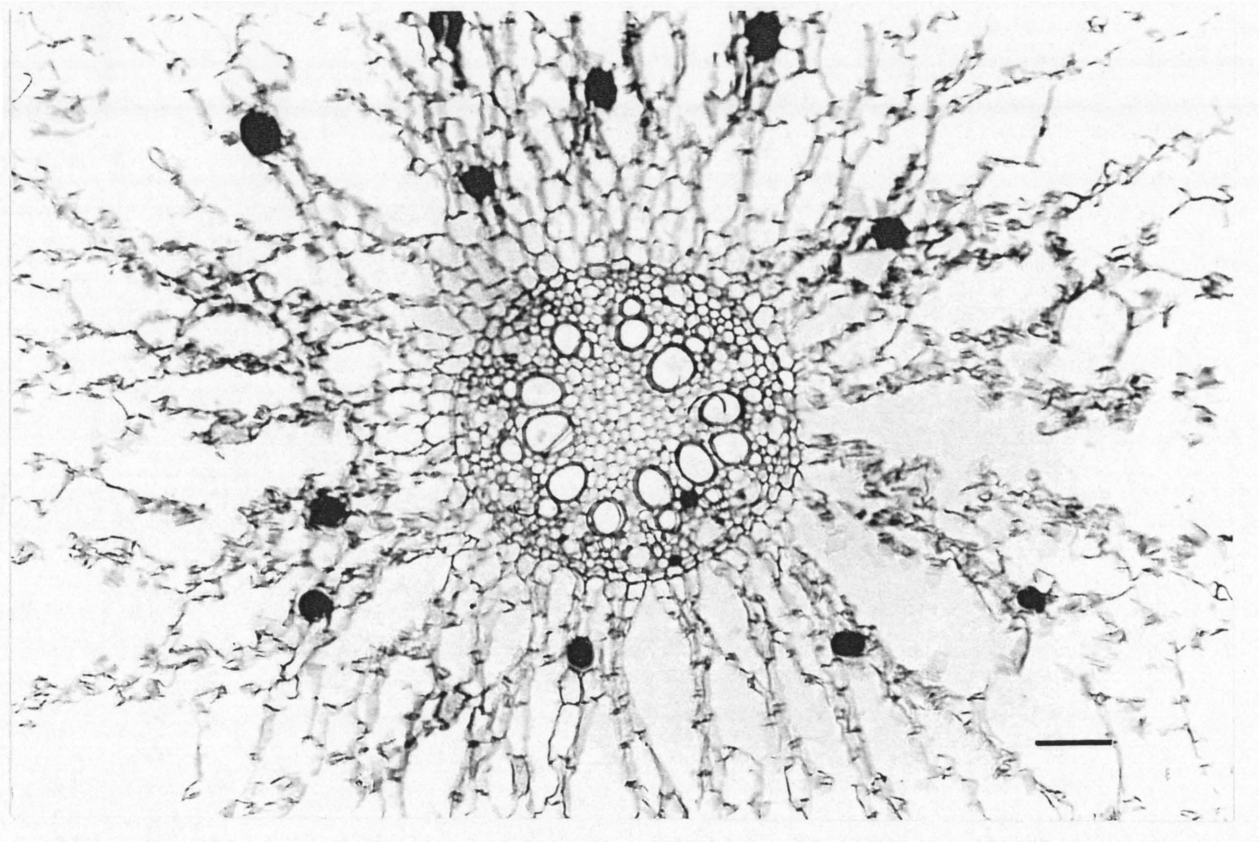


Figure 5.18 Light micrograph of TS root of *Z. rehmannii*, stelar and cortical regions. Scale bar = 55 µm

CHAPTER 6

MORPHOLOGY OF FLORAL AND FRUITING STRUCTURES

6.1 Introduction

Characteristic to the family Araceae, is the inflorescence (Figure 6.0) consisting of a large, often conspicuously coloured bract (spathe), which subtends or envelops a spadix of numerous infinitesimal sessile flowers. Members display considerable diversity in flower characters: uni- or bisexual, presence or absence of perianth, stamens one to six - fused or free, presence or absence of staminodes among female flowers, locules one to many, ovules anatropous, amphitropous or orthotropous on basal, apical, axile or parietal placentas.

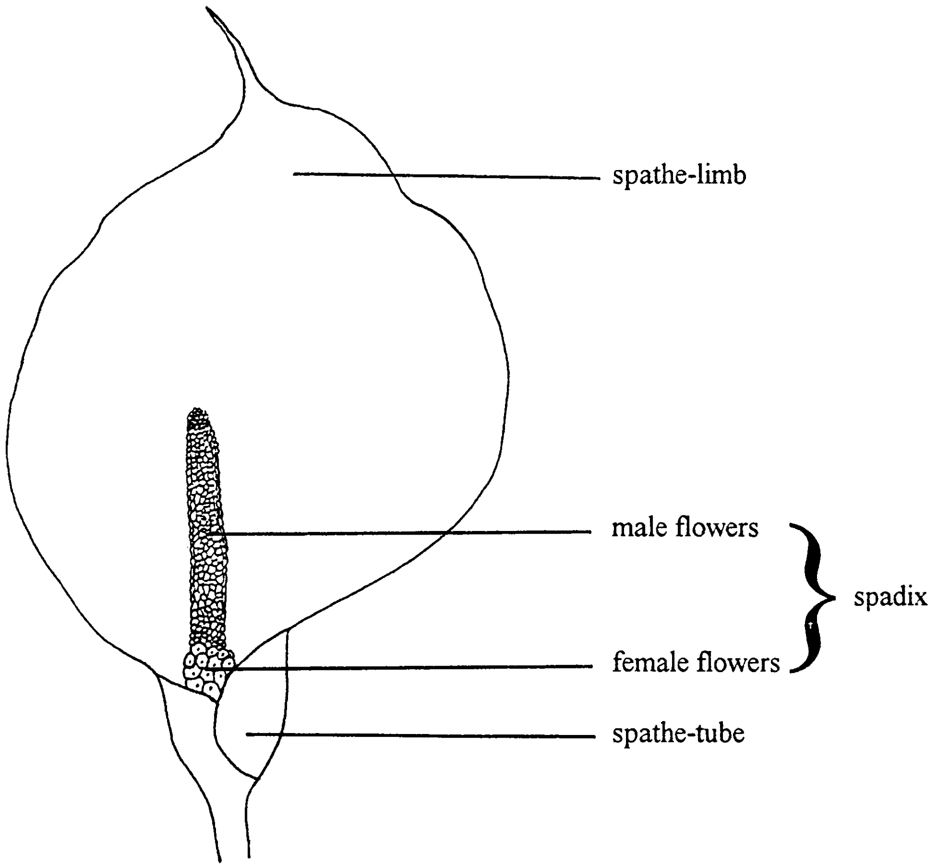


Figure 6.0 General morphology of the aroid inflorescence

The diversity of the family makes suprageneric classification difficult. The Schottian system (Schott 1860) focused purely on floral morphology (quoted in Nicolson 1960). Engler (1920) recognised eight subfamilies on the basis of vegetative and floral morphology as well as anatomy, and his system included ideas on evolution (quoted in Nicolson 1982). Hutchinson (1973) like Schott emphasised floral morphology. Grayum's (1990) cladistic treatment of the family based on vegetative and floral characters suggests five subfamilies. Bogner & Nicholson (1991) divided the Araceae into nine subfamilies using evidence from morphology. Their classification system emphasises habit, reticulate versus striate venation, the nature of the spathe and spadix, bisexual versus unisexual flowers and the presence or absence of a perigon. Since the details of floral morphology form the basis of aroid classification, variation in morphology needs to be well documented.

This chapter focuses firstly on the morphology of floral structures and secondly on the fruiting structures in *Zantedeschia*. Variation shown by individual species with regard to a particular character is discussed in the relevant section. The taxonomic importance of characters is highlighted in the description, and is further elaborated upon under the taxonomic inference.

6.2 Materials and methods

The study of the morphology of floral and fruiting structures was based on field observations of natural populations in South Africa between 1992 and 1995. Descriptions are based on plants in the wild, those kept in cultivation, herbarium specimens and material preserved in formalin-acetic-acid-alcohol (FAA) in the ratio 1:1:18. The description is that for the genus, with taxonomic differences among species being emphasised.

Ten infructescences of *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata* were collected from single populations in KwaZulu-Natal. These were used to assess the number of fruit per infructescence as well as the number of seeds per fruit. The number of ovules per ovary was compared with the number of seeds per fruit to determine the percentage seed set.

6.3 Floral structures

6.3.1 Inflorescences

Inflorescences are contemporary with the leaves. There is usually only a single inflorescence per leaf axil arising from a sheath. Rarely is a second inflorescence initiated at a leaf axil. Each leaf axil does not develop an inflorescence. Inflorescences develop mostly from the uppermost leaves, when leaves are mature. The inflorescence emerges rapidly and reaches its full height in about two weeks after bud emergence. Usually, the plant has only one or two inflorescences. The rate at which inflorescences on a plant emerge varies, thereby preventing selfing.

6.3.2 Peduncles

Inflorescences are borne on upright peduncles. Peduncle length is variable among species as well as within a species, being equal to or slightly longer than the leaves. The peduncle is generally green, but in *Z. albomaculata* subsp. *albomaculata* may be purple, or if green, then mottled with purple or white. In *Z. jucunda*, *Z. valida* and sometimes in *Z. pentlandii* peduncle bases are also mottled with purple. The peduncle is held erect until pollination is achieved. When the berries are mature, the weight of the infructescence causes the penduncle in all species except *Z. aethiopica* to bend towards the ground, so that the infructescence comes to lie on the ground. In *Z. aethiopica,* the peduncle remains firm and erect at berry maturity.

6.3.3 Spathes

Spathes are cylindrical or funnel-shaped, convolute at the base, variously coloured and a purple-coloured blotch at the base is present in some species. Typically, spathe shapes can be differentiated into two types: cylindrical (Figure 6.1) and funnel-shaped (Figure 6.2). The length to width ratio of the cylindrical spathe is approximately 2.5–6:1 and that of the funnel-shaped spathe is 1–1.5:1. The points at which measurements were made are indicated in Figures 6.1 & 6.2. Table 6.1 summarises spathe characters of taxonomic importance among species.

Z. albomaculata, *Z. odorata* and *Z. rehmannii* can be distinguished by their cylindrical spathes. Spathes are funnel-shaped in the remaining species. Generally, in all species, the margins of the limb, in the open spathe prior to fruit set, tend to overlap thereby enclosing the spadix. The spathe of *Z. odorata* (Figure 6.3), although cylindrical, is distinct from those of *Z. albomaculata* and *Z. rehmannii* in that the margins do not overlap, hence the spathe is open towards the base.

When pressed open, spathes may be grouped into two categories on the basis of their length to width ratios, namely cordate versus ovate. In all species (Figure 6.4), except

Table 6.1 Spathe characters of diagnostic importance in *Zantedeschia*

Taxon	**Spathe** **Shape**	**Colour**	**Purple -coloured blotch at base of spathe interior**
Z. aethiopica	funnel	white, sometimes with a purplish tinge on the outside	absent
Z. albomaculata subsp. *albomaculata*	cylindrical	white, cream, pale yellow, sometimes coral pink	present or absent
Z. albomaculata subsp. *macrocarpa*	cylindrical	cream	present or absent
Z. elliotiana	funnel	golden yellow	present or absent
Z. jucunda	funnel	golden yellow	present
Z. odorata	cylindrical	white	absent
Z. pentlandii	funnel	lemon, chrome yellow	present
Z. rehmannii	cylindrical	white, shades of pink to dark maroon	present or absent
Z. valida	funnel	white	present

Z. odorata (Figure 6.5) and *Z. rehmannii*, spathes are cordate. In the latter species, the spathes are ovate. Although spathes of *Z. albomaculata* are folded into a cylinder appearing longer than broad, when opened out, their lengths and widths are about the same.

The apex of the spathe is diagnostic in separating *Z. albomaculata* subsp. *macrocarpa* from the typical subspecies. In *Z. albomaculata* subsp. *albomaculata* (Figure 6.6), the apex of the spathe tapers and recurves whereas in *Z. albomaculata* subsp. *macrocarpa* (Figure 6.7), the apex is truncate. However, a few specimens of *Z. albomaculata* subsp. *albomaculata* [Wood 431 (NH), Strey 4874 (NH)] were found to have truncate spathes.

Spathe colour is also of diagnostic significance at infrageneric level. The funnel-shaped spathes of Z. *elliotiana*, Z. *jucunda* and Z. *pentlandii* are yellow and can therefore be easily separated from the white spathes of Z. *aethiopica* and Z. *valida*. The separation of species with cylindrical spathes, on the basis of colour is less useful as many of the shades intergrade.

The presence or absence of a purple-coloured blotch (Figure 6.8) is the third character of taxonomic importance. Its presence in Z. *jucunda*, Z. *pentlandii*, Z. *valida* and its absence in Z. *aethiopica* and Z. *odorata* is a consistent diagnostic character. The purple-coloured blotch is inconsistent in spathes of Z. *albomaculata*, Z. *elliotiana* and Z. *rehmannii* and is therefore of little diagnostic value in these species. The presence of the purple-coloured blotch in Z. *valida* is valuable in separating this species from Z. *aethiopica*. The length of the blotch equals that of the female zone on the spadix.

During fruiting, the spathe is persistent, turning green in all species except Z. *aethiopica* and Z. *odorata* in which only the lower half of the spathe is persistent, the upper half withers away exposing the berries.

Variations in spathes observed in wild populations

In the wild, spathes of Z. *aethiopica* were found to have pink or purple streaks on the outside (Figure 6.9). This pattern was not observed on spathes of any of the other species. There have been recent reports of a pink cultivar "Pink marshmallow" of Z. *aethiopica* (Figure 6.10), which is not known in the wild. It is probably a variation of the cultivated form. Pink coloration in Z. *aethiopica* is a polymorphic character as plants raised from seeds of the pink form often produce white spathes. The pink or purple streaks on the outside of spathes suggest that the species has genes for pink or purple coloration. Ae cultivar of *Z. aethiopica*, "Green Goddess" (Figure 6.11) has been successfully propagated for its green and white spathes. Similarly, efforts are being made locally to bulk produce the "pink marshmallow".

In a natural population of *Z. albomaculata* subsp. *albomaculata* in KwaZulu-Natal, cream to yellow spathes were observed to have white spots (Figure 6.12). This is not surprising when one considers that the spathe is a modified leaf and may therefore have the potential to produce maculations as do the leaves. Plants with maculate and those with immaculate leaves, both were observed to produce maculate spathes. This suggests that plants with immaculate leaves also carry genes for maculations. In horticulture, spathe maculation holds promise for producing colourful spathes through the manipulation of genes, such as the purple ones of *Z. rehmannii* with white maculations.

Another sport in the form of double spathe which is occasionally found in natural populations, may be introduced as a garden ornamental. In general, the outer spathe is leaf-shaped, about twice as long as the inner one and lacks a spadix (Figure 6.13). Not much is known about this phenomenon, and as such the stability of this character needs assessment. Nevertheless, the anomaly has tremendous potential for horticultural purposes.

6.3.4 Spadices

The spadix is typically cylindrical, narrowing towards the apex (Figure 6.14). Size of spadices vary depending on the size of the spathe, being usually shorter than the spathe.

Spadices are sessile or sometimes shortly stipitate and monoecious. The spadix in *Z. odorata* (Figure 6.5) is consistently shorter and broader, being about 2.5 times longer than wide. In the remaining species, the spadix is about 8–10 times longer than wide (measurements at male phase). Such spadices, though inconsistent, have been observed in a few spathes of *Z. aethiopica*, *Z. jucunda* and *Z. pentlandii*. In *Z. odorata*, the stout stipe prior to fruit set is conspicuous as opposed to *Z. aethiopica* in which the stipe is sessile to subsessile.

6.3.5 Androecium

Each male flower comprises one to three anthers affixed to the spadix. Perianth segments are absent. Anthers (Figure 6.15) are sessile, free, oblong, 1.5–2 mm long, truncate at the apex and characterised by two terminal pores. Pollen is white and extruded through the pores in a fine thread (Singh *et al.*, Appendix 4).

6.3.6 Staminodes

Staminodes are interspersed among ovaries in *Z. aethiopica* and *Z. odorata*. Its presence is valuable in separating these two species from the remaining ones. Staminodes (Figure 6.16) are spathulate, tapering proximally towards the base. They can be differentiated from anthers (Figure 6.15) by their shape and the lack of terminal pores through which pollen is released.

The number, arrangement and structure of staminodes are similar in *Z. aethiopica* and *Z. odorata*, thus offering no difference for species separation. The possible role of staminodes in scent production and/or defence is discussed by Singh *et al.* (Appendix 4).

In a few specimens of *Z. albomaculata* subsp. *macrocarpa,* one to two staminodes were found among ovaries in the male-female transition zone. However, the ovaries lower down were devoid of staminodes, unlike in *Z. aethiopica* and *Z. odorata* where ovaries are consistently surrounded by three staminodes. No scent was perceived in the inflorescences of *Z. albomaculata* subsp. *macrocarpa* with staminodes.

6.3.7 Gynoecium

Ovaries are arranged in a spiral on the spadix (Fig. 6.14), are ovoid in shape, superior and green to white. Perianth parts are lacking. There are three locules per ovary, with 1–12 anatropous ovules of axile or subapical placentation. The style is short, 0.1–1 mm. Stigmas are truncate and covered by stigmatic papillae (Figure 6.17).

6.4 Fruiting structures

6.4.1 Infructescences

The infructescence gradually expands in size both laterally and vertically, the extra girth coming from the increase in berry size. Berries are supported by a persistent spathe. In *Z. aethiopica* and *Z. odorata* the upper part of the spathe withers away and berries are supported by the lower portion which turns green (Figure 6.18). In the remaining species, the entire spathe turns green (Figure 6.19). The peduncle in *Z. aethiopica* remains upright when berries are ripe (Figure 6.18). In the remaining species the penduncle bends downwards so that the infructescence comes to lie on the ground (Figure 6.19). The open end of the spathe comes to face downwards, such that the berries make contact with the soil. Berries disintegrate from apex to base. The spathe degenerates simultaneously from apex to base so that berries are consecutively released.

6.4.2 Berries

Berries are generally obovoid in shape, but this may vary due to pressure from the expanding neighbouring berries. In *Z. aethiopica* berries were found to be 1.5 times longer than wide, whereas in *Z. albomaculata* subsp. *albomaculata* berries are 1.3 times wider than long (Table 6.2). Berry dimension is important in separating these two species.

Berry colour is diagnostic in *Z. aethiopica.* Only in *Z. aethiopica* does the mature berry turn orange, soft and juicy when ripe. When all the berries are ripe, the infructescence appears orange. In the remaining species, berries remain green and their pericarp remains firm until disintegration. For further details on sequence of berry development in *Z. aethiopica*, see Singh *et al.* (Appendix 4).

Table 6.2 Comparison of ovary, ovule, berry and seed number in *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata*

	Z. aethiopica	*Z. albomaculata* subsp. *albomaculata*
Mean number of ovaries per inflorescence	70.1	17.3
Mean number of ovules per ovary	8.9	6.9
Mean number of berries per infructescence	84.5	16.6
Mean length of berry (mm)	12.49	10.22
Mean width of berry (mm)	8.45	12.88
Mean number of seeds per berry	4.30	4.19
% success (ovule to seed)	48.28	60.7

Percent success of ovule to seed was calculated as follows:

$$\% \text{ success} = \frac{\text{Number of seeds per berry}}{\text{Number of ovules per ovary}} \times \frac{100}{1}$$

Mean number of ovaries, ovules, berries and seeds were calculated from ten heads of *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata*. A comparison of the values for the two taxa are summarised in Table 6.2.

The number of berries per infructescence was found to correlate with the number of ovaries per inflorescence, which is lower in *Z. albomaculata* subsp. *albomaculata*. The higher number of berries in *Z. aethiopica* implies a higher number of seeds which might explain the comparative wide geographical range of this species.

6.4.3 Seeds

Seeds are ovoid to widely ovoid, verrucose, one to ten per berry. Although the mean number of seeds per ovary was found to be approximately the same for both taxa (Table 6.2), success of ovule fertilisation was 12.42% lower in *Z. aethiopica* than in *Z. albomaculata* subsp. *albomaculata*. When the number of berries per infructescence is considered, then the lower rate of ovule success in *Z. aethiopica* does not disfavour the species in any way. In both taxa, however, the ovule fertilisation was lower than 65%.

In all species, seeds were found to be viscid. However, in *Z. aethiopica*, seeds are surrounded by copious amounts of mucilage. This probably aids in avian dispersal. Since the seeds of *Z. aethiopica* may be avian dispersed, it may account for the species being widespread in South Africa. In the remaining species, seed dispersal is rather passive, by means of mere disintegration on the ground. This may explain why many of these species have more restricted ranges (see Chapter 8).

6.5 Taxonomic implications

6.5.1 Floral characters

In this study, floral characters considered to be important in separating species include: spathe shape and colour, presence of the purple-coloured blotch at the base of the spathe and presence of staminodes among ovaries.

Cylindrical versus funnel-shaped spathes are useful in demarcating groups of species. Spathe colour is important in separating species with funnel-shaped spathes. The presence of a purple-coloured blotch at the base of the spathe within was found to be taxonomically significant in distinguishing *Z. valida* from *Z. aethiopica*. Its presence in the cylindrical spathes is of little diagnostic use in the absence of vegetative characters.

The presence of staminodes in *Z. aethiopica* and *Z. odorata* enables the separation of these species from *Z. valida*. One or two staminodes present in the male-female transition zone of *Z. albomaculata* subsp. *macrocarpa* suggests that these may be traces of the loss of staminodes in this species or mere anomalies of the anthers in this zone.

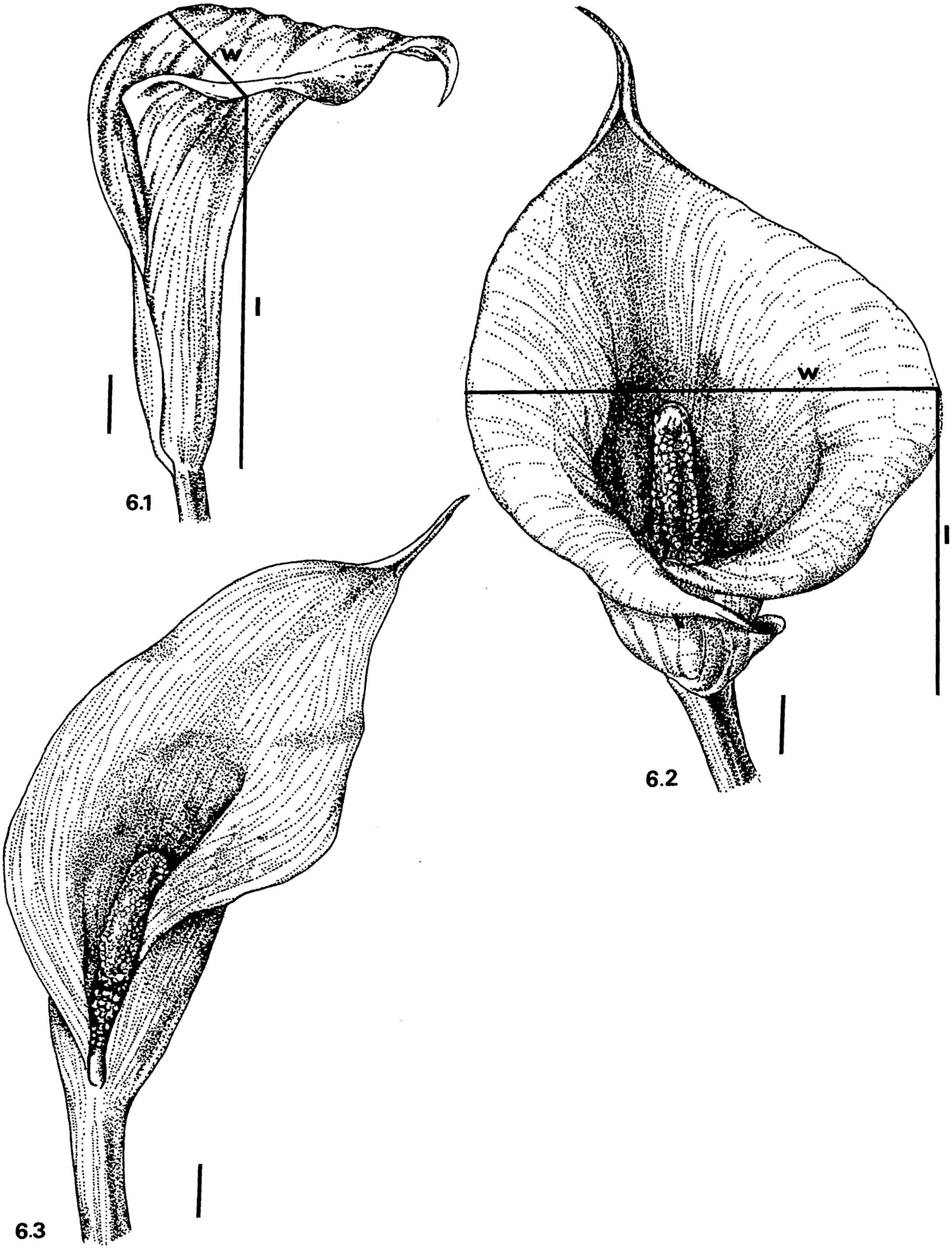
6.5.2 Fruit characters

Fruit characters of diagnostic value include berry size and colour, peduncle position when fruit are mature, greening of the spathe during fruiting, and the mechanism of seed dispersal.

Berry size was found to be important in separating *Z. aethiopica* from *Z. albomaculata* subsp. *albomaculata*. Dimensions of fruits in other species may be valuable in demarcating species and for indicating relationships among species.

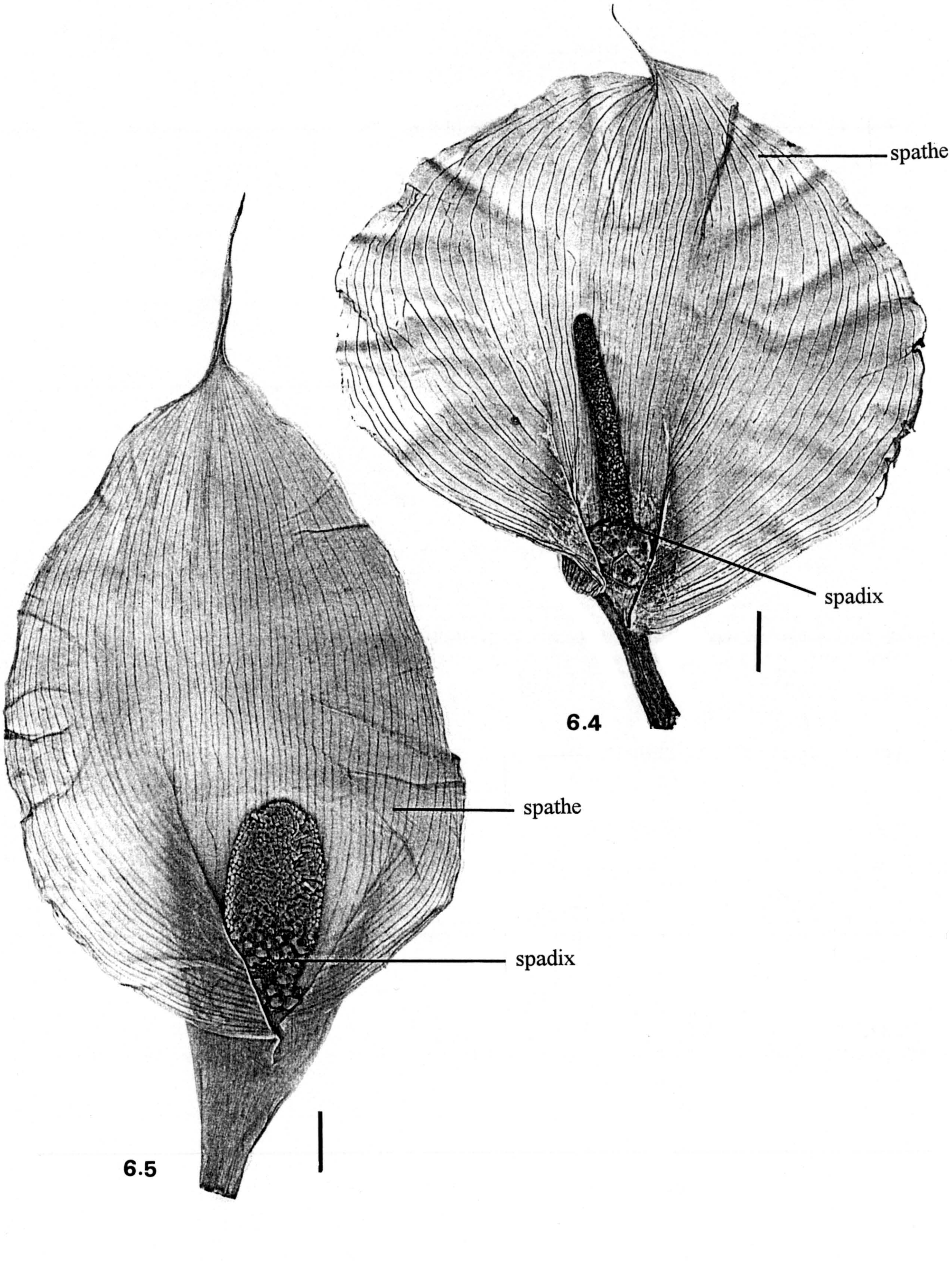
Change in colour of berries from green to orange in *Z. aethiopica* is useful in separating this species from the remaining species in which berries remain green. Berries in Z. *aethiopica* become soft, mucilaginous and orange in colour, seemingly in preparation for a specialised disperser (most probably birds). In the other species, seed dispersal is by disintegration of the berries on the ground, and the pericarp remains firm and green. In *Z. aethiopica*, the penduncle remains erect when berries are ripe, whereas in other species, the penduncle bends towards the ground. Only the lower half of the spathe in *Z. aethiopica* and *Z. odorata* turns green, whereas in the remaining species, the entire spathe turns green.

On the basis of floral and fruiting characters, *Z. aethiopica* is distinct from the remaining species. Its closest relative appears to be *Z. odorata* which differs in its cylindrical spathe open towards the base, short and stout spadix, fruits remaining green and firm on ripening, the penduncle bends towards the ground, and its restricted distribution. Floral and fruiting characters in *Zantedeschia* are valuable in demarcating species or groups of species and in reflecting relationships among them.



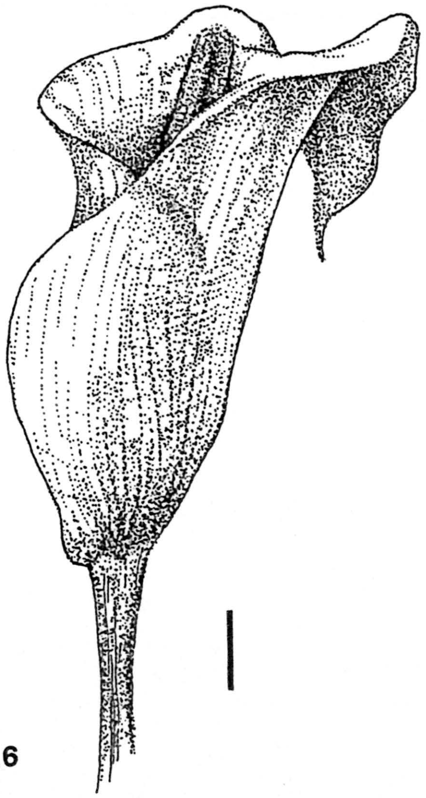
Figures 6.1–6.3 Spathe shapes of diagnostic value

6.1 *Z. rehmannii*, cylindrical. Scale bar = 10 mm 6.2 *Z. elliotiana*, funnel-shaped. Scale bar = 10 mm
6.3 *Z. odorata*, limb of spathe does not overlap. Scale bar = 12 mm

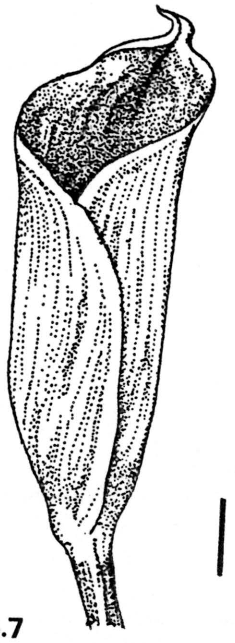


Figures 6.4–6.5 Photocopies of spathes showing shapes when pressed open

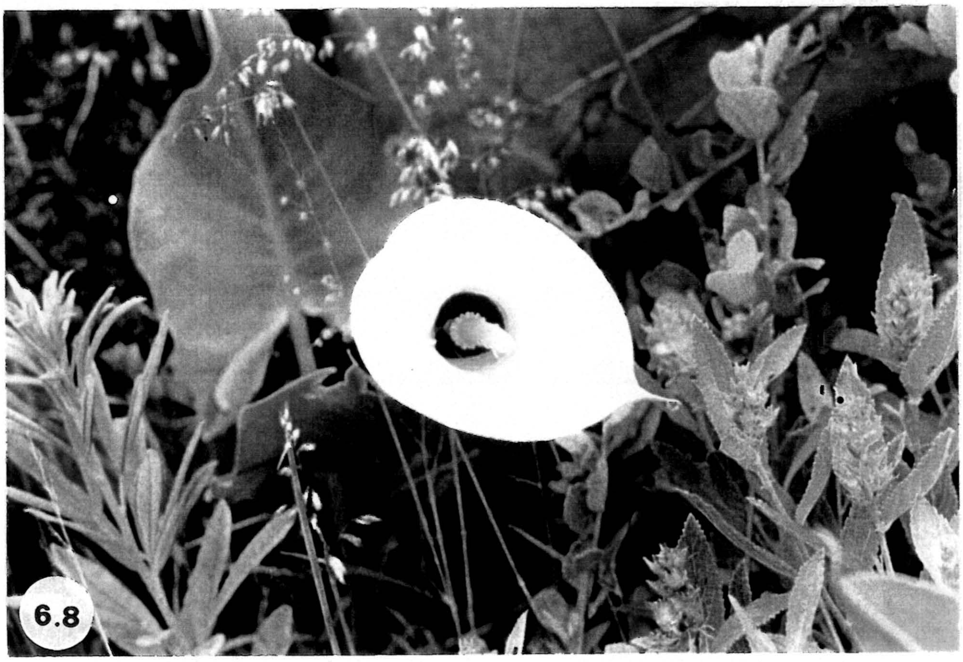
6.4 *Z. jucunda*, cordate. Scale bar = 10 mm
6.5 *Z. odorata*, ovate. Scale bar = 10 mm



6.6



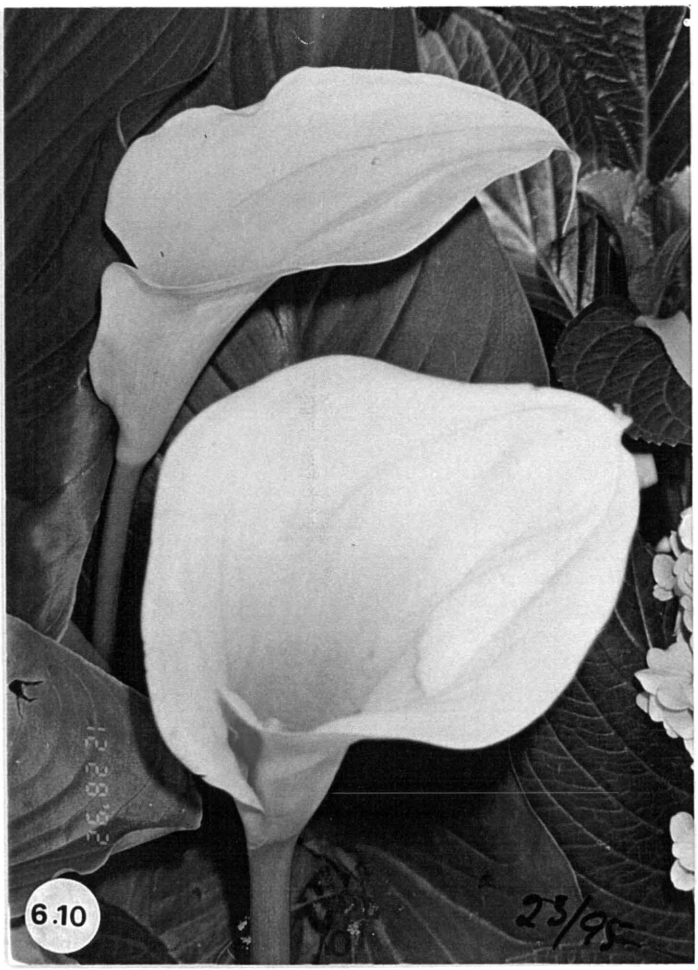
6.7



6.8

Figures 6.6–6.8 Spathe characters

6.6 *Z. albomaculata* subsp. *albomaculata*, limb of spathe reflexed. Scale bar = 10 mm
6.7 *Z. albomaculata* subsp. *macrocarpa*, limb of spathe truncate. Scale bar = 10 mm
6.8 *Z. valida*, purple-coloured blotch at base of spathe within



Figures 6.9–6.11 Variations in spathe colour

6.9 *Z. aethiopica*, purple streaks on outside of spathe
6.10 *Z. aethiopica*, "pink marshmallow", cultivar (Photograph by Rosemary Rudman)
6.11 *Z. aethiopica*, "Green Goddess", cultivar (From slide taken by Nancy Gardiner)


6.12


6.13

Figures 6.12–6.13 Variations in spathe form

6.12 *Z. albomaculata* subsp. *albomaculata*, white maculations on spathe
6.13 *Z. albomaculata* subsp. *albomaculata*, double spathe

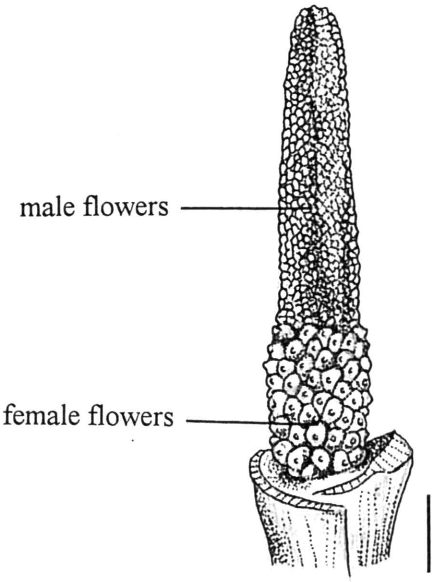
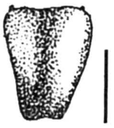
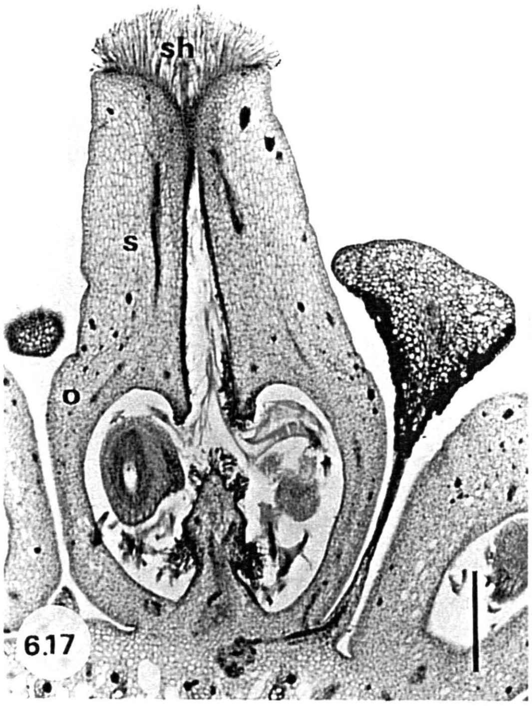


Figure 6.14 *Z. pentlandii*, spadix structure (spathe removed)
Scale bar = 15 mm



6.15 *Z. rehmannii*, anther
Scale bar = 1.5 mm

6.16 *Z. odorata*, staminode. Scale bar = 2 mm



6.17 *Z. aethiopica*, LS pistil showing stigmatic hairs. Scale bar = 1 mm
o = ovary; s = style; sh = stigmatic hairs


6.18


6.19

Figures 6.18–6.19 Fruiting characters

6.18 *Z. aethiopica*, upright peduncle, upper half of spathe withers
6.19 *Z. rehmannii*, peduncle bends towards the ground, entire spathe turns green

CHAPTER 7

POLLINATION BIOLOGY

7.1 Introduction

Pollination biology is an integral component of each of the disciplines of ecology, systematics and evolution (Estes *et al.* 1983). It provides a medium for understanding diversity. Pollination biology is also a basic science that provides theoretical knowledge for plant breeding.

The wide range of pollination strategies such as fungus mimicry (Meeuse & Morris 1984), odour and carrion mimicry (Kite 1995), trap mechanism (Dormer 1960) and heat mimicry (Moodie 1976; Robacker *et al.* 1988; Bay 1995) makes pollination biology in the Araceae a fertile field of research. While cantharophily (beetles) or myophily (flies) are common in the family, melittophily (bees) does occur to a lesser degree. Both fly and bee pollination syndromes were found among species of *Anthurium* (Croat 1980) while in a single species such as *Arum dioscoridis* Sm., beetles and flies have been implicated as pollinators (Grayum 1986).

Observations in *Zantedeschia* suggest that pollination is achieved mainly through beetle activity. The purpose of this chapter is to review and examine pollination strategies in *Zantedeschia*.

7.2 Materials and methods

Refer to Materials and Methods in Singh *et al.* (Appendix 4).

7.3 Breeding system

In this study, *Zantedeschia* is regarded as having a preference for outbreeding. Selfing is prevented, by the temporal separation of the maturing of the stamens and pistils (dichogamy) (Wyatt 1983), with the female flowers maturing before anther dehiscence (protogyny). Self-pollination in *Z. albomaculata* subsp. *albomaculata* has resulted in seed set (Singh *et al.*, Appendix 4). The stigmatic surface in this species has been observed to remain receptive during pollen release from anthers on the same spadix. This is in keeping with Baker & Baker's (1983) suggestion that the structure and the timing of the maturation of the male and female flowers may be altered to achieve pollination. In *Z. aethiopica*, the stigmatic surface degenerates before anther maturity, thus preventing selfing.

7.4 Floral reward/deceit mimicry

Observations on *Zantedeschia* illustrate modes specialised to achieve pollination, which may be interpreted as floral rewards or deceit mimicries. The presumed role of five characters in attracting beetles are speculated upon.

7.4.1 Stigmatic exudate

Simpson & Neff (1983) concluded that stigmatic exudates serve as a reward in plants that have a very short or rudimentary style and a relatively broad stigma. In *Zantedeschia* these morphological features are present. Furthermore, a stigmatic exudate is present when the stigmas are receptive. Although in this study, the exudates of *Zantedeschia* have not been tested for its constituents, it is felt that as in *Anthurium seibertii* Croat (Croat 1980), sugar levels in the exudates are probably high thus serving as a reward to insect visitors.

7.4.2 Spathe as a place to breed

The araceous spathe is ideally designed as a breeding place for insects. In *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata*, several beetles were observed at the base of single spathes. It is possible that the gravid females may be seeking a place in the spathe to lay their eggs. The male beetles probably enter the spathes to mate with the females.

7.4.3 Floral aroma

Second to the Orchidaceae, the Araceae is an important family in respect to scent production (Vogel 1990). Odours in the Araceae range from vile to sweet and fragrant. Meeuse *et al.* (1984) reported both a sweet fragrance and a vile odour in different parts of the same inflorescence of *Sauromatum guttatum* Schott (voodoo-lily). In *Z. aethiopica* and *Z. odorata,* a faint freesia-like scent is perceived during stigma receptivity (contrary to Perry 1989). Details on the possible sites of scent emission are discussed by Singh *et al.* (Appendix 4).

The correlation of odour and heat production with pollination in the family is reported in many studies (Moodie 1976; Meeuse *et al.* 1984; Robacker *et al.* 1988). Hatch & Millerd (1957) found that although spadices of *Zantedeschia* are identical to aroids with special type of respiration, there was no difference in the process of respiration in *Z. aethiopica.* The spadix tissue in *Z. aethiopica* is similar to that in other plant tissues, which is in contrast with the spadices of other scent producing aroids (Hatch & Millerd 1957). It is probable that *Zantedeschia* has dispensed with the production of heat during scent emission.

7.4.4 Markings on the spathe

The exact function (if any) of the purple-coloured blotch within the spathe is still unknown. Red and purple often add to the impression of rotting carrion, thereby attracting insects, but provides nothing for the insects in return (Gibbons 1984).

The presence or absence of the purple-coloured blotch at the base of the spathe is summarised for the genus in Table 6.1 (p. 58). Purple marking is constantly present in spathes of *Z. jucunda*, *Z. pentlandii* and *Z. valida*. The coloration extends from the base of the spathe to a height equalling that of the female zone and may therefore be correlated with activity in the female zone. For instance, it probably mimics the remains of dead flesh and aids in the attracting carrion beetles thereby effecting pollination. Alternatively, the marking could represent a group of beetles mating at the base of the spathe, thus inviting other beetles to join in. The blotch is however, absent in spathes of *Z. aethiopica* and *Z. odorata*. The presence of scent in these two species may be responsible for attracting pollinators.

The purple-coloured blotch is not consistent in spathes of *Z. albomaculata*, *Z. elliotiana* and *Z. rehmannii* and these species are also non-scented. Dark spathes in *Z. rehmannii* serve to attract carrion beetles and therefore the blotch in these spathes is redundant. This may explain the absence of the purple-coloured blotch in dark spathes. Many white to cream spathes of *Z. rehmannii* were recorded on herbarium labels as having the purple-coloured marking at the base. However, some light coloured spathes of *Z. albomaculata* were found to lack the purple-coloured blotch. What then is responsible for insect attraction in these spathes? Perhaps too much emphasis is being placed on the purple-coloured blotch as a beetle attractant. To explain attracting mechanisms in spathes lacking blotches, extensive field observations are necessary.

7.4.5 Dead arachnids/insects within spathes

In all species, dead spiders, bees and flies were found at the base of the spathe, apart from living beetles. The spathe probably provides a place for insects to trap food. The decaying bodies of the victims may also attract carrion insects into the spathe.

7.5 Possible role of staminodes in scented species

Gottsberger (1977) reported that beetles visiting flowers may feed on pollen, on nectar or on flower organs like petals, tepals, stamens and carpels and thereby cause considerable damage to flowers. In *Zantedeschia*, only scented species bear staminodes among their ovaries.

Engler (1884) suggested that the tepaloid staminodes among the ovaries in *Z. aethiopica* have a protective function (quoted in Grayum 1990). Staminodes may provide protection against herbivores. Lateral walls of anthers and staminodes (Figure 7.1) were found to be lined with several tannin cells. The ovaries, however, lack tannin. Chemically, tannins may have the potential to reduce the digestibility of proteins or if absorbed have toxic side effects (Ellis 1990). Furthermore, secondary substances such as tannins may have evolved in response to natural selection for defence against herbivores and insects (Whittaker & Feeny 1971). Therefore, it is suggested that tannins in the staminodes of *Z. aethiopica* and *Z. odorata* act as antifeedants to beetles, thus protecting the ovaries.

It is likely that with the loss of scent in the other species, there was subsequent loss of staminodes. In addition, the spadix, anthers, staminodes and ovaries in all species contain raphides of calcium oxalate which may also deter herbivory.

7.6 Pollen morphology and extrusion

Pollen exine sculpturing is psilate in *Zantedeschia* (Figure 7.2). Grayum (1986) found a positive correlation between psilate pollen and beetle pollination in the Araceae. He further suggests that pollen is attached onto the smooth hard bodied insects such as beetles through the agency of sticky secretions of the stigma or, of the inner spathe surface as in *Dieffenbachia* Schott. Pollen grains in *Zantedeschia* are held together in a thread by a sticky substance. Whether pollen is also held together electrostatically is unknown. Presumably, the release of pollen in threads requires only one end of the thread to attach itself to the insect body, for the entire thread to be transported. In *Z. albomaculata* subsp. *albomaculata*, pollen has been observed to fall in large masses onto the stigma, in the absence of vectors.

The mechanism for the release of pollen in flowering plants is achieved by shrinkage of the endothecial layer as cells lose water (Fahn 1974). In general, the inner periclinal walls of the endothecial cells or fibrous layer are thickened and this forces the anther slits to open during dehydration (Fahn 1974). Squeezing of pollen grains through pores in *Z. aethiopica* and other poricidal members of the Araceae is due to the thickening being on the outer rather than the inner periclinal walls of the endothecial cells (Weberling 1989). The inverse position of the thickening probably creates an inward pressure during water loss, thereby compressing the pollen sac which releases the pollen in threads through the pore.

7.7 Breeding behaviour

Crosses between species were not attempted in this study as several species failed to flower under greenhouse conditions. Furthermore, most endemic species are located far away from the centre of study, making frequent visits difficult.

Bagging experiments in the greenhouse indicated that *Z. aethiopica* is self-incompatible. Bagged inflorescences of *Z. albomaculata* subsp. *albomaculata* set seed, inferring that selfing occurs in this species. Self compatibility or incompatibility could not be established in the other species as they failed to flower under greenhouse conditions. Nevertheless, these observations have given rise to a few questions requiring further study. Is self-pollination in *Z. albomaculata* subsp. *albomaculata* habitual or a fail-safe mechanism when cross pollination has failed? Is it possible that only species with cylindrical spathes are self-compatible, while those with funnel-shaped spathes require cross pollination? Is selfing restricted to the *Z. albomaculata* group, where temporal separation of sexes is lacking? This information will be of particular importance to plant breeders. The gap in knowledge may be filled in by future collaborative research with horticulturists, plant breeders, geneticists, and amateur botanists.

7.8 Hybridisation

Letty (1973) was of the opinion that occasionally plants of hybrid origin between *Z. aethiopica* and *Z. albomaculata* occurred in the former Transvaal and in Lesotho where the two species overlap. This is contrary to reports by Traub (1948). He recorded that although seeds developed between crosses of *Z. aethiopica* and other summer rainfall species (discoid tubers), they failed to germinate. Crosses between species with discoid tubers were however successful. During this study no apparent hybrids of *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata* were found in areas where the two species overlap. The species appeared to be reproductively isolated.

Interspecific hybridisation occurs readily in taxa with discoid tubers (Traub 1948). Chi (1990) and Yao (1992) reported that incompatibility between species with discoid tubers and *Z. aethiopica* is indicated by abortion of the embryo and endosperm and by albinism in rescued hybrids (quoted in Yao *et al.* 1994). Since *Z. aethiopica* does not breed true with species with discoid tubers, Letty's (1973) record of hybrids between *Z. aethiopica* and *Z. albomaculata* is doubtful.

Crosses between *Z. aethiopica* and *Z. odorata* did produce viable seeds but the seedlings were virescent (Yao *et al.* 1994). These authors also reported that hybridisation of *Z. odorata* with species with discoid tubers produced better developed embryo and endosperm than *Z. aethiopica* but albinism in the hybrids persisted.

7.9 Post pollination floral changes

Zantedeschia can be grouped under Gori's (1983) pollination-induced temporal pattern of floral change. This means that after pollination, there is a rapid change in floral characters. Gori (1983) argues that this pattern of floral change is quite distinct from simple floral senescence and suggests that these changes have important adaptive significance for species possessing them. Post pollination floral changes in *Zantedeschia* were found to provide characters of diagnostic value. The changes will be discussed as per character.

7.9.1 Floral scent

In *Z. aethiopica* and *Z. odorata,* the scent which was perceptible at stigma receptivity disappears after anther dehiscence.

7.9.2 Colour of spathe

Part of or the entire spathe turns green as the berries mature. In *Z. aethiopica* and *Z. odorata*, only the lower half of the white spathe turns green, while the upper half dries and falls off. In the remaining species, the entire spathe which was either shades of white, yellow or red, turns green wrapping itself tightly around the berries.

7.9.3 Berry colour

Berries in *Z. aethiopica* change from green to orange, probably out of the visible range of insects into the visible range of birds. In all other species berries remain green.

7.9.4 Staminodes

In *Z. aethiopica* and *Z. odorata*, the staminodes disintegrate after pollination, becoming hidden in between the enlarging berries.

7.9.5 Anthers

The male zone degenerates and eventually senesces once all pollen has been released.

7.9.6 Stigmatic surface

The stigmatic surface glistens during stigma receptivity, but after pollination, the surface degenerates and turns brown.

Pollinators are able to recognise post pollination floral changes and visit only unpollinated flowers (Gori 1983). It is probable that the changes in *Zantedeschia*, no longer offer beetles a place for foraging or brooding in the spathe (as berries enlarge), hence forcing them to seek spathes with unpollinated flowers.

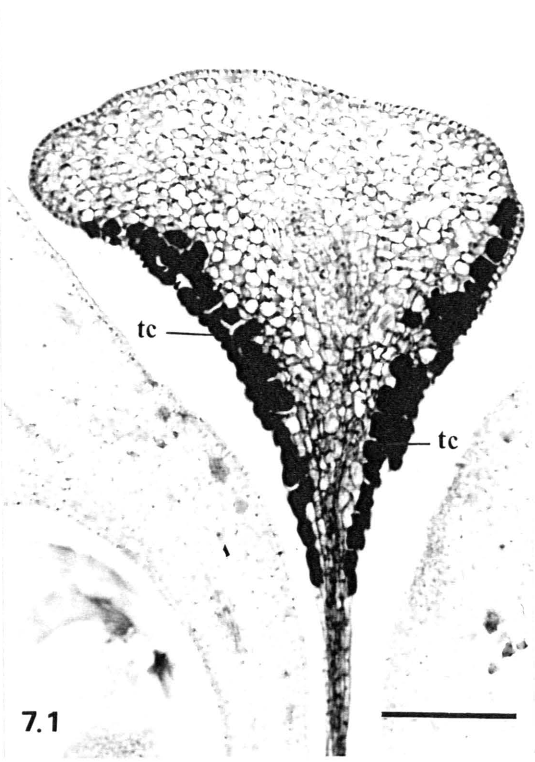
In this study, *Z. aethiopica* formed the basis for understanding pollination biology in the genus. For a detail report on the pollination and the development of flowers in *Z. aethiopica*, see Singh *et al.* (Appendix 4).

7.10 General inferences

From the studies made on members of the genus, particularly *Z. aethiopica*, the following broad inferences are presented.

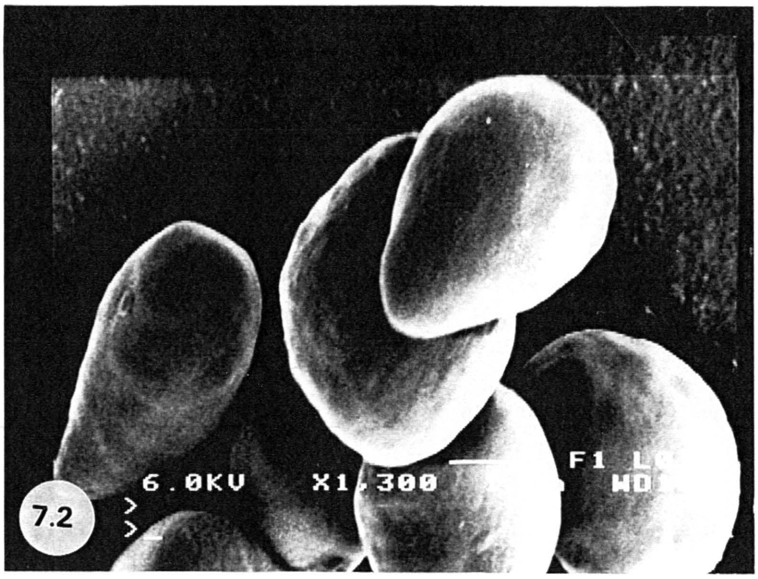
- Members of the genus are usually outbreeders. Selfing is a fail safe mechanism in some species when cross pollination fails.
- All species are beetle-pollinated. Beetles use the base of the spathe (female zone) as a place for breeding. The stigmatic exudate sticks to the bodies of beetles. Pollen adheres to the sticky exudate on the beetle body and is transported in this way.
- The stigmatic exudate may also provide a source of sugar for the beetles during their stay in the spathe.

Several suggestions made in this study, regarding pollinators, rewards for insect visitors, pollen, method of pollen transfer, self-compatibility versus self-incompatibility, chemistry of the exudate, post pollination changes and insects, need confirmation and further examination. These desiderata which require a major effort will no doubt provide the information necessary for an evolutionary study of the group.



7.1

Figure 7.1 *Z. aethiopica*, LS staminode showing tannin cells (tc) in lateral walls. Scale bar = 1 mm



7.2

Figure 7.2 Scanning electron micrograph of pollen grain of *Z. aethiopica* . Scale bar = 28 µm

CHAPTER 8

PHYTOGEOGRAPHY

8.1 Introduction

Patterns of distribution displayed by taxa are useful in the interpretation of the origin, migration and evolution of species as well as in taxonomic decisions. *Zantedeschia* is restricted to Africa south of the equator, with a concentration of species in southern Africa. Among the eight species, only *Z. albomaculata* subsp. *albomaculata* extends into Zimbabwe, Malawi, Angola, Zambia and Tanzania. Members of the genus prefer subtropical to warm temperate climates. Species display a variety of geographical patterns from wides to endemics, allopatry to sympatry, and disjuncts to vicariants. In this chapter, the phytogeography of species is discussed in terms of geology, ecology and its value in circumscribing taxa.

8.2 Materials and methods

Distribution maps were prepared from specimens housed at the National (PRE), Natal (NH) and H.G.W.J. Schweickerdt (PRU) herbaria using the Mappit computer programme (NBI, Pretoria), for the Flora of Southern Africa region (FSA).

8.3 Geographical distribution

8.3.1 Widespread species

Z. aethiopica and *Z. albomaculata* subsp. *albomaculata* may be regarded as widespread in southern Africa. *Z. aethiopica* is the most vigorous species, occurring mainly along the coast of South Africa from the Western Cape Province through to the Northern Province (Map 1, p. 124). In this large area the species has been recorded from Western Cape, Eastern Cape, KwaZulu-Natal, the Free State, North West Province, Gauteng, Mpumalanga, Northern Province, Swaziland and Lesotho. The wide geographical range of this taxon may be attributed to its comparative ability to inhabit moist as well as more mesophytic habitats. Furthermore, *Z. aethiopica* does not seem to have a preference for any particular altitude, soil type or rainy season. It occurs from sea level to high altitudes about 2000 m above sea level, in the winter and summer rainfall areas.

In the FSA region, *Z. albomaculata* subsp. *albomaculata* ranges from Eastern Cape Province to the Northern Province (Map 6, p. 128). This species extends into Lesotho, Swaziland, Zimbabwe, Zambia, Angola, Tanzania and Malawi (Figure 8.1). *Z. albomaculata* subsp. *albomaculata* does not occur in the winter rainfall region of the Cape. In KwaZulu-Natal and Mpumalanga, the species was found growing sympatrically with *Z. aethiopica* and appears to be reproductively isolated.

8.3.2 Endemics

8.3.2.1 Broad endemics

The distribution pattern of *Z. albomaculata* subsp. *macrocarpa* (Map 7, p. 129) and *Z. rehmannii* (Map 8, p. 129) are rather similar. Both species are concentrated mainly in Mpumalanga, extending into Gauteng, KwaZulu-Natal, the Free State and Swaziland. Unlike *Z. albomaculata* subsp. *albomaculata*, these species do extend further south beyond KwaZulu-Natal, into the Eastern Cape.

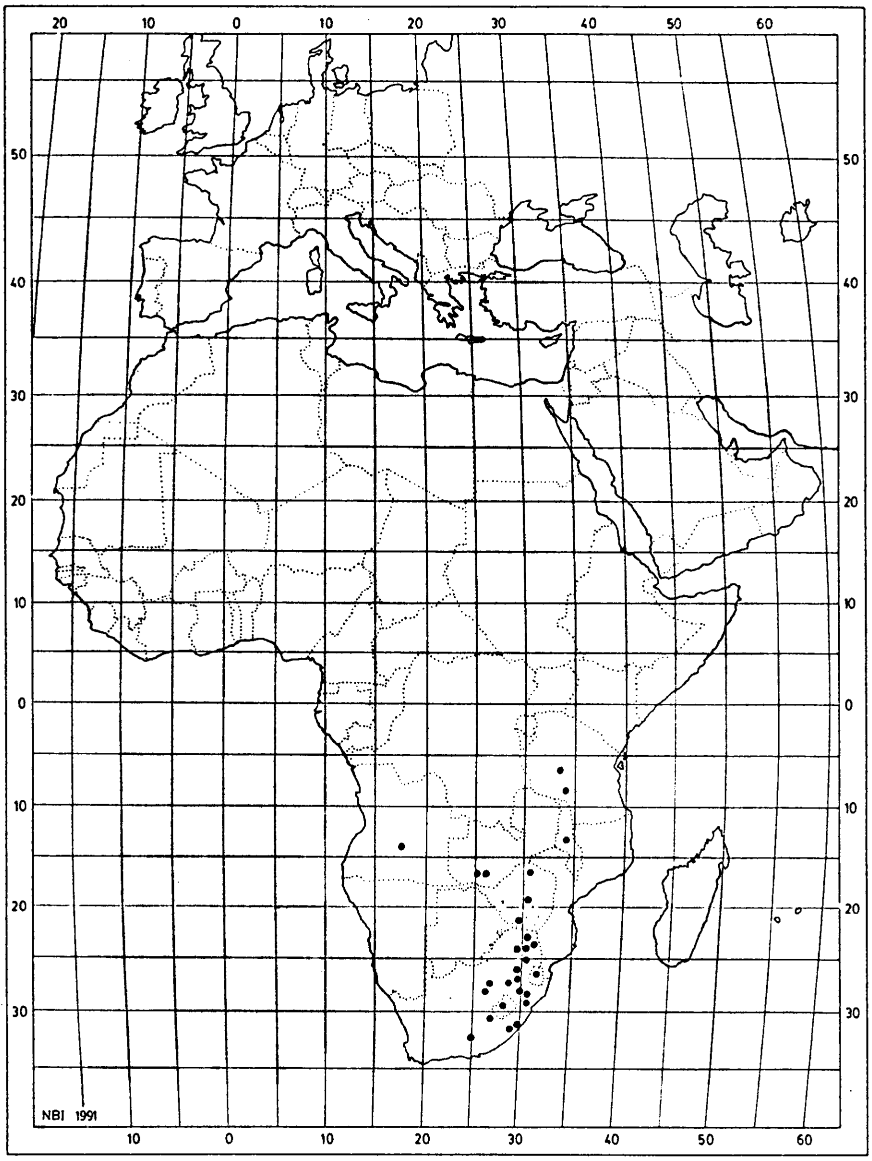


Figure 8.1 Distribution of *Z. albomaculata* subsp. *albomaculata* in southern and south-central Africa

8.3.2.2. Narrow endemics

Z. jucunda, *Z. pentlandii*, *Z. valida* and *Z. odorata* are endemic to relatively small areas in South Africa. The former two species are endemic to Mpumalanga, *Z. valida* to Northern KwaZulu-Natal and *Z. odorata* to the Western Cape.

Z. jucunda and *Z. pentlandii* are restricted to a small area in Mpumalanga. They occur on substrates derived from rocks of the Dsjate Subsuite, part of the Rustenburg Suite of the Eastern Bushveld Complex. The region is characterised mainly by gabbro-norite with seams of magnetite (iron and vanadium), chromite and plantiniferous rocks. The two species occur in the same general area but are strictly allopatric with *Z. jucunda* (Map 5, p. 127) being confined to a small area in the Lulu Mountains in Sukukuniland (grids 2429 and 2430), whereas *Z. pentlandii* (Map 4, p. 126) occurs further south on rocky outcrops near Roosenekal in the Lydenburg District (grid 2530). Allopatry is important in isolating these two taxa reproductively.

A specimen referred to as *Z. pentlandii* [Batten s.n. (PRE 36456)] was reported to have been collected at Tsolo in the Transkei. Locality details on the label states "Transkei, Tsolo" and is followed by a question mark. The specimen consists of two young leaves and no flowering material. Since young leaves in this species are similar to those of *Z. albomaculata* subsp. *albomaculata*, which is common in the Transkei, it is difficult to confirm the identity of the specimen. Batten in Batten & Bokkelman (1966) has painted *Z. pentlandii* which she cites as being collected at Tsolo. She received the plant from a lady who worked for her neighbour (pers comm.). The plant was said to have been collected at Tsolo.

North of Tsolo, there is a great sill of gabbro-norite at Insizwe, Mount Ayliff, Tabankulu and Ingeli in the former Transkei (Du Toit 1954). Since the rock types in the area is rather similar to those in Mpumalanga, it is likely that *Z. pentlandii* could grow in this area. Should *Z. pentlandii* occur in the wild at Tsolo, then the species shows a disjunction of more than 650 km. Disjunction due to long distance dispersal is highly unlikely considering that seed dispersal in this species is by means of fruit disintegration on the ground. Attempts to locate the *Z. pentlandii* population at Tsolo have hitherto been in vain. Disjunction in the species is therefore dispensable until the existence of a population in the Transkei is confirmed.

Z. valida is restricted to the region bordered by the Biggarsberg, Giants Castle and Collin's Pass (grids 2829 and 2929) in KwaZulu-Natal (Map 3, p. 126). The species occurs in a moist dark brown, clay-loam soil which is moderately permeable.

Z. odorata is endemic to the dolerite outcrops in the Nieuwoudtville District (grid 3119AC) in the Western Cape (Map 2, p. 125). The doleritic boulders break down to form a red, slowly permeable clay soil which has a high water holding capacity. During the rainy season the soil retains water well while in the dry season the clay hardens and cracks.

Except for plants of *Z. aethiopica*, *Z. albomaculata* and *Z. rehmannii* growing in open grassland, all *Zantedeschia* tubers are buried beneath boulders or in the crevices, so that in the period of dryness the tubers are kept cool. In the rainy season, the tubers themselves are kept moist by the moisture in the soil around it.

8.3.3 Species not found in the wild

Z. elliotiana is known only from cultivated material and is not known from the wild. The species was described from a plant cultivated from seed of unknown origin. Two possibilities exist as to why this species does not occur in the wild. Firstly, the plant may be of hybrid origin. The possible parents being *Z. albomaculata* subsp. *albomaculata*, which contributes genes for ovate-orbicular leaves, and *Z. pentlandii* or *Z. jucunda* which contributes genes for funnel-shaped yellow spathes. Secondly, habitat destruction or human collecting pressure may have reduced the species to an isolated population which is easily missed in the wild, or perhaps it has become extinct; although at this stage evidence is overwhelmingly in favour of it being a hybrid of cultivation.

Experimental hybridisation of *Z. pentlandii* or *Z. jucunda* and *Z. albomaculata* subsp. *albomaculata* may assist in supporting the hypothesis that *Z. elliotiana* is a hybrid between these species. The combination of ovate-orbicular leaves and funnel-shaped spathes clearly defines *Z. elliotiana* as distinct and it is for this reason that the taxon is still upheld in this study.

8.4 Centre of genetic diversity

The greatest concentration of species is in the Lydenburg grid (2530) in Mpumalanga (Figure 8.2). This geographical degree square contains four species which include *Z. aethiopica*, *Z. albomaculata*, *Z. rehmannii* and the endemic, *Z. pentlandii*. It is probable that species originated in this province, radiating into neighbouring provinces and countries. It is probable that *Z. aethiopica* and *Z. odorata* have originated in the winter rainfall region whereas the remaining species have their origin in the summer rainfall region. Eight grids between the 24^0 and 30^0 latitudes and 28^0 and 32^0 longitudes, contain the three species, *Z. aethiopica*, *Z. albomaculata* and *Z. rehmannii*. Northwards above the 24^0 latitude and southwards below the 30^0 latitude, the concentration of species decreases to two or one. The number of species per degree square is likely to change when specimens from other herbaria in southern Africa are incorporated into the database and as collections increase.

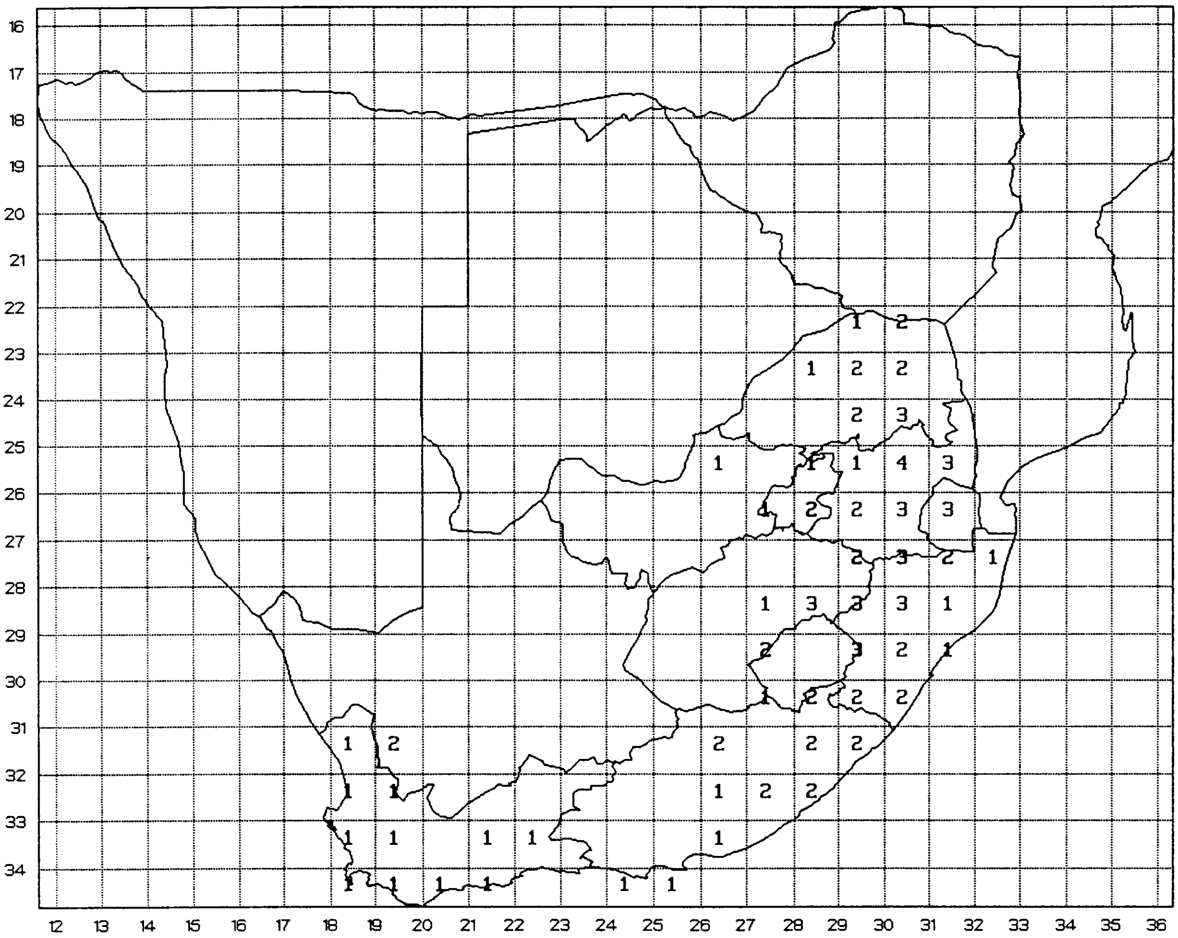


Figure 8.2 Distribution of *Zantedeschia*. The number of species per geographical degree square is indicated for the FSA region.

8.5 Ecological distribution

The preference of *Zantedeschia* species for particular vegetation types was interpreted on the basis of Rutherford & Westfall's (1986) biomes of southern Africa (Figure 8.3). Table 8.1 outlines the biomes in which species occur. It is clear that members of the genus do not grow in the Desert and Nama-Karoo biomes, probably due to aridity. The mean annual rainfall in the Desert (13—85 mm) and Nama Karoo (100—520 mm) biomes is probably too low and inconsistent to support the growth of these herbs.

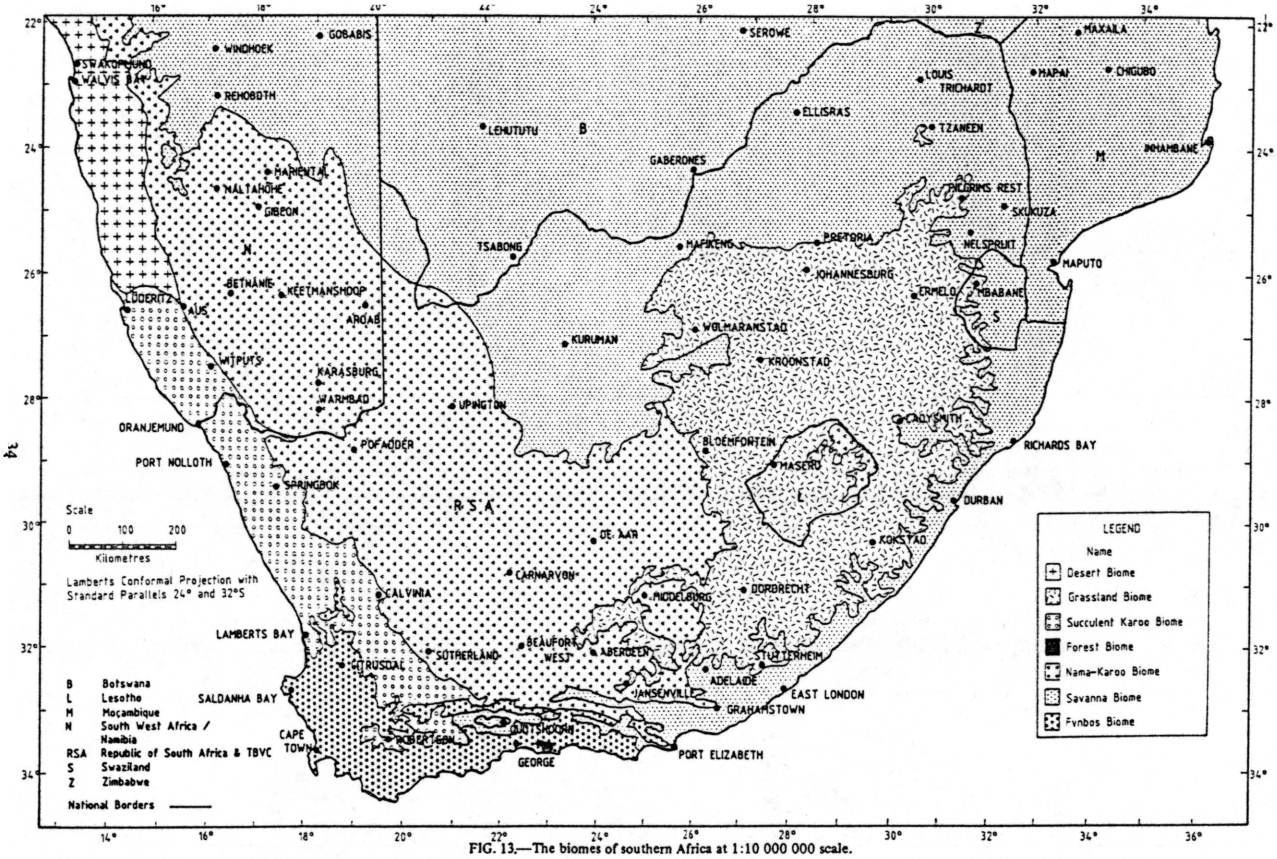


FIG. 13.—The biomes of southern Africa at 1:10 000 000 scale.

Figure 8.3 Biomes of southern Africa (ex Rutherford & Westfall, 1986)

On the other hand, the genus thrives well in grassland (400—2000 mm), savanna (235 mm) and fynbos (210—3000 mm). Although the annual rainfall in forest (525—725 mm) is high, species tend not to grow inside the forest, most probably due to low light intensity. Occasionally, *Z. aethiopica*, *Z. albomaculata* subsp. *albomaculata* and *Z. rehmannii* may be found growing on forest margins and in plantations where there is sufficient light.

All members of the genus occur in areas with a seasonal rainfall. *Z. odorata* is dependent on the winter rains in the Cape for its vegetative growth and flowering whereas the closely related *Z. aethiopica* occurs in both winter and summer rainfall areas. Species with discoid tubers occur only in the summer rainfall area.

Table 8.1 Biomes in southern Africa in which *Zantedeschia* occurs

Species	Biomes		
	grassland	savanna	fynbos
Z. aethiopica	x	x	x
Z. albomaculata subsp. *albomaculata*	x	x	
Z. albomaculata subsp. *macrocarpa*	x		
Z. jucunda	x		
Z. odorata			x
Z. pentlandii	x	x	
Z. rehmannii	x		
Z. valida	x		

Stebbins (1974) gives the following account of the response of species to a deteriorating environment: the surviving species becomes adapted to drought or cold and the rhythm of flowering and seed production is altered to correspond with the favourable growing season. Changes in flowering are likely to include shortening of various reproductive stages, and consequently the structure of the inflorescences, flowers and fruits.

Such changes are evident in *Z. aethiopica*. Flowering of *Z. aethiopica* coincides with the rainy season. Although, under favourable conditions, plants may flower throughout the year, vegetative growth and flowering is profuse between September and May in the summer rainfall area. Plants in the winter rainfall area have adjusted their flowering rhythm to between August and January, a period just after the winter rains. There appears to be no other phenological difference between plants of *Z. aethiopica* in the summer and winter rainfall areas.

Wright's (1940) principle on adaptive radiation (quoted in Stebbins 1974), may well apply to *Z. odorata*. His premise was that the division of a population into several small subpopulations is most advantageous in rapid evolution. The subpopulations are sufficiently isolated from each other and can become differentiated under the influence of differential selection pressures. Migration can occur often between these subpopulations so that adaptive gene complexes arising in one subpopulation can spread to other subpopulations.

Z. aethiopica displays a range of phenotypic responses to the environment. For example, plants in shaded areas may reach a height of 2,5 m and have large laminae whereas those in direct sunlight tend to be about 60 cm tall with reduced laminae. *Z. odorata* closely resembles *Z. aethiopica* in morphology and cytology (Yao *et al.* 1994). The former species probably originated as a subpopulation of *Z. aethiopica* (sensu Stebbins). Phenotypic plasticity permitted the subpopulation to persist in an environment that has changed in an unfavourable way. The subpopulation adapted to a particular microclimate at Klipkoppies in Nieuwoudtville. Plants of *Z. odorata* can be separated from *Z. aethiopica* by a cylindrical spathe with a long limb, a dwarf-like spadix borne on a distinct stout stipe and a different fruiting phenology. Fruiting in *Z. odorata* differs from *Z. aethiopica* in that berries of the latter turn orange and soft when ripe, while those of *Z. odorata* remain green and firm until eventually disintegrating on the ground. The question that may be asked if these differences in *Z. odorata* are adaptations to a deteriorating environment? What ecological conditions are likely to promote a change in phenology, bearing in mind that in all other species, seed dispersal is by simple disintegration as in *Z. odorata*? In species in isolated habitats such as *Z. odorata*, dispersal by disintegration may be a favourable way of securing progeny over a short period of time. Since *Z. aethiopica* has a longer flowering period than all other species, seed dispersal through an agent may be risked.

In accordance with Wright's principle, *Z. odorata* may have become sufficiently isolated from *Z. aethiopica* and its floral and fruiting structures have become modified under the influence of differential selection pressures. For example, a short thicker spadix in a slightly open spathe may be an adaptation to strong winds which are common in the Western Cape. Shortening of the flowering season from late July to August or from August to September may reflect on the rainfall seasonality. Flowering is reduced to barely two months.

The extent to which floral and fruiting characters have become differentiated in response to environmental constraints can only be determined by detailed phenological study of *Z. odorata*, and *Z. aethiopica* from various habitats in the winter and summer rainfall areas. The difficulty with such a study, is to determine whether a population of *Z. aethiopica* is wild or naturalised in an area, as this species becomes naturalised easily in suitable habitats. For instance, a collection of *Z. aethiopica* [Singh & Patterson-Jones 51 (NH)] in Cloudskraal (3119AC), the same quarter degree square in which *Z. odorata* occurs was considered by Perry to be introduced (pers. comm.). The population is growing on Table Mountain sandstone.

The heterogeneous patterns of distribution exhibited by species of *Zantedeschia* are partly related to the geology and ecology of an area, as well as to the species ability to tolerate different climates. Distribution patterns were found to be useful in confirming the identity of species.

CHAPTER 9

DISCUSSION

9.1 Introduction

In the preceding chapters, four basic sources of taxonomic evidence—morphology, anatomy, pollination biology and phytogeography were reviewed for the genus *Zantedeschia* with emphasis on characters of diagnostic importance. These themes illustrate the homogeneity and heterogeneity of species.

In this chapter, taxonomic characters are summarised and discussed in relation to interspecific relationships and evolutionary trends. Based on relationships, two sections as suggested by Letty over two decades ago (Letty 1973) are proposed for formal acceptance (Singh *et al.*, Appendix 5). The typical section, *Zantedeschia* contains *Z. aethiopica* while *Z. albomaculata*, *Z. elliotiana*, *Z. jucunda*, *Z. pentlandii*, *Z. rehmannii* and *Z. valida* are grouped into Section *Aestivus*. Evidence is presented for incorporating *Z. odorata*, a more recently described species from Nieuwoudtville (Perry 1989), in Section *Zantedeschia*.

Some of the ideas on relationships and evolutionary trends presented here are no doubt speculative, but I have not hesitated to present them. It is hoped that these may stimulate future research to test their validity. Based on the attributes studied, an evolutionary diagram, indicating possible phylogenetic relationships among species, is suggested.

---

* Formal descriptions of Sections in Latin are included in Appendix 5

9.2 Morphology

In the genus *Zantedeschia*, macromorphology provided multifarious characters for species recognition. It is possible to identify species using vegetative characters in combination with that of floral morphology. Attributes of value in distinguishing species are discussed below.

Majority of *Zantedeschia* species can be easily identified by their vegetative characters. Vegetative attributes of particular diagnostic importance are tuber and leaf types.

Stebbins (1974) offers the following hypothesis for the development of storage organs. Rhizomes and tubers are adapted to an alternation between a dormant period and a period of vegetative growth. As rhizomatous geophytes undergo a long period of vegetative growth, there is no adaptive value in storing large amounts of food. Such growth forms are best adapted to mesic or wet conditions and, in dry regions occupy sandy porous soils having roots that penetrate depths. The stem tuber is a modification of the rhizome in response to a shorter growing season, in which case there is a need to store food during the long dormant period.

In the light of Stebbins' suggestions, *Z. aethiopica* has rhizome-like tubers which explains the ability of this species to inhabit wet areas and to remain vegetative during all seasons, provided there is sufficient moisture. Species in Section *Aestivus* have discoid tubers and have a definite dormant period during the dry season (April to August). Despite its long period of dormancy (November to June), tubers of *Z. odorata* are rhizomatous as in *Z. aethiopica.* This is contrary to the expectation that this species should have discoid tubers in order to survive the long unfavourable period.

Perry's (1989) illustration of tubers of third year seedlings of *Z. odorata* kept in cultivation appear to be similar to species with discoid tubers in Section *Aestivus*. This is in contradiction to the narrow tubers found in the wild. The slender tuber may be an adaptation to growth in rock crevices. An interesting experiment would be to study tuber development in plants of *Z. aethiopica*, *Z. odorata* and one species in Section *Aestivus*, germinated from seeds. In addition, tubers should be observed during the dormant and growing seasons for any signs of transformation in shape.

The tubers of species in Section *Aestivus* are all discoid. Therefore, on tuber disposition alone, *Z. aethiopica* and *Z. odorata* in the wild can be separated from the remaining species. In most cases, herbarium taxonomists cannot appreciate the value of tuber types in this group, as tubers are awkward to dig up, and are therefore lacking in herbarium material. Therefore, there is greater reliance on leaf characters for identification.

Leaf characters which include shape and the presence or absence of maculations can be extensively employed in demarcating *Zantedeschia* species or groups of species. *Z. rehmannii*, *Z. albomaculata, Z. jucunda*, *Z. pentlandii* and *Z. elliotiana* can be identified by their distinct leaf shapes. *Z. aethiopica*, *Z. odorata* and *Z. valida* form a group on the basis of their ovate-cordate leaves which can be separated from the rest of the species. It is not always possible to separate *Z. albomaculata* subsp. *albomaculata* from *Z. albomaculata* subsp. *macrocarpa* on leaf shape alone, as the former subspecies displays wide plasticity in leaf shape, sometimes approaching those of subspecies *macrocarpa* and even those of *Z. elliotiana*.

In combination with leaf shapes, the presence of maculations in *Z. jucunda* and *Z. elliotiana*, and its absence from *Z. odorata*, are valuable in recognising these species. Since maculations may be present or absent on the laminae of some species, its usefulness as a distinguishing character is reduced. Since maculations are polymorphic, its stability as a distinct feature is further reduced.

In *Zantedeschia*, floral characters of value in recognising species include spathe shape and colour, presence or absence of staminodes and the purple-coloured blotch at the base of the spathe interior.

Spathe shape, namely cylindrical versus funnel-shaped is diagnostic for species identification in both fresh and herbarium specimens. Among species with funnel-shaped spathes, two groups may be recognised on the grounds of colour – white versus yellow. Colour is of little use in separating cylindrical spathes.

Spadices in *Z. odorata*, as opposed to the remaining species, are consistently dwarf (Figure 6.5, p. 68). Dwarfism in the spadix may be an adaptation to severe winds which are typical in the Cape winter rainfall area. With the increase in the diameter of the spadix, the spathe limbs do not overlap, thus the spathe is open to the base, unlike in the remaining species. The slight openness in the spathe may not offer insects an enclosed shelter for foraging or breeding, hence insect activity within the spathe is reduced. Except for a few small beetles in some spathes, insect activity in *Z. odorata* was fairly low in comparison to *Z. aethiopica*.

The presence of staminodes in members of Section *Zantedeschia* are useful in separating them from those in Section *Aestivus*. Staminodes may be homologous with a perianth, offering protection to the naked ovaries. The lack of staminodes in Section *Aestivus* is probably due to reduction in floral structure. Through reduction only certain structures of the plant are changed, the rest remains well differentiated (Dahlgren *et al.* 1985). In Section *Aestivus*, the structure of the anthers and ovaries and their arrangement on the spadix is similar to that of Section *Zantedeschia*, with the exception of staminodes.

Staminodes are considered as non functional stamens and as such lack the ability to produce pollen. However, Yao (1992) reports that staminodes in emasculated spadices of *Z. odorata* produced pollen. Examination of the male-female transition zone on the spadix of *Z. odorata* indicated that due to vertical compression of the spadix, ovaries in this zone are surrounded by three staminodes as well as by anthers. It is therefore likely that the spadix was emasculated above this zone and that the pollen reported from the staminodes by Yao (1992) was in fact shed from the anthers surrounding ovaries in the transition zone.

The purple-coloured blotch at the base of the spathe within, is absent in members of Section *Zantedeschia*. Its absence in spathes of *Z. aethiopica* and *Z. odorata* and its presence in *Z. valida*, all of which have immaculate ovate-cordate leaves and white spathes, is valuable in differentiating these species. In spathes of *Z. jucunda* and *Z. pentlandii*, the purple-coloured blotch is consistently present, whereas it may be present or absent in *Z. albomaculata, Z. elliotiana* and *Z. rehmannii*. Letty (1973) recorded the purple-coloured blotch as being absent in spathes of *Z. rehmannii* and *Z. elliotiana*, and further, considered it to be a key difference between the latter species and the yellow-flowered arums, *Z. jucunda* and *Z. pentlandii*. In this study, contrary to that reported by Letty (1973), the purple-coloured blotch has been found to be present in some spathes of *Z. elliotiana* and *Z. rehmannii*. This character, which is restricted to members of Section *Aestivus* is therefore not stable for determining species.

9.3 Vegetative anatomy

The anatomy of the vegetative organs proved to be fairly homogeneous among all species, except for minor differences in leaf details. Although species are morphologically distinct, they form a closely knit group on the basis of anatomy.

A striking feature was the presence of collenchyma as girders and strands which is uncommon among monocotyledons. Its presence however, in the stems of the family Commelinaceae (Tomlinson 1969) as strands only, characterises this family. Other major monocotyledonous groups such as the Palmae (Tomlinson 1969), Juncaceae (Cutler 1969) and Cyperaceae (Metcalfe 1971) are devoid of collenchymatous cells. In the Cyperaceae, girders and strands of sclerenchyma are present and these are equivalent to the collenchymatous structures in *Zantedeschia*. The potential value of the collenchyma girders and/or strands as a taxonomic character could only be assessed when more species in the family Araceae are investigated.

In subfamily Philodendroideae, there are seven tribes, five of which are monogeneric (Table 9.6, p. 119). The number of monogeneric tribes suggests that the subfamily is either heterogeneous or, that many taxa are isolated (French & Tomlinson 1981d). A study of the vegetative anatomy of each tribe will reflect the diversity of the subfamily. Therefore, although the anatomy of *Zantedeschia* is less useful at subgeneric level, it may well be of relevance in establishing relationships in this complex subfamily.

9.4 Pollination biology

Preliminary studies on pollination provided valuable information for the taxonomic separation of *Z. aethiopica* from the remaining species. Stigma receptivity in *Z. odorata* extends into the stage of pollen dehiscence on the same spadix (Yao 1992), hence spontaneous selfing is possible. This overlap in maturity of male and female flowers was also observed in *Z. albomaculata* subsp. *albomaculata*. Self-compatibility in *Z. odorata* is useful in separating it from *Z. aethiopica*, which has been observed to be clearly self-incompatible (Singh *et al.*, Appendix 4). The faint freesia-like scent in these two species, among other attributes, supports their classification into Section *Zantedeschia*.

9.5 Phytogeography

Adaptation to summer or winter rainfall conditions may provide a clue to species identity in *Zantedeschia*. In addition, fifty percent of the species are endemic to particular localities in South Africa. Locality details of endemic species are useful in confirming the identity of herbarium specimens. Chemical analysis of soil samples from the range of endemics may explain further the preference of these species for particular soil types or geological substrates. For a view on the possible origin of the genus, see discussion on the origin of *Zantedeschia* in southern Africa (p. 118).

9.6 Chromosomal evidence

Zantedeschia has a base chromosome number of $x = 16$ or 17 (Grayum 1990), with $n = 16$ (Petersen 1989) and $2n = 32$ (Marchant 1971; Yao *et al.* 1994). Chromosomes in the genus are small (Marchant 1971), about 2 µm, calculated from micrographs in Marchant (1971) and Yao *et al.* (1994).

Yao *et al.* (1994) provided chromosomal evidence to explain relationships within the genus. These authors have reported the following information. The karyotype of *Z. aethiopica* "Childsiana" (a cultivar of *Z. aethiopica*) which is essentially the same as that of *Z. aethiopica*, is distinctly different from those of plants of Section *Aestivus*. In addition to metacentric and submetacentric chromosomes, *Z. aethiopica* and *Z. odorata* have telocentric and subtelocentric chromosomes which are lacking in Section *Aestivus*. The difference between the karyotypes of *Z. aethiopica* and *Z. odorata* lies in the number of metacentric and submetacentric chromosomes. *Z. aethiopica* has 14 metacentric and 4 submetacentric chromosomes whereas *Z. odorata* has 8 metacentric and 10 submetacentric chromosomes. Karyotypes of plants in Section *Aestivus* were found to be uniform. It must be noted that chromosome counts and karyotypes of *Z. jucunda* and *Z. valida* are not yet published. Therefore, information on members in Section *Aestivus* is based on the remaining species only.

Compatibility between *Z. aethiopica* and *Z. odorata* and incompatibility patterns between either of these species with plants of Section *Aestivus*, correlate closely with the karyotype classifications of species (Yao *et al.* 1994). Interspecific hybridisation occurs readily within Section *Aestivus* (Traub 1948). Based on karyological evidence, Yao *et al.* (1994) concluded that *Z. odorata* is somewhat intermediate between *Z. aethiopica* and plants of Section *Aestivus*, although closer to *Z. aethiopica*. Relationships based on characters recorded in Table 9.1 (p. 109) indicates that *Z. odorata* displays characters of both sections but resembles *Z. aethiopica* in majority of character states.

9.7 Macromorphological adaptations to the environment

Vegetative features in *Zantedeschia*, particularly in the summer rainfall species, represent obvious adaptations to a dry environment. Some of these are considered below.

Plants of *Zantedeschia* are deciduous, tuberous herbs with leaves evanescent during the dry season. They can therefore survive the unfavourable period as tubers. Discoid tubers in most species of *Zantedeschia* are an adaptation to long periods of dryness. Rhizomatous tubers in *Z. aethiopica* enables the plant to be evergreen in constantly moist areas.

Leaves of *Zantedeschia* are thin and amphistomatic, which increases photosynthetic activity. In addition, except for leaves of *Z. rehmannii*, leaves of the remaining species are broad which increases the surface area for photosynthesis. Large flat leaves are more likely to cool below dew point at night, and become covered with moisture (Raschke 1960). This reduces the effect of transpiration.

The maculate areas of the lamina lack stomata and well-developed palisade and spongy mesophyll cells. Essentially, the maculation is non-functional in photosynthesis. It is a form of variegation. Variegated plants have been of considerable interest to research workers for their study of plastid heredity (Manenti 1975), and is of particular interest to plant breeders for their showiness. Probably all major families contain some variegated species (Evenari 1989). In addition to spathe coloration, variegation in *Zantedeschia* has also been the basis for the successful trade of container or garden plants. This has been achieved through the development of new cultivars through hybridisation of variegated and non-variegated species. Another aroid, *Caladium* Vent. has been commercially exploited for its variegated leaves.

Evanari (1989) attributes variegation in many plants to the somewhat pronounced degeneration and sometimes complete destruction of the chloroplasts which are initially 'normal'. He concludes that the biochemical defects of the mutated plastids are expressed in the lack of certain polypeptides and enzymes that are needed for the buildup of Photosystem I in photosynthesis. Evanari (1989) also discusses the different ways in which variegation may be inherited.

In a study of the variegated leaves of *Acer negundo* L. (Aceraceae), Manenti (1975), found that the mesophyll in white and white-yellow areas of the leaf has no visible chloroplasts and that the leaf blade in these areas are thinner than the rest of the leaf, a situation similar to that observed in *Zantedeschia* (see Figures 5.10, p. 49 and 5.12, p. 50). Certain types of variegation are affected by environmental conditions such as light and temperature (Evanari 1989). For instance, in a variegated variety of *Arabidopsis* sp.

(Cruciferae) low light intensity and short days lead to a decrease of variegation, whereas continuous light induces the plastids to become white (Evanari 1989), and this could possibly be explained by the fact that environmental stresses can change gene expression by stimulating the formation of new proteins and/or the repression of normally present proteins (Sachs & Ho 1986).

Are maculations in *Zantedeschia* a result of environmental factors as suggested by Sachs & Ho (1986) or are they predetermined with a definite functional role? The function of maculations which is probably a consequence of malformed plastids may be to reduce the surface area of leaves, thereby conserving moisture by decreasing transpiration. For example, if all maculations on a lamina of *Z. jucunda*, *Z. elliotiana* or *Z. albomaculata* subsp. *albomaculata* were combined, it would probably account for one third to half the surface area of the lamina, which constitutes a considerable area of the leaf. It is further speculated that maculations reflect, rather than absorb sunlight, which helps to keep the leaf surface cool. Hence, maculations may be interpreted as an adaptation to intense sunlight.

The possibility of maculations serving as a deterrent against herbivores cannot be ruled out. Maculations on the leaves of *Gasteria* Duval may serve as a camouflage in the shrubby plant cover and stony habitats (Van Jaarsveld 1989). The camouflage strategy in *Gasteria* may be in response to herbivory (Van Jaarsveld 1987). When the habit and habitat of *Gasteria* are considered, camouflage seems a reasonable explanation for maculations in the genus. In the wild, very few immaculate or maculate plants of *Zantedeschia*, showed signs of phytophagous feeding. However, the laminae of plants kept in cultivation are profusely eaten by caterpillars. Caterpillars feeding on *Zantedeschia* leaves are not deterred by the presence of maculations in some species. There is therefore a need for further understanding of variegation in plants of *Zantedeschia* in the wild.

9.8 Position of *Z. odorata*

Evidence from various disciplines suggest that *Z. odorata* exhibits characters of both Section *Zantedeschia* and Section *Aestivus*. Table 9.1 summarises the differences between the two sections and highlights the attributes of *Z. odorata*.

Table 9.1 Summary of characters used to separate *Z. aethiopica* (Section *Zantedeschia*) from the summer rainfall species (Section *Aestivus*). States applicable to *Z. odorata* are indicated to show characters shared with both sections.

Section *Zantedeschia*	Section *Aestivus*
usually evergreen, deciduous under extreme dryness, short period of dormancy or no dormancy	regularly deciduous during the dry season, long period of dormancy (***Z. odorata***)
purple-coloured blotch constantly absent from base of spathe within (***Z. odorata***)	purple-coloured blotch constantly present or inconsistently present
staminodes interspersed among ovaries (***Z. odorata***)	staminodes not regularly dispersed among ovaries, if present restricted to the male-female transition zone
berries turn orange, soft and mucilaginous	berries remain green and firm until disintegration (***Z. odorata***)
upper half of spathe disintegrates, only the lower half turns green (***Z. odorata***)	entire spathe turns green, wrapping itself tightly around the maturing berries
tuber rhizomatous (***Z. odorata***)	tuber discoid
delicate freesia-like scent (***Z. odorata***))	no scent
Karyotype morphology: metacentric, submetacentric, telocentric and subtelocentric chromosomes (***Z. odorata***)	Karyotype: only metacentric and submetacentric chromosomes
summer and winter (***Z. odorata***) rainfall	summer rainfall
stigma receptivity does not overlap with anther dehiscence on the same spadix	stigma receptivity overlaps with anther dehiscence on the same spadix?
interspecific hybridisation does not occur (***Z. odorata***)	interspecific hybridisation readily occurs

Z. odorata shares more characters with *Z. aethiopica* than with members of Section *Aestivus.* A possible explanation for this may be the suggested evolution of *Z. odorata* from the widespread *Z. aethiopica* (Chapter 8, p. 95), through modification in characters following selective pressure. For instance, *Z. odorata* may have become adapted to selfing in the absence of pollinators and to seed dispersal by disintegration in the absence of dispersers. An alternative explanation that seems more likely is convergent evolution where *Z. aethiopica* and *Z. odorata* share similar attributes which have differentiated along different lines. Differences in spathe shape, spadix dimensions and seed dispersal mechanism in *Z. odorata* may be due to adaptive responses to the environment. In cases where several attributes are shared between taxa, convergence is less obvious and this strengthens the initial presumption that taxa share a common ancestry (Dahlgren *et al.* 1985). Thus the close resemblance of *Z. odorata* to *Z. aethiopica* in many characters (Table 9.1), supports the assumption that the species were derived from a common ancestor. Selection pressure could also have been responsible for many of the similarities between these two species. Similarities in characters from morphology, pollination biology, phytogeography, cytology and hybridisation suggest that *Z. odorata* should be grouped within Section *Zantedeschia.*

9.9 *Z. albomaculata* complex

Letty (1973) recognised three subspecies of *Z. albomaculata* based on leaf shape, spathe shape, berry number and size, and geographical distribution. In this review, *Z. albomaculata* subsp. *valida* was found to be distinct within the complex and has been raised to species level, *Z. valida* (Singh *et al.*, Appendix 5).

Z. albomaculata subsp. *macrocarpa* differs from the typical species in having triangular-hastate, sparsely maculate leaves and medium-sized, straw-coloured spathes which are truncate at the apex (Letty 1973). Sometimes leaf and spathe shape in plants of *Z. albomaculata* subsp. *albomaculata* are the same as those of *Z. albomaculata* subsp. *macrocarpa*. This implies that in the absence of mature fruit, it would be impossible to separate the two species.

Engler (1915) upheld these two subspecies as distinct species. *Z. macrocarpa* according to Engler had immaculate leaves and yellow spathes whereas *Z. albomaculata* had maculate leaves and white spathes. Traub (1948) agreed with Brown's (1902) view that the distinction of these two taxa on the basis of number and size of fruit is debatable. It is more valuable to note biological differences between the two taxa that would warrant them specific rank than to emphasise minor differences such as the size of fruit (Traub 1948).

Difficulty in the use of fruit size is unavoidable since fruit size is relative to seed development. For instance, a berry with many seeds will be larger than one with few seeds. Secondly, in *Z. albomaculata* subsp. *albomaculata*, berries may be up to 18 mm in length, whereas in *Z. albomaculata* subsp. *macrocarpa*, berries may be up to 20 mm long (Letty 1973). Berry length in the two subspecies is therefore rather similar. Lastly, the stage of maturity at which the berry is measured is important. During observations of herbarium specimens, it became apparent that the number of fruit is more useful in delimiting the two subspecies. *Z. albomaculata* subsp. *macrocarpa* was found to have relatively fewer berries, about half the number found in *Z. albomaculata* subsp.

albomaculata. Generally, leaf shape, spathe shape and colour, and number of fruit are specific to each subspecies. It would, however, be interesting to study the range of phenotypic variation in both subspecies as well as the hybrids between them.

9.10 Phylogenetic relationships

Table 9.2 represents an assessment of the hypothesized character conditions as primitive or advanced, in the family, as proposed by Grayum (1990). *Zantedeschia* displays a mixture of both character states. There is a tendency for members of the genus to be primitive in vegetative characters, yet advanced in floral morphology. The genus as a whole is primitive in its distichous leaves, lack of a geniculum, paracytic stomata, lack of compound and cortical vascular bundles, absence of stem endodermis, prisms and trichosclereids, one to many locules per ovary, many ovules, anatropous ovule, endosperm in seed and monad pollen. Advanced characters in *Zantedeschia* include reticulate venation, presence of “laticifers” and bifurines, enclosing spathe, monoecious spadix, aperigonate flowers, stout anthers, stamens fewer than four, anther dehiscence through apical pores, globose and psilate pollen.

Characters of which both the primitive and advanced states are found in the genus are outlined in Table 9.3. *Z. aethiopica* and *Z. odorata* exhibit primitive characters in comparison to the remaining species, making Section *Zantedeschia* less modified than Section *Aestivus*. *Z. rehmannii* is most advanced in regard to its leaf shape.

Table 9.2 Summary of taxonomically useful characters in the Araceae (sensu Grayum 1990). Text in bold indicates the state for *Zantedeschia*, text in italics implies state is unknown for *Zantedeschia*.

Characters	Primitive state	Advanced state
Growth habit	**rhizomatous** or caulescent	**tuberous**, epiphytic, vining
Phyllotaxy	**distichous**	spiral
Geniculum	**absent**	present
Leaf form	**simple, cordate**	**lanceolate**; compound or lobed
Leaf venation	parallel	**reticulate**
Stomata	**paracytic**	anomocytic, tetracytic
Compound vascular bundles	**absent**	present
Cortical vascular bundles	**absent**	present
Stem endodermis	**absent**	present
Tricosclereids	**absent**	present
Secretion vessels	absent or single cells	**"laticifers"**
Bifurines	absent	**present**
Prisms	**absent**	present
Spathe	Type I	Type II, **III** & IV
Spadix	hermaphoditic	**monoecious**
Perigonium	present	**absent** or fused
Locules of ovary	2 or 3	**one or many**
Ovules per locule	**many**	few or one
Placentation	**axile**	parietal, basal, apical
Stamen length	elongate	**stout**
Number of stamens	4—6	**fewer** or more
Anther dehiscence	longitudinal	apical, lateral, **poricidal**
Staminodia in female flowers	**present**	**absent** or fused
Ovule type	**anatropous**	orthotropous
Nucellus type	*crassinucellate*	*tenuinucellate*
Megaspore units	*tetrads*	*dyads*
Endosperm in seed	**present**	absent
Cells of chalazal chamber	*6—8*	*1—4*
Base chromosome number	x = 7 or 14	x = 15, **16**, **17**, 18, 19, 20, etc.
Pollen aperature type	*monosulcate*	*zonate, forata, inaperturate*
Pollen type	boat-shaped	**globose**
Pollen size	*medium-sized*	*small, large, very large*
Pollen unit	**monads**	tetrads
Exine sculpturing	foveolate-reticulate	striate, **psilate**, spinose, etc.
Pollen starch content	*absent*	*present*
pollen nuclear number	*II*	*III*

Spathe types: I = unmodified, bractlike, II = expanded and/or coloured
III = enclosing spadix, IV = constricted

Table 9.3 Characters of which both primitive and advanced states are found among species of *Zantedeschia*.

Characters	Primitive state	Advanced state
Growth habit	*Z. aethiopica, Z. odorata*	All other species
Leaf form	All other species	*Z. rehmannii*
Staminodia among female flowers	*Z. aethiopica, Z. odorata*	All other species

9.10.1 Phylogeny of *Zantedeschia*

Data gathered during this review of characters was used to develop an intuitive phylogeny for the genus (Figure 9.1).

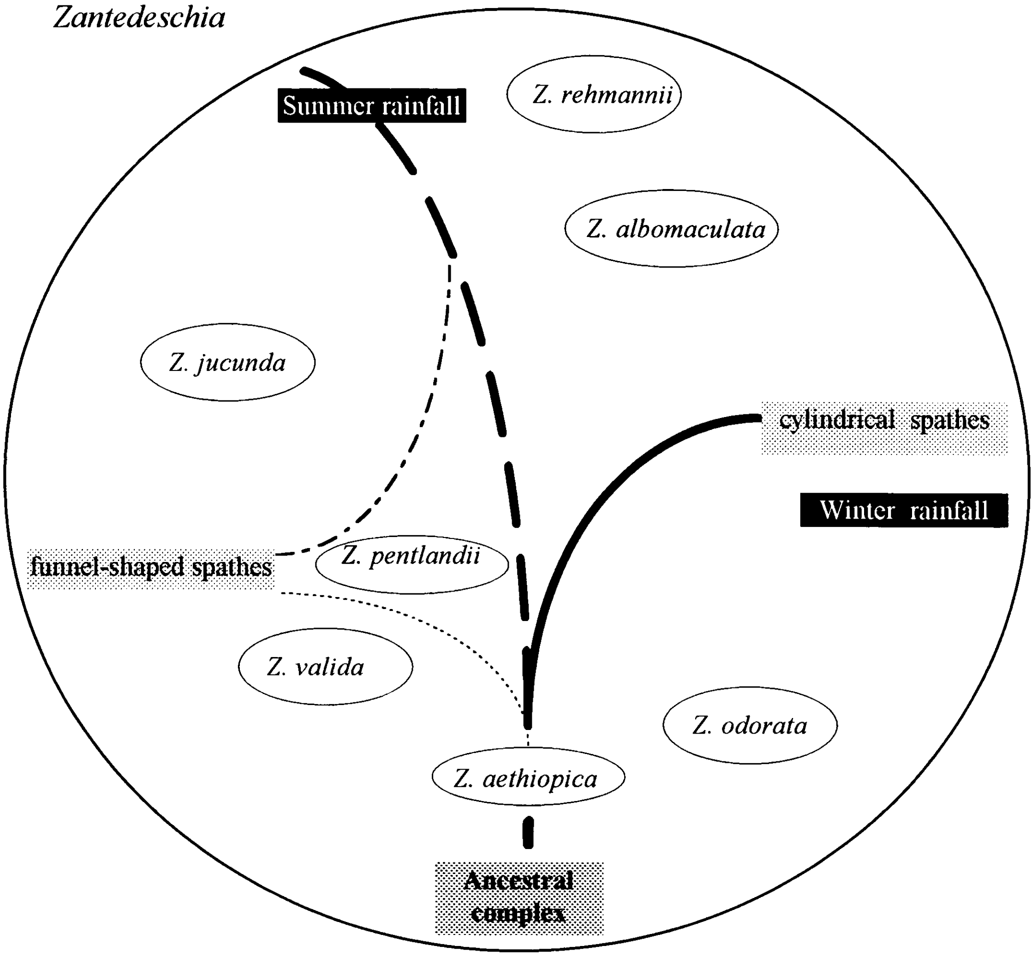


Figure 9.1 Phylogeny of *Zantedeschia* species. Species were grouped intuitively using overall similarity.

9.10.2. Preliminary cladistic analysis

Hennig 86 version 1.5 was used to derive possible phylogenetic relations among species. Sixteen characters (Table 9.4), mainly morphological, all equally weighted were used in the analysis. *Z. elliotiana*, a species suspected to be of garden origin, was excluded. Since there is no distinct sister group for *Zantedeschia*, characters for an ancestral type were hypothesised. An alternative sister group would be a member from the *Philodendron* Alliance as proposed by Mayo *et al.* (in press).

Table 9.4 Characters and character states in *Zantedeschia* (used in Figure 9.2)

1. Storage organs: rhizomatous (0), tuberous (1)
2. Phenology: evergreen (0), potentially evergreen (1), deciduous (2)
3. Leaf shape: ovate-cordate (0), oblong-elliptic to cordate (1), oblong to triangular-hastate (2), lanceolate (3)
4. Maculation on leaf: absent (0), mostly absent (1), mostly present (2), present (3)
5. Spathe colour: white (0), cream (1), yellow (2) white through to purple (3)
6. Spathe shape: funnel-shaped (0), cylindrical (1)
7. Spathe closure: closed (0), open on one side (1)
8. Spathe apex: tapering (0), elongate (1), truncate (2)
9. Spathe greening: entire spathe withers (0), upper portion of spathe withers, lower portion turns green (1), entire spathe turns green (2)
10. Scent: present (0), absent (1)
11. Purple blotch: absent (0), present or absent (1), present (2)
12. Spadix length: long tapering to appendix (0), long (1), short (2)
13. Staminodes: 4 or 5 (0), 3 (1), 0 (2)
14. Infructescence: erect (0), pendulous (1)
15. Fruit colour: red (0), orange (1), green (2)
16. Chromosomal count (according to Yao *et al.* 1994): 3A (0), 3B (1), 2B (2)

Table 9.5 Data matrix of 16 characters for 8 taxa of *Zantedeschia*

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Z. aethiopica	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0
Z. albomaculata subsp. *albomaculata*	1	2	2	2	3	1	0	1	2	1	1	1	2	1	2	2
Z. albomaculata subsp. *macrocarpa*	1	2	2	1	1	1	0	2	2	1	1	1	2	1	2	2
Z. jucunda	1	2	2	3	2	0	0	1	2	1	2	1	2	1	2	2
Z. odorata	0	2	0	0	0	1	1	1	1	0	0	2	1	1	2	1
Z. pentlandii	1	2	1	1	2	0	0	1	2	1	2	1	2	1	2	2
Z. rehmannii	1	2	3	1	3	1	0	2	2	1	1	1	2	1	2	2
Z. valida	1	2	0	1	0	0	0	1	2	1	2	1	2	1	2	2

Data analysis resulted in two equally parsimonious trees of 35 steps, ci 85 and ri 86. Both trees generally agreed with the intuitive phylogeny. Tree 1 (Figure 9.2) was similar to Tree 0 in all respects except that the position of *Z. albomaculata* subsp. *albomaculata* and *Z. albomaculata* subsp. *macrocarpa* were interchanged.

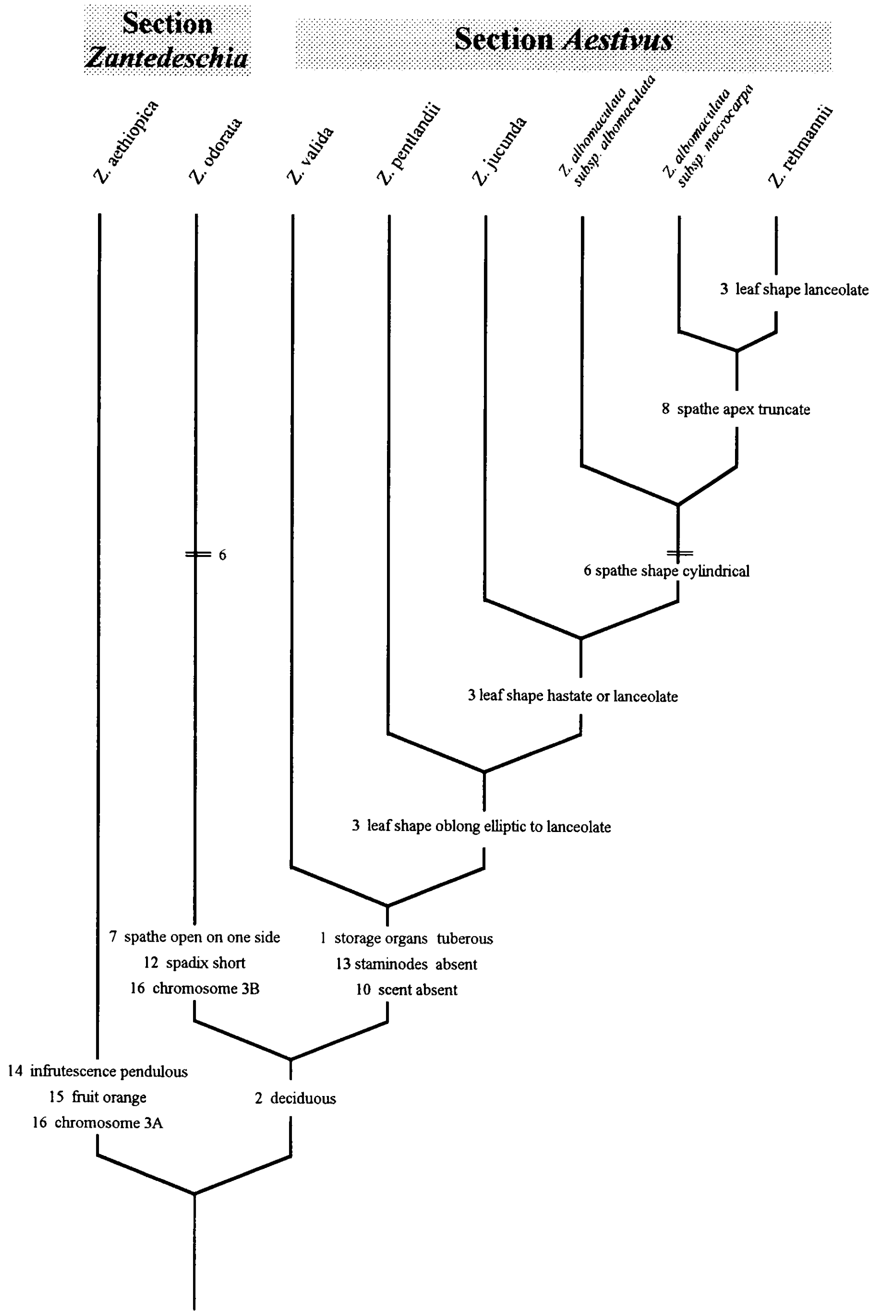


Figure 9.2 Cladogram of *Zantedeschia* species generated by Hennig 86. Characters and the state for each species, used in the cladogram are recorded in Tables 9.4. and 9.5 respectively. Convergence is indicated by a double line.

From the cladogram (Figure 9.2) there appears to be two main lines in *Zantedeschia* and these are assigned sectional ranks. Rhizomatous tubers, staminodes among ovaries and the presence of scent in *Z. aethiopica* and *Z. odorata* suggest that the species are closely related to the hypothetical ancestral type. The two species are grouped into Section *Zantedeschia* and the remaining species comprise Section *Aestivus*.

Within Section *Aestivus*, there seems to be two further lines of separation based on spathe shape. Cylindrical spathes in *Z. albomaculata* and *Z. rehmannii* separate them from the funnel-shaped spathes in *Z. jucunda*, *Z. pentlandii* and *Z. valida*. Among taxa with funnel-shaped spathes, *Z. jucunda* and *Z. pentlandii* are more closely allied on the basis of spathe colour. *Z. valida* is similar to *Z. aethiopica* in leaf and spathe characters. However, the purple-coloured blotch at the base of the spathe interior and the lack of staminodes, are distinctive in *Z. valida*. Cylindrical spathes in *Z. odorata* is regarded as having evolved by convergence.

9.11 Position of tribe Zantedeschieae within subfamily Philodendroideae

Despite differences in morphology, species of *Zantedeschia* are closely related anatomically and undoubtfully share a common ancestor. The genus is thus considered to be monophyletic. Characters such as a non constricted spathe, ovules anatropous, seeds with endosperm, and stamens free, isolate the genus into a tribe of its own, the Zantedeschieae, within the taxonomically difficult subfamily Philodendroideae. A review of eight subfamilies incorporating data from various disciplines is presented by Jacobsen in the monumental treatment of the families of monocotyledons (Dahlgren *et al.* 1985). Petersen (1989) correlates chromosomal data with the phylogeny of the subfamilies using the classification of Bogner & Nicolson. Based on cytological data, Petersen (1989) suggests a rearrangement of the position of some tribes so that the classification will be in better accordance with the phylogeny. In his detailed review of the relationships between infrafamilial taxa, Grayum (1990) groups the aroids into five subfamilies using cladistics. For a detail discussion on the evolution and phylogeny of Araceae, refer to Grayum (1990).

Genera within Subfamily Philodendroideae are listed in Table 9.6, according to the classification by Bogner & Nicolson (1991). *Anubias*, *Bognera*, *Aglaonema*, *Aglaodorum*, *Dieffenbachia* and *Zantedeschia* have been grouped into the '*Aglaonema* alliance', one of five informal "alliances" suggested by Grayum (1990). These genera appear not to fit into any other alliance and thus form a heterogenous group.

9.12 Origin of *Zantedeschia* in southern Africa

The Araceae is considered to have a West Gondwanaland-Laurasian distribution (Raven & Axelrod 1974). These authors regard the aroids as one of the many families that migrated between Africa and South America prior to or during the Paleocene after which period, the floras of the two continents became distinct. Genera of the '*Aglaonema*' alliance are distributed in America, Southeast Asia or Africa (Table 9.6), hence they link Africa to South America and Africa to South East Asia. The poor representation of aroids in Africa is presumably due to drought during the Neogene and Quartenary times, which tended to disrupt the African Flora (Raven & Axelrod 1974).

Table 9.6 Classification of Subfamily Philodendroideae (Bogner & Nicolson 1991)

Tribe	Subtribe	Genera	Number of species	Distribution
Philodendreae	Homalomeninae	*Furtadoa* M. Hotta	2	Southeast Asia
		Homalomena Schott	140	Southeast Asia, America
	Schismatoglottidinae	*Schismatoglottis* Zoll. & Moritzi	100	America & Asia
		Piptospatha N.E. Br.	10	Western Malaysia
		Hottarum Bogner & Nicolson	3	Borneo
		Bucephalandra Schott	1	Borneo
		Phymatarum M. Hotta	2	Borneo
		Aridarum Ridley	7	Borneo
		Heteroaridarum M. Hotta	1	Sarawak
	Philodendrinae	*Philodendron*	500	Tropical America
Anubiadeae		*Anubias*	7	Central & Western Africa
		Bognera Mayo & Nicolson	1	South America
Aglonemateae		*Aglaonema* Schott	21	Indomalaysia
		Aglaodorum Schott	1	Western Malaysia
Diffenbachieae		*Dieffenbachia* Schott	25	Tropical America
Zantedeschieae		*Zantedeschia*	8	Central & southern Africa
Typhonodoreae		*Typhonodorum*	1	East African coast, Madagascar
Peltandreae		*Peltandra* Raf.	3	North America

It is difficult to speculate where the ancestral form of subfamily Philodendroideae originated. However, it is suggested that *Zantedeschia* fragmented from a widespread ancestral form of the subfamily in West Gondwanaland. Aridity has probably forced the genus southwards into southern Africa, where on acquiring a suitable niche, the genus has become established as an endemic.

9.13 Conclusion

The taxonomic information presented in this study will aid herbarium taxonomists in plant identifications. It would also be useful to aroid systematists in determining intergeneric relationships, particularly in resolving discrepancies within the heterogeneous subfamily Philodendroideae. Since horticulture is based on, and is heavily constrained by, the characters of species which have evolved in their native habitat (Rees 1980), the survey of characters presented for this horticulturally important group, will benefit plant breeders. It is therefore hoped that this integrated assessment of taxonomic characters for the genus *Zantedeschia* will be appreciated by taxonomists, aroid systematists, plant breeders and keen gardeners.

CHAPTER 10

CONCLUSIONS

- *Zantedeschia* is a monophyletic genus.
- Eight species and two subspecies are grouped into two sections. *Z. albomaculata* subsp. *valida* is raised to specific rank as *Z. valida*.
- Vegetative morphology, particularly tuber type and leaf shape, is important in separating species or groups of species. *Z. odorata* and *Z. aethiopica* are distinct in having rhizomatous tubers. On leaf morphology, *Z. rehmannii* is distinct.
- Floral morphology, especially spathe shape and colour, staminodes, the purple-coloured blotch at the base of the spathe interior and floral odour provide useful diagnostic characters for species delimitation. Cylindrical spathes in *Z. albomaculata*, *Z. rehmannii* and *Z. odorata* are easily distinguishable from the funnel-shaped spathes in the remaining species. Staminodes among ovaries, the consistent lack of the purple-coloured blotch at the base within the spathe and a faint freesia-like scent are restricted to *Z. odorata* and *Z. aethiopica*.
- The homogeneity among species is evident from the study of vegetative anatomy. The description provided for the genus will be useful in a comprehensive comparative study of the anatomy of the family.
- *Z. aethiopica* displays distinct post pollination changes, useful in taxonomy. This supports the view that pollination biology in other species requires further examination.
- Patterns of distribution are useful in species delimitation. Six of the eight species occur in the summer rainfall areas with the greatest concentration in the Eastern Transvaal and KwaZulu-Natal. Four species are endemic to particular habitats in South Africa. Their restricted distribution is useful in confirming the identity of a species.

CHAPTER 11

TAXONOMIC TREATMENT [*]

---

[*] prepared for the *Flora of Southern Africa*. Partly adapted from Letty (1973).

0748 000

ZANTEDESCHIA

by Y. SINGH*

Zantedeschia Spreng., in Syst. Veg. 3: 765 (1826); Baill. in Bull. Soc. Linn. Paris 1: 254 (1880); Engl. in Bot. Jahrb. 4: 64 (1883); Pflanzenr. 4, 23 Dc: 61 (1915); Marloth, Fl. S. Afr. 4: 52 (1915); Traub, Plant Life 4: 12 (1948); Adamson & Salter, Fl. Cape Penins. 132 (1950); Phill., Gen. S. Afr. Flow. Pl. edn. 2: 161 (1951); Bailey, Cycl. Hort. p. 3534 (1963); Letty in Bothalia 11: 5 (1973); Dyer, Gen.S.Afr. Flow. Pl.: 894 (1976); Mayo, F.T.E.A. : 16 (1985) *nom. cons.* Type species: *Z. aethiopica* (L.) Spreng.

Calla L., Sp. Pl. 968 (1753), pro parte.
Aroides Heist. ex Fabricius, Enum. Pl. Hort. Helmst. ed. 2,2:42 (1763); Kuntze, Rev. Gen. 2: 737 (1891) (as "*Arodes*").
Colocasia Link, Diss. Bot. Sverin 77 (1795); Handb. 1: 267 (1829).
Richardia sensu Kunth in Mem. Mus. Hist. Nat. Paris 4: 433, t. 20 (1818); Engl. in DC., Mon. Phan. 2: 326 (1879); N.E.Br. in Fl. Cap. 7: 36 (1897); Fl. Trop. Afr. 167: 8 (1901); Phill., Gen. S. Afr. Flow. Pl. ed. 1: 125 (1926).

Terrestrial, acaulescent, perennial herbs with rhizomatous or discoid tubers. *Cataphylls* two, broad at base, tapering towards the apex, green, sometimes mottled or striped with purple on the outside, whitish on inside, margins folded inwardly. Outer cataphyll about half the length of inner one. Inner cataphyll up to half the length of the petiole. *Leaves* deciduous or evergreen, several, glabrous, radical, rosulate petiolate; petiole with well-developed sheath about one third to half its length, lacking apical pulvinus, base sometimes mottled or striped with purple or white, sometimes with trichomes; lamina variable lanceolate, ovate, orbicular; maculate or immaculate, base cuneate, truncate, hastate or cordate, apex acute or obtuse with a subulate tip. *Inflorescence* appearing with leaves, usually subequal to or taller than leaves. *Peduncle* usually as long as, or longer than the leaves, green, base sometimes mottled with purple or white, sometimes setulose. *Spathes* cylindrical to funnel-shaped, convolute at the base, up to 170 mm long, white, cream, yellow, pink or red, with or without a purple-coloured blotch at the base inside, persistent, green when berries are mature; limb spreading, truncate to acute, terminating in a subulate tip. *Spadix* shorter than spathe, monoecious, free, sessile or sometimes more or less stipitate, apical part staminate, basal portion pistillate, sometimes with staminodes interspersed among ovaries. *Flowers* unisexual, without a perianth, densely congested. *Stamens* free, anthers sessile, oblong, laterally compressed, truncate at the apex, dehiscing by apical pores; pollen white, emitted in long fine threads. *Ovaries* numerous, spirally arranged, 3-locular; ovules 1-8 per locule, with axile or subapical placentation; style short, about 1 mm long, terete; stigma capitate. *Fruit* a berry; clustered, few to many seeded, green or orange when ripe, up to 20 mm in diameter, usually surrounded by and contained in the partial or entire spathe. Seed mucilaginous, subglobose or ovoid, cream to brown, verrucose, with abundant endosperm.

A genus of 8 species and 2 subspecies, 7 of which are confined to southern Africa. *Z. albomaculata* subsp. *albomaculata* extends into Zimbabwe, Zambia, Angola, Malawi and Tanzania. Two sections, *Zantedeschia* and *Aestivus*, are distinguished. *Z. aethiopica* and *Z. odorata* form Section *Zantedeschia*, whereas the remaining species are grouped in Section *Aestivus*.

Key to species and subspecies of *Zantedeschia*

1a Female flowers interspersed with staminodes; spathe interior without a purple-coloured blotch at base
  2a Spathe funnel-shaped; spadix 50-75 mm long, 5-7 mm wide; peduncle erect during fruiting; berries turn orange and soft when ripe; widespread in South Africa .... 1. ***Z. aethiopica***
  2b Spathe cylindrical; spadix 25-35 mm long, 5-10 mm wide; peduncle bending to the ground during fruiting; berries remain green and firm when ripe; restricted to the Nieuwoudtville District in the Western Cape .... 2. ***Z. odorata***
1b Female flowers usually lacking staminodes (if present restricted to ovaries in zone between male and female); spathe interior with or without a purple-coloured blotch at base
  3a Spathe funnel-shaped, interior with a purple-coloured blotch at base
    4a Spathe white; leaf lamina ovate to orbicular-cordate .... 3. ***Z. valida***
    4b Spathe yellow; leaf lamina variously shaped
      5a Leaf lamina usually immaculate, oblong-hastate, glaucous green .... 4. ***Z. pentlandii***
      5b Leaf lamina always maculate, triangular-hastate to ovate-orbicular, deep green
        6a Leaf lamina triangular-hastate .... 5. ***Z. jucunda***
        6b Leaf lamina ovate-orbicular .... 6. ***Z. elliotiana***

---

[*] Natal Herbarium, National Botanical Institute, Botanic Gardens Road, Durban, 4001 South Africa

3b Spathe cylindrical, interior with or without a purple-coloured blotch at base
  7a Leaf lamina oblong, ovate or triangular-hastate
    8a Leaf lamina oblong to ovate-hastate; spathe tapering to apex .... 7a. *Z. albomaculata* subsp. *albomaculata*
    8b Leaf lamina triangular-hastate; spathe truncate at apex .... 7b. *Z. albomaculata* subsp. *macrocarpa*
  7b Leaf lamina narrowly lanceolate, cuneate at base .... 8. *Z. rehmannii*

1. Zantedeschia aethiopica (*L.*) *Spreng.*, Syst Veg. 3: 765 (1826); Baill. in Bull. Soc. Linn. Paris 1: 254 (1880); Engl. in Bot. Jahrb. 4: 64 (1883); Pflanzenr. 4, 23 Dc: 62 (1915); Marloth, Fl. S. Afr. 4: 52 (1915); Traub in Plant Life 4: 12 (1948); Adamson & Salter, Fl. Cape Penins. 132 (1950); Letty in Flow. Pl. Afr. 30: t. 1190 (1954-55); Letty in Bothalia 11: 9 (1973). Lectotype: Specimen in Hort. Cliff. Herb. (BM; PRE, photo!).

Calla aethiopica L., Sp. Pl. 968 (1753); Mill., Dict. ed. 8 (1768); Ait., Hort. Kew. ed. 1, 3: 318 (1789); Sims in Bot. Mag. t. 832 (1805).

Aroides aethiopicum (L.) Heist. ex Fabric., Enum. Pl. ed. 2: 42 (1763); Kuntze, Rev. Gen. 2: 740 (1891) (as "Arodes").

Colocasia aethiopica (L.) Link, Diss. Bot. Sverin 77 (1795); Handb. 1: 267 (1829).

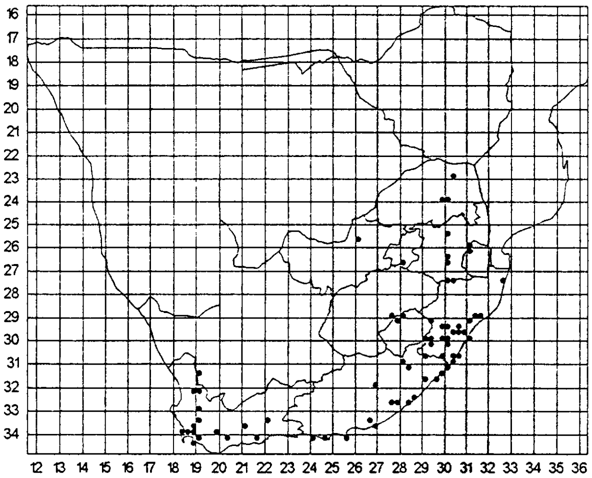
Otosma aethiopica (L.) Rafin., New Fl. Amer. 2: 90 (1836); Fl. Tellur. 4: 8 (1836).

Richardia africana Kunth, Mem. Mus. Hist. Nat. Paris 4: 433, t. 20 (1818); Engl. in DC., Mon. Phan. 2: 326 (1879); N.E. Br. in Fl. Cap. 7: 36 (1897); nom. illegit. Type: same as *Z. aethiopica*.

Zantedeschia aethiopica var. *minor* Engl. in Pflanzenr. 4, 23 Dc: 63 (1915). Type based on Gard. Chron. 27: 755, fig. 153 (1890) of *Z. aethiopica* "Little Gem."—var. *umganiensis* Leicht. & Engl. in Pflanzenr. 4, 23 Dc: 64 (1915). Type: KwaZulu-Natal, Howick Falls, 1899, *Nelson*.

Deciduous or evergreen herb up to 1.5 m tall. *Tubers* rhizomatous. *Leaves* evergreen or deciduous, 0.4-1.5m long; petiole green, lamina more or less spreading and leathery, usually broadly ovate-cordate, 150-200 (-600) mm long, 100-150 (-200) mm broad at the base, apex acute or obtuse, the length of the lamina above the basal lobes usually more than twice the width, usually immaculate. *Peduncle* 300-600 mm (-1,5 m) long, green, glabrous, triangular in cross-section. *Spathes* about 150 mm long, 120 mm broad, white inside, bright green at base outside merging into white upwards, longitudinally veined, folded from slightly below the insertion of the spadix into a wide-mouthed funnel, limb obliquely spreading, ending in a green recurving 20 mm long apiculus. *Spadix* sessile, male zone about 70 mm long, anthers bright yellow, 1,5-2 mm long, 1-1,5 mm broad with 2 pores, pollen white; female zone about 18 mm long; *ovaries* interspersed with spathulate staminodes, about 4 mm long, globose, pale yellow-green grading to whitish at the tip, tapering to a short style 1,5 mm long, 3 locular, each locule with 1-4 ovules. *Fruits* numerous, 12 mm long, 10-12 mm in diam. across the top, green at first, becoming soft and orange coloured when ripe, tapering to a triangular base with a short persistent style at the apex, seeds 1 - 12. Figure 1.

Z. aethiopica is widespread in southern Africa, extending from the Western Cape Province, eastwards through the Eastern Cape, KwaZulu-Natal, Lesotho to the Northern Province (Map 1). The species grows in grassland, savanna and forest margins, from sea level to high altitudes, with a preference for moist habitats and stream banks. Flowering between August and October in the winter rainfall region and between August and February in the summer rainfall areas. However, under favourable conditions plants may flower throughout the year.



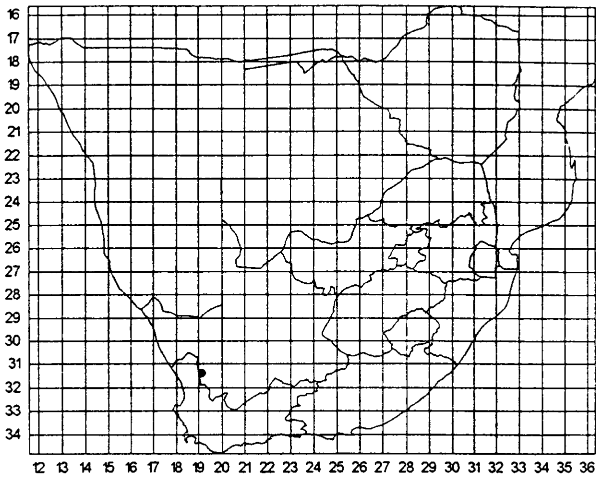
Map 1.— **Zantedeschia aethiopica**

Vouchers: *Abbott 6131* (NH); *Bester 1276* (NH); *Braun 878* (PRE, SWZ); *De Winter 768* (PRE); *Dieterlin 583* (NH, PRE); *Codd* 8519 (PRE); *Dyer 1904* (PRE); *Hanekom* 734(PRE); *Hargreaves 4054* (ROML); *Heath 437* (SWZ); *Heywood 190* (NH); *Letty 320* (PRE); *Schmitz 5954, 8039* (ROML); *Singh 77* (NH); *Singh & Baijnath 39* (NH, PRE); *Singh & Patterson-Jones 51* (NH, PRE), *52* (NH); *Singh, Van Wyk & Baijnath 46* (NH); *Stam* 53 (PRE), *Strey* 9281, *Stielau 189, 5838* (NH).

2. Z. odorata *P.L. Perry* in S. Afr. J. Bot. 55: 447 (1989). Isotype: Western Cape, Nieuwoudtville Reserve, among dolerite outcrops, *Perry & Snijman 2147* (PRE!).

Deciduous perennial herb up to 0.75 m tall. *Tubers* rhizomatous, erect, up to 40 mm long and 25 mm wide. *Roots* numerous, more basal ones becoming contractile towards the end of the growing season. *Leaves* erect, 2-5, up to 600 mm long; petiole up to 280 mm long and 100 mm wide, sheathing for about 100 mm at the base, semi-terete above, light green; lamina broadly ovate-cordate up to 270 mm long, 80-160 mm wide at base, apex obtuse or acute, often ending in a curved green apiculus about 15 mm long, immaculate. *Peduncle* erect, up to 550 mm long and 15 mm wide at the base, roughly triangular in cross section, light green, spongy, upper part becoming flaccid as fruit ripens and bends towards the ground. *Spathes* up to 125 mm long and 80 mm wide, ovate, spreading, green towards the base on the outside shading to white towards the apex, white inside with a curved green apiculus about 25 mm long; margins somewhat undulate, tube usually open to the base. *Spadix* shortly cylindrical up to 35 mm long, on a stout stipe 8-10 mm long and 5-6 mm diameter; male zone apical up to 25 mm long and about 12 mm wide towards the base, tapering to 7 mm apically. Anthers yellow, about 15 mm broad with two pores through which strings of white pollen are emitted. Female zone basal, about 10 mm long and 13 mm wide. *Ovaries* broadly ovoid to globose about 3 mm long and wide, pale green, interspersed with spathulate staminodes. Style 0.75 mm long, white. *Stigma* capitate, white, becoming brown with age. *Ovules* up to 12 in 3 locules, pear-shaped about 1 mm long, soft, white. *Berries* up to 35 in a cluster about 75 mm long and 40 mm wide surrounded by the persistent lower portion of spathe, with persistent style 1-2 mm long; becoming fawn and soft as they wither on the ground. *Seed* irregularly ovoid, 4-5 mm long and 3-4 mm wide, light chestnut-brown, 3-4 per berry. Figure 2,1.

Z. odorata is restricted to a limited area known as Klip Koppies in Nieuwoudtville in the Western Cape (Map 2). The outcrops are formed by large dolerite boulders which break down to form a red clay soil which retains water well in the rainy season. The plants grow in crevices between the boulders, where at least the lower part of the plant is in cool shade. The roots are in seasonally very wet soil or sometimes in standing water. Flowering late July and August.



Map 2.— **Zantedeschia odorata**

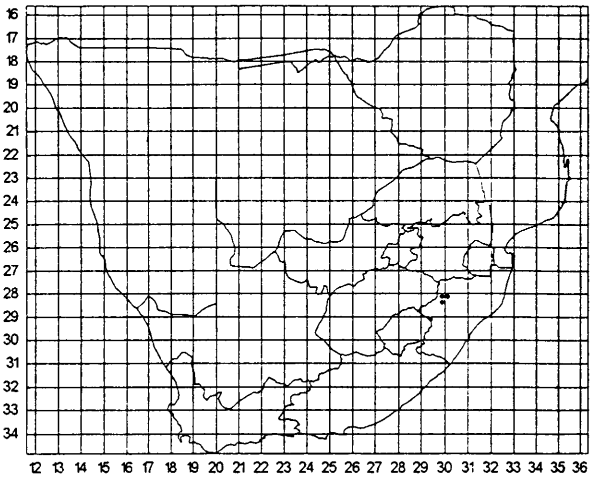
Vouchers: *Oliver & Mauve 41* (PRE); *Perry & Snijman 2147* (PRE); *Singh & Patterson-Jones 50* (NH, PRU).

3. Z. valida (*Letty*) *Y. Singh* in S. Afr. J. Bot. (under review). Type: KwaZulu-Natal, Farm Blanerne, Elandslaagte, 29 km N. of Ladysmith, *Letty* 492 (PRE, holo!).

Z. albomaculata subsp. *valida* Letty in Bothalia 11: 25 (1973).

Deciduous perennial herb, robust, up to 0.75m tall. *Tubers* discoid. *Leaves* up to 750 mm; petioles up to 450 mm long; lamina thick textured up to 300 mm long, up to 240 mm broad at midway between apex and base of midrib, ovate-cordate to ovate-orbicular-cordate with apiculate apex, usually immaculate (rarely maculate). *Peduncle* up to 750 mm long, green or sometimes stained or mottled with purple. *Spathes* vary in size up 150 mm long, 120 mm broad, white inside, yellow at base outside merging into white upwards, longitudinally veined, veins towards the base green, folded from slightly below the insertion of the spadix into a wide-mouthed funnel, limb obliquely spreading, ending in a green recurving 20 mm long apiculus. *Spadix* sessile, about 65 mm long; male zone about 50 mm long, anthers yellow; female zone about 15 mm long, 5 mm wide midway; *ovaries* 3 locular, 2-3 ovules. *Berries* numerous, medium sized about 10 mm diam., green in colour when ripe. Figure 2,2.

Restricted to the region bordered by the Biggarsberg, Giants Castle and Collin's Pass in KwaZulu-Natal (Map 3). Plants grow among rocks on the mountain clefts and foothills as well as on the banks of streams and in vleis. Flowers from October to March with the peak in November.



Map 3.— **Zantedeschia valida**

Vouchers: *Letty 492, s.n.* (PRE); *Marais 360* (PRE); *Mitchell-Innes s.n.* (PRE); *Singh & Baijnath 53* (NH).

4. Z. pentlandii (*Watson*) *Wittm.* in Gartenfl. 17: t. 1456 (1898); Letty, Wild Flows. Transv. 9, t. 6 (1962); Letty in Bothalia 11: 15 (1973). Type: Bot. Mag. t. 7397 (1895)

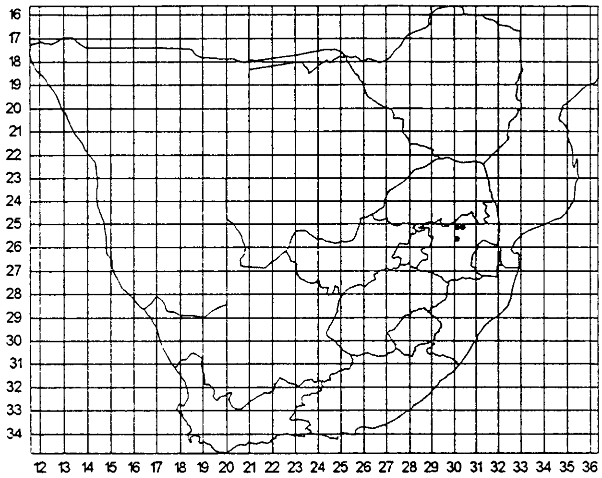
Calla pentlandii Whyte ex Watson in Gard. Chron. 12: 124 (1892), nomen subnudum.

Richardia pentlandii Watson in Gard. Chron. Ser. 3, 15: 590 (1894); Hook. f. in Bot. Mag. t. 7397 (1895). *R. angustiloba* sensu N.E.Br. in Fl. Cap. 7: 36 (1897); Fl Trop. Afr. 8: 169 (1901)), partly; sensu Phillips in Flow. Pl. S. Afr. 1: t. 10 (1921). *R. sprengeri* Comes in Att. R. Ist. Incorazz. Napoli. Ser. V. Vol 3. Mem. 7 (1902). Type: Hort. Sprenger, Naples (K).

Zantedeschia macrocarpa sensu Engl. in Pflanzenr. IV, 23 Dc: 67 (1915); *Z. angustiloba* sensu Marloth, Fl. S. Afr. 4: 54, t. 13 (1915); sensu Traub in Plant Life 4: 16 (1948), partly; sensu Batten and Bokelmann, Wild Flows. E. Cape Province 9, t. 4, 2 (1966).

Deciduous perennial herb, robust, up to 0.6 m tall. *Tubers* discoid. *Leaves* up to 600 mm long, usually shorter than the peduncles, petioles up to 300 mm long, sheathing at the base; lamina oblong-elliptic to oblong-lanceolate, hastate, obtuse to acute, abruptly apiculate, up to 350 mm long and 150 mm wide, usually immaculate (seldom maculate). *Peduncle* up to 600 mm long, mottled with purple at base. *Spathes* up to 130 mm long, lemon-chrome yellow with a dark purple-coloured blotch at the base inside, slightly marked with green outside at the junction with the peduncle, and at the apiculate apex, regularly funnel-shaped; limb loosely folded, seldom recurved backwards, with a 5-20 mm long apiculus. *Spadix* shortly stipitate, usually less than half as long as the spathe; male zone slightly more than two thirds of the length, anthers yellow; female portion less than one third of the length; *ovaries* 3-locular, 5-8 ovules in each locule. *Berries* few in number, green in colour when ripe, with up to 20 seeds. Figure 2,3.

Restricted to the Mapoch region of Mpumalanga (Map 4), comprising the northern part of the Belfast District and adjoining part of the Lydenburg District. Plants often grow in dense colonies wedged between rocks. Tubers are relatively superficial and plants can be dug out easily. Flowering from November to December.



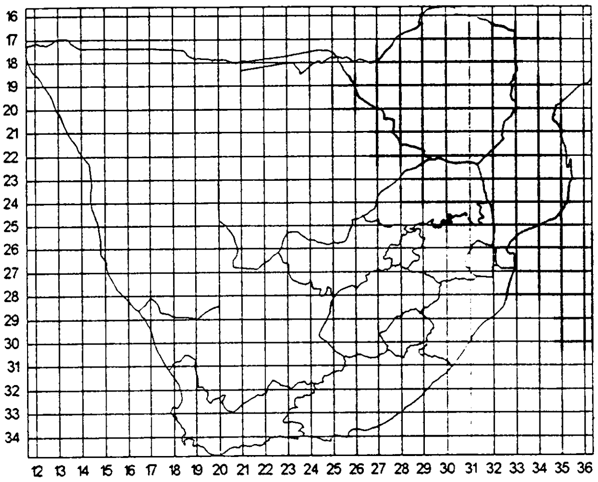
Map 4.— **Zantedeschia pentlandii**

Vouchers: *Cameron* 406 (PRE); *Codd* 8227 (NH); *Letty* 333, 334, 335 (PRE); *du Plessis 36447, 36446* (PRE); *Singh, Van Wyk & Baijnath* 42 (NH, PRU).

5. Z. jucunda *Letty* in Bothalia 7: 455 (1961); Letty in Wild Flows. Tvaal. 12, t. 7 (1962); Bothalia 11: 13 (1973). Type: Transvaal, Lydenburg District, Sekhuhuniland, summit of Lulu Mountains, Farm Het Fort, *Barnard & Mogg 991* (PRE, holo!).

Deciduous perennial herb, up to 0,8 m tall. *Tubers* discoid. *Leaves* up to 800 mm long; petioles 100-300 mm long; lamina triangular-hastate 170-300 mm long, 50-150 mm broad across the base, densely maculate with long white translucent spots, apex acute with a subulate tip, the length of the blade above the basal lobes usually less than twice the width. Peduncle up to 800 mm long. *Spathes* about 100-160 mm long, golden-yellow with a purple-coloured blotch at the base inside, very slightly rugose within, deep yellow without, folded from below the insertion of the spadix into a cup-shaped funnel; limb spreading, slightly recurved backwards and tapering to a subulate tip. *Spadix* 30-40 mm long; male zone apical, about 20-25 mm long; female zone basal, about 25 mm long; *ovaries* subglobose, sessile, about 24 in number, 3 locular, 5-8 ovules. *Berries* about 1-3 cm in diam., green in colour when ripe. Figure 2,4.

Restricted to the Magnet Heights region of the Lulu mountains, Sekhukhuniland in Mpumalanga (Map 5). Plants tend to grow scattered, either solitary or in small clumps, but never as gregarious as Z. pentlandii. Tubers tend to be more deeply seated than in the other species and plants can be dug out only with difficulty. Flowers from November to January.



Map 5.— **Zantedeschia jucunda**

Vouchers: *Barnard & Mogg 991* (PRE); *Barnard 180, 181* (PRE); *Government Commissioner s.n.* (PRE); *Singh, Van Wyk & Baijnath 49* (NH, PRU).

6. **Z. elliotiana** (*Watson*) *Engl.* in Pflanzenr. 4, 23 Dc: 61 (1915); Burtt Davy in Kew Bull. 234 (1924), partly, excluding specimen cited; Traub in Plant Life 4: 20 (1948); Letty in Bothalia 11: 14 (1973). Neotype: Hort. Kew Gardens 27th April, 1897, type of Bot. Mag. t. 7577 (K).

Richardia elliotiana Watson in Gard. Chron. 12: 124 (1892); Mottet in Rev. Hort. 67: 38 (1895); De Duren in Rev. Hort. Belg. 23: 13, t. (1897); Hook. f. in Bot. Mag. t. 7577 (1898); N.E. Br. in Fl. Trop. Afr. 8: 167 (1901).

Calla elliotiana Watson in garden and Forest 5: 330 (1892); Knight in J. Roy. Hort. Soc. 12: Proc. 58 (1890), nom. nud.

Deciduous perennial herb up to 0,6 m tall. *Tubers* discoid. *Leaves* up to 600 mm long; lamina up to 270 mm long and 270 mm broad, sometimes slightly longer than broad, orbicular, ovate, deeply cordate, apiculate, green with many translucent spots; petiole more or less as long as the lamina, occasionally much longer. *Peduncle* about 400 mm long. *Spathes* up to 130 mm long, funnel-shaped above, campanulate below, bright "golden yellow" throughout, immaculate and smooth within, tip caudate. *Spadix* up to 70 mm long, lengths of male and female zones variable, pollen white, ovaries green. *Berries* up to 25 mm in diam., green when ripe. Figure 2,5.

Known only from cultivated specimens; has not been found in the wild. It is probably a hybrid of garden origin. Suspected parents include *Z. pentlandii* or *Z. jucunda* and *Z. albomaculata* subsp. *albomaculata*. Flowers from November to January.

Vouchers: *Galpin 11820* (PRE); *Marloth 7697* (PRE); *O'Connor s.n.* (PRE); *Singh, Van Wyk & Baijnath 44* (NH); *Wood 8909* (NH)— all cultivated in the Transvaal.

7. **Z. albomaculata** (*Hook.*) *Baill.* in Bull. Soc. Linn. Paris 1: 254 (1880); Letty in Bothalia 11: 17 (1973). Type: Hort. Kew, type of Bot. Mag. t. 5140 (1859); (K, holo).

Deciduous perennial herb, 0.4-0.75 m tall. *Tubers* discoid. *Leaves* up to 750 mm long; petiole 200 - 400 mm long, sheathed to up to half the length, green or purple or striped and mottled with purple or white at the base, sometimes with soft hairs towards the base; lamina oblong or triangular, base hastate or saggitate, 100-400 mm long and 25-90 mm broad; lower lobes variable from short and rounded to long triangular with round apex, or strap-shaped with a blunt or acute apex, maculate or immaculate. *Peduncle* up to 750 mm long, green or sometimes stained or mottled with purple, sometimes with soft hairs towards the base. *Spathes* 25-170 mm long, seldom without a dark purple-coloured blotch at the base inside, varying in colour from white through ivory, cream, straw-coloured to pale yellow and, seldom, coral pink, the colour outside greenish at the base, intensifying upwards as the spathe matures; tube sometimes open to the base, mostly convolute, broadening towards the apex; limb subtruncate to gradually tapering, apiculate, somewhat recurved. *Spadix* sessile or stipitate; ovaries not interspersed with staminodes, 3-locular with 3-4 ovules per locule. *Berries* few to many, up to 20 mm in diam., crowded, 4-8 seeded, green when ripe.

7a. subsp. **albomaculata**.

Letty in Bothalia 11: 18 (1973); Mayo in F.T.E.A : 36 (1985).

Richardia albomaculata Hook. in Bot. Mag. t. 5140 (1859); Schott, Prodr. 325 (1860); Van Houtte in Fl. des Serr. 13: 97, t. 1343 (1860); 21: 165, t. 2258 (1875)); Engl. in DC., Mon. Phan. 2: 327 (1879); N.E. Br. in Fl. Cap. 7: 37 (1897). Type Hort. Kew ex Messrs Backhouse of York, originally from "Natal", type of Bot. Mag. t. 5140 (K, holo). *R. hastata* Hook. in Bot. Mag. t. 5176 (1860); Engl. in DC., Mon. Phan. 2: 328 (1879); Watson in Gard. Chron. ser. 3, 12: 123 (1892); N.E.

Br. in Fl. Cap. 7: 38 (1897); Fl. Trop. Afr. 8: 168 (1901). Type: Hort. Kew ex Messrs. Veitch of Exeter, originally from "Natal", type of Bot. Mag. t. 5176 (K, holo). *R. angustiloba* Schott in J. Bot. Lond. 3: 35 (1865); Engl. in DC., Mon. Phan. 2: 329 (1897); N.E.Br. in Fl. Cap. 7: 37 (1897), Fl. Trop. Afr. 8: 169 (1901). Type: Angola, Pungo Andongo, between Calemba and Quisonde, on left bank of river Cuanza, *Welwitsch* 230 (BM, holo; K). *R melanoleuca* Hook.f. in Bot. Mag. t. 5765 (1869); Engl. in DC., Mon. Phan. 2: 328 (1879); Watson in Gard. Chron. 12: 124 (1892); N.E. Br. in Fl. Cap. 7: 38 (1897); Phill. in Flow. Pl. S. Afr. 4: t. 141 (1924). Type: Hort. Bull., Chelsea, from "Africa", type of Bot. Mag. t. 5765 (K, holo). — var. *tropicalis* N.E. Br. in Fl. Trop. Afr. 8: 168 (1901). Lectotype: Malawi, Namisa, *Cameron* s.n. (K).

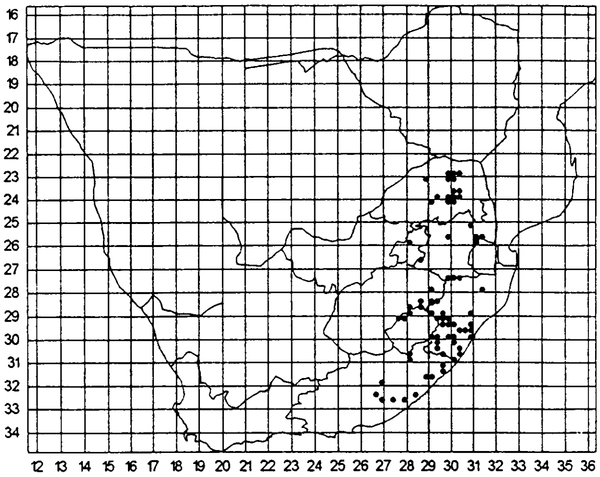
Calla oculata Lindl. in Gard. Chron. 40: 788 (1859). Type: no specimen extant: "Messrs. Veitch received it from Natal".

Zantedeschia albomaculata (Hook.) Baill. in Bull. Soc. Linn. Paris 1: 254 (1880); Engl. in Bot. Jahrb. 4: 64 (1883); Pflanzenr. 4, 23 Dc: 67, t. 30 E-G (1915); Bailey, Cycl. Hort. 3534 t. 4028 (1919); Phill. in Flow. Pl. S. Afr. 19: t. 735 (1939); Traub in Plant Life 4: 14 (1948). — forma *latifolia* Engl. in Bot. Jahrb. 4: 64 (1883). Syntypes: Transvaal, Houtbosch, *Rehmann* 93, 94 (Z). *Z. hastata* (Hook.) Engl. in Bot Jahrb. 4: 64 (1883); Dur. & Schinz, Consp. Fl. Afr. 5: 477 (1894); Traub, l.c. 4: 20 (1948). *Z. angustiloba* (Schott) Engl. in Bot. Jahrb. 4: 64 (1883); Dur. & Schinz, l.c. 5: 477 (1895); Engl. in Pflanzenr. 4, 23 Dc: 67 (1915); Traub, l.c. 4: 16 (1948). *Z. melanoleuca* (Hook. f.) Engl. in Bot. Jahrb. 4: 64 (1883); Pflanzenr. 4, 23 Dc: 67 (1915); Bailey, Cycl. Hort. 3536 (1919); Traub, l.c. 4: 22 (1948). —var. *tropicalis* (N.E. Br.) N.E. Br. ex Engl. in Pflanzenr. 4, 23 Dc: 68 (1915); Traub, l.c. 4: 24 (1948). *Z. chloroleuca* Engl. & Gilg in Warburg, Kunene Exp. 180 (1903). Type: Angola, *Baum* 398. *Z. oculata* (Lindl.) Engl. in Pflanzenr. 4, 23 Dc: 68 (1915). *Z. tropicalis* (N.E. Br.) Letty in Bothalia 7: 456 (1961).

Aroides albomaculatum (Hook.) Kuntze, Rev. Gen. Pl. 2: 740 (1891) (as *Arodes albomaculatum*). *A. hastatum* (Hook.) Kuntze, l.c. (1891) (as *Arodes hastatum*); Rendle, Cat. Afr. Pl. Welw. 2, 1: 90 (1899). *A. angustilobum* (Schott) Kuntze, l.c. 740 (1891) (as *Arodes angustilobum*); Rendle, l.c. 90 (1899).

Leaves oblong hastate, conspicuously maculate or immaculate. *Spathes* white, ivory or cream, rarely pale yellow or coral pink, sometimes with a distinct green midvein extending into the mucron, rarely with white maculations on the outside, usually with a purple-coloured blotch at the base inside, limb gradually tapering to the apex, somewhat recurved. *Berries* numerous, medium sized, up to 18 mm in diam., green in colour when ripe. Figure 2,6.

In the FSA region, this subspecies extends from the Eastern Cape Province, through KwaZulu-Natal, northern Lesotho, north eastern Free State, Swaziland, south-eastern and eastern Transvaal (Map 6). It also occurs in Zimbabwe, Malawi, Zambia, Angola and Tanzania. Plants grow in vleis, on rocky hillsides, forest margins and in marshy ground along streams. Tubers can survive in a depauperate state under fairly dry conditions. Flowering from November to April with a peak in December.



Map 6.— **Zantedeschia albomaculata** subsp. **albomaculata**

Vouchers: *Admiraal s.n.* (PRE); *Abbott 5441* (NH); *Codd* 10690 (PRE); *Compton 28455, 30347* (NH); *Dieterlen 306* (PRE); *Dyer & Verdoorn 2375* (NH); *Gerstner s.n.* (NH); *Guillarmod 4645* (PRE); *Hargreaves 3494* (ROML); *Hargreaves & Kali 3923* (ROML); *Heath 435* (SWZ); *Hoener 1690* (PRE); *Killick* 3887 (PRE); *Kluge 641* (PRE, PRU); *Marais 306* (PRE); *Plowes 2378, 2388, 2390, 2398* (NH); *Singh 82, 85, 86* (NH); *Strey 4874, 6129, 6222, 6288, 6256, 7038I* (NH); *Wood 431, 1370* (NH); *Zietsman 1440* (PRE).

7b. subsp. **macrocarpa** (Engl.) Letty

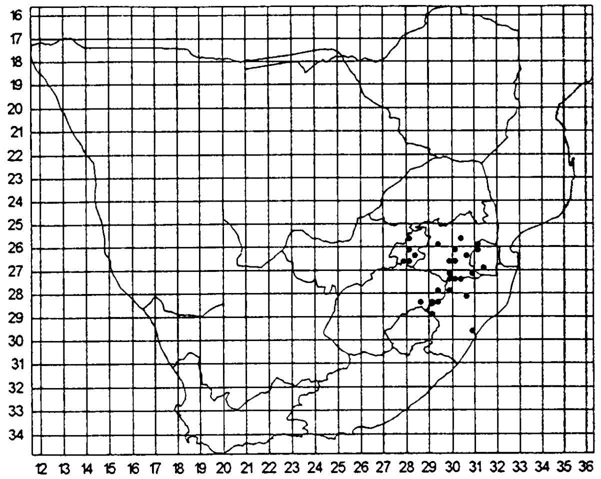
Letty in Bothalia 11: 23 (1973).

Z. macrocarpa Engl. in Bot. Jahrb. 4: 64 (1883); Dur. & Schinz, Consp. Fl. Afr. 5: 477 (1895); Engl. in Pflanzenr. 4, 23: 67 (1915). Type: Trigardsfontein, *Rehmann* 82 (B, holo; Z, PRE, photo!). *Z. melanoleuca* var. *concolor* Burtt Davy in Kew. Bull.: 233 (1924), Type: Hort. Sander & Co. (K), *Z. oculata* sensu Burtt Davy l.c. 234 (1924), partly; sensu Letty, Wild Flows. Tvaal. 8, t. 4 (1962). *Z. angustiloba* sensu Traub in Plant Life 4: 16 (1948), partly.

Richardia macrocarpa (Engl.) Watson in Gard. Chron. 12: 124 (1892). *R. angustiloba* sensu N.E. Br. in Fl. Cap. 7: 37 (1897), partly; Fl. Trop. Afr. 8: 169 (1901), partly.

Leaves triangular-hastate, lower lobes bluntly triangular, sparsely maculate or immaculate. *Spathes* cream, usually with a purple-coloured blotch at the base inside, limb truncate at the apex, somewhat upright. *Berries* few, large sized, up to 20 mm in diam., green in colour when ripe. Figure 2,7.

Occurs only in the FSA region, found in KwaZulu-Natal, Lesotho, eastern Free State, Swaziland, Mpumalanga and Gauteng (Map 7). It inhabits grassy vleis and marshy grounds beside streams. Flowering from November to April with a peak in December.



Map 7.— **Zantedeschia albomaculata subsp. macrocarpa**

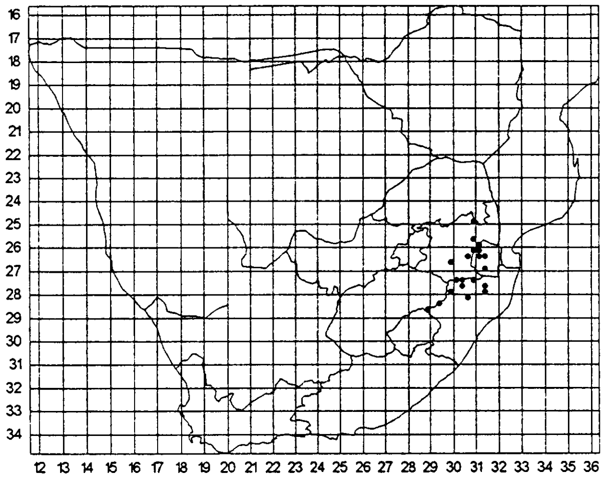
Vouchers: *Codd 4771, 8088, 10724* (PRE); *Codd & Dyer 6259* (PRE); *Galpin 1360* (NH); *Killick & Marais 2136* (PRE); *Letty 327* (NH), *337, 340* (PRE); *Pott-Leendertz 5148* (PRE); *Shepherd 63* (NH); *Singh, Van Wyk & Baijnath 47* (NH); *Steel 572* (PRE); *Young A373* (NH).

8. Z. rehmannii *Engl.* in Bot. Jahrb. 4: 63 (1883) (as "Rehmannii"); Pflanzenr. 4, 23 Dc: 65, fig. 30 A-D (1915); Marloth, Fl. S. Afr. 4: 53, t. 13 (1915); Traub in Plant Life 4: 25 (1948); Letty, Wild Flows. Tvaal. 8, t. 3 (1962); Letty in Bothalia 11:5 (1973). Type: "New Castle", *Rehmann* 80 (Z, holo.)

Richardia rehmannii (Engl.) N.E.Br. ex Harrow in Gard. Chron. 4: 570 (1888), as "Lehmanni"; Watson in Gard. Chron. 12: 124 (1892); N.E. Br. in Gard. Chron. 13: 568 (1893), as "Rhemannii"; Krelage in Gard. Chron. 14: 564 t. 94 (1893), as "Lehmanni"; Watson in Gard. Chron. 16: 364 (1894); Krelage in Gartenfl. 43: 12, fig. 7 (1894); Hook. f. in Bot. Mag. t. 7436 (1895); N.E.Br. in Fl. Cap. 7: 36 (1897); Spreng. in Wien I11. Garten Zeit. 415 (1901), as "Stehmanni"; Medley Wood, Natal Plants 6: t. 512 (1912); Phill. in Flow. Pl. S. Afr. 1: t. 15 (1921).

Deciduous, perennial herb, (-0.25) 0.4-0.6 (-0.8) m tall. *Tubers* discoid. *Leaves* up to 600 mm long; petioles 100-200 mm long, sheathing at the base for about 30-70 mm; lamina lanceolate, acuminate, subulate at the apex, cuneate at the base, 150-400 mm long, 20-70 mm broad, dark green, usually immaculate (seldom maculate),. *Inflorescence* shorter than, subequal to or taller than leaves. *Peduncle* up to 600 mm long, green, glabrous, channelled. *Spathes* 110-120 mm long, 15-20 mm broad, folded from the base for two thirds of its length into a narrow cylinder, colour ranging from white through shades of pink to dark maroon (almost black), usually without purple area at the base within, limb slightly spreading, recurved, with a tapering tip. *Spadix* usually stipitate about half as long as the spathe; male zone about 22 mm long, anthers yellow, pollen white; female zone about 8 mm long, not interspersed with staminodes. *Ovaries* 3 loculed, 2-4 ovules per locule. *Berries* with up to 6 seeds, green in colour when ripe. Figure 2,8.

Z. rehmannii is distributed from Harrismith in the Free State, northern KwaZulu-Natal, through Swaziland to southern and eastern Transvaal (Map 8). This species grows among rocks on grassy hillsides at medium and quite high altitudes, in semi-shade at forest margins and in sandy runnels. Flowering from September until February, with a peak in November to January.



Map 8.— **Zantedeschia rehmannii**

Vouchers: *Compton 28320* (PRE), *28456* (NH, PRE); *Codd & Dyer 6268, 6286* (PRE); *Codd 6395, 8084* (PRE); *Gerstner 5188 (NH, PRE), s.n.* (NH); *Haygarth 5577* (NH); *Heath 117* (SWZ); *Jordaan 633, 2110* (NH); *Letty 331* (PRE); *MacDevette 463* (NH); *Retief & Herman 135* (PRE); *Shepherd 95, 97* (NH); *Williams 121* (NH); *Wood 5204* (NH).

REFERENCES

BROWN, N.E. 1900. Aroideae. *Flora Capensis* VII: 32–39.

BROWN, N.E. 1902. Aroideae. *Flora of Tropical Africa* VIII. 167–169.

BURTT DAVY, J. 1924. New or noteworthy South African Plants - VI. *Kew Bulletin*. 223–235.

ENGLER, H.G.A. 1915. *Das Pflanzenreich* IV, 23Dc: 61–69. Berlin

LETTY, C. 1973. The genus *Zantedeschia*. *Bothalia* 11: 5–26.

MAYO, S.J. 1985. Araceae. *Flora of Tropical East Africa*. 36–38.

PERRY, P.L. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447–451.

TRAUB, H.P. 1948. The genus *Zantedeschia*. *Plant Life* 4: 9–32.

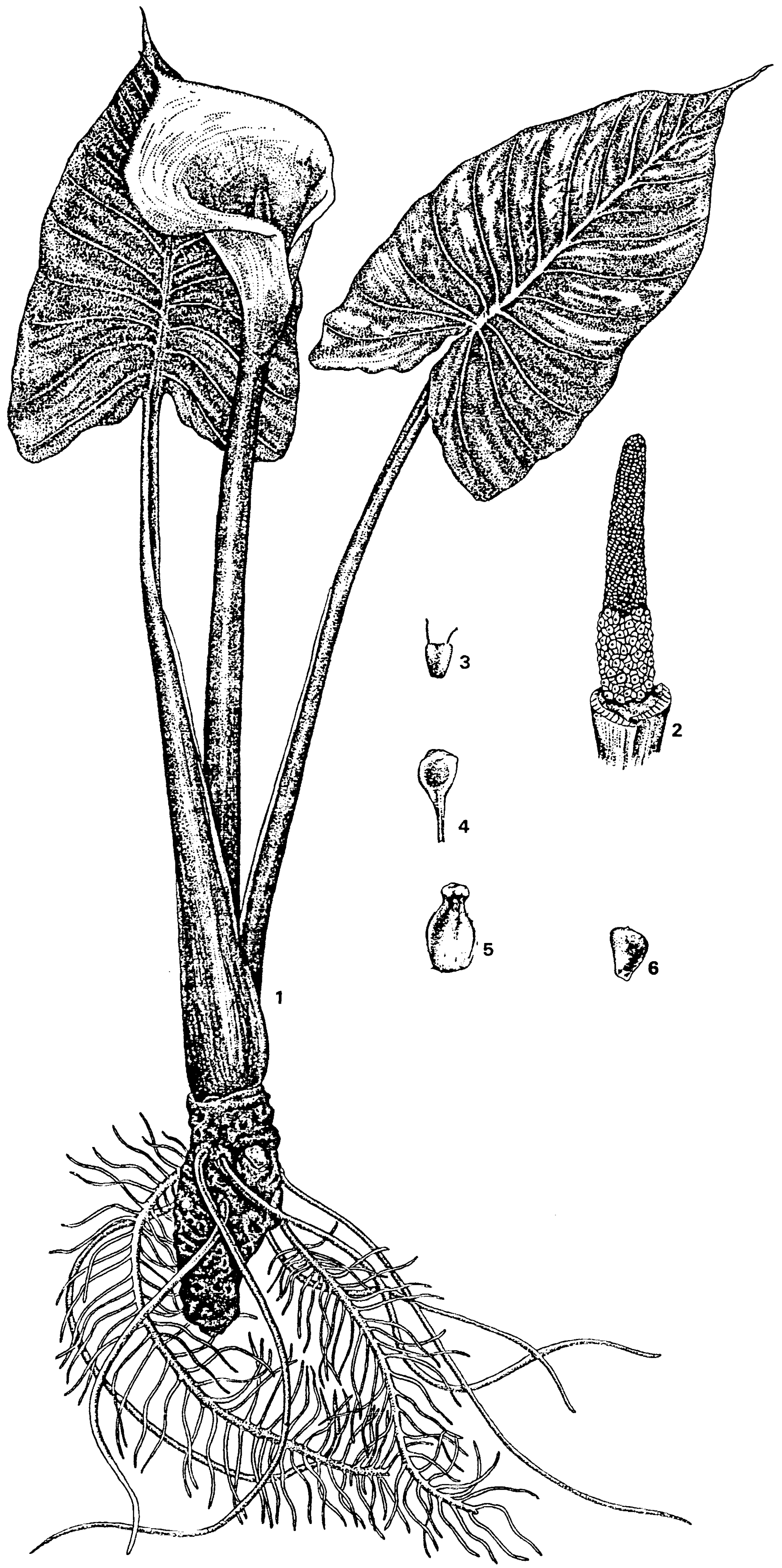


Figure 1.— **Zantedeschia aethiopica**: 1, habit, x 0.2; 2, spadix, x 0.7; 3, anther adaxial side, x 4; 4, staminode adaxial side, x 4; 5, ovary, x 3; 6, berry, x 0.8. Artist N. Anghar.

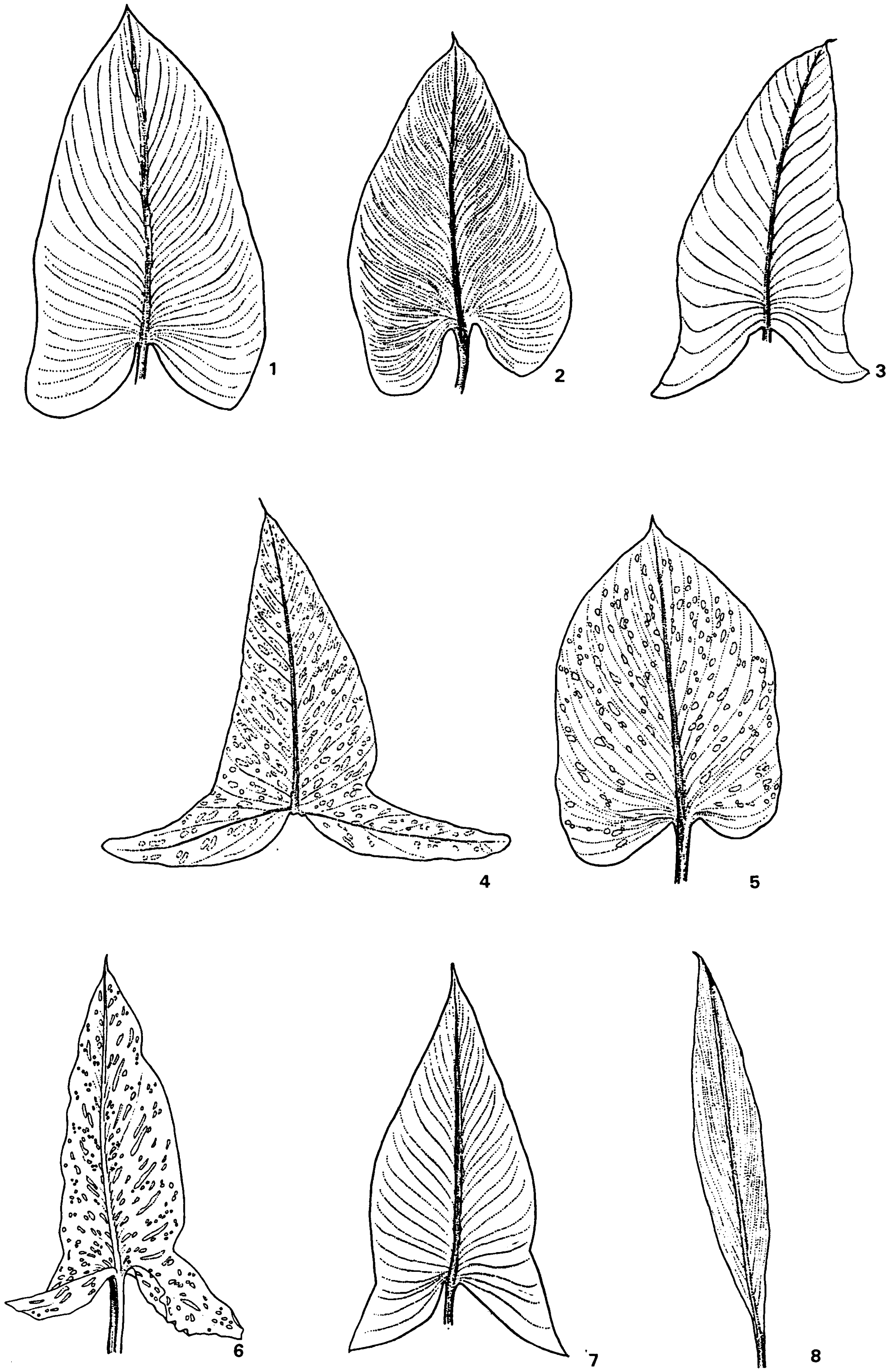


Figure 2.—**Zantedeschia**: leaf shapes. 1, **Z. odorata**, x 0.20; 2, **Z. valida**, x 0.15; 3, **Z. pentlandii**, x 0.20; 4, **Z. jucunda**, x 0.25; 5, **Z. elliotiana**, x 0.3; 6, **Z. albomaculata** subsp. **albomaculata**, x 0.25; 7, **Z. albomaculata** subsp. **macrocarpa**, x 0.15; 8, **Z rehmannii**, x 0.2 Artist: A. Anghar.

REFERENCES

ANCIBOR, E. 1979. Systematic anatomy of the vegetative organs of the Hydrocharitaceae. *Botanical Journal of the Linnean Society*. 78: 237–266.

AYENSU, E.S. 1970. Comparative anatomy of *Dioscorea rotundata* and *Dioscorea ayenensis*. In: *New research in plant taxonomy*, edited by Robson, N.K.B., Cutler, D.F. and Gregory, M. pp. 127–136, Academic Press, London.

BAKER, H.G. & BAKER, I. 1983. Floral nectar sugar constituents in relation to pollinator type. In: *Handbook of experimental biology*. (ed.) Jones, C.E. & Little, R.J., Scientific and Academic Editions, New York, 117–141.

BATTEN, A. & BOKKELMAN, H. 1966. *Wild flowers of the eastern Cape Province*. Books of Africa, Cape Town.

BAY, D.C. 1995. Thermogenesis in the aroids. *Aroideana* 18: 32–39.

BOGNER, J. 1987. Morphological variation in aroids. *Aroideana* 10: 4–16.

—— & NICOLSON, D.H. 1991. A revised classification of Araceae with dichotomous keys. *Willdenowia* 21: 35–50.

BRIDSON, D. & FORMAN, L. 1989. *The herbarium handbook*. Royal Botanic Gardens, Kew.

BROWN, N.E. 1902. Aroideae. *Flora of Tropical Africa* VIII. 167–169. London.

BUTTERFIELD, H.M. 1948. The *Zantedeschia* (Calla) industry in California. *Plant Life* 4: 34–35.

CHI, H.W. 1990. A study of incompatibility within the genus *Zantedeschia*. M.Hort.Sc. thesis, Massey University, Palmerston North, New Zealand. (quoted in Yao, *et al.* 1994).

CORR, B.E. 1993. *Zantedeschia* research in the United States: past, present and future. *Acta Horticulturae* 337: 177–187.

CROAT, T. B. 1980. Flowering behaviour of the neotropical genus *Anthurium* (Araceae). *American Journal of Botany* 67: 888–904.

——— 1991. A revision of *Anthurium* Section *Pachyneurium* (Araceae). *Annals of the Missouri Botanical Garden* 78: 539–855.

CUTLER. D.F. 1969. Anatomy of the monocotyledons, Vol. IV. Juncales. (ed. C.R. Metcalfe). Clarendon Press, Oxford.

DAHLGREN, R.M.T., CLIFFORD, H.T. & YEO, P.F. 1985. *The families of monocotyledons: structure, evolution and taxonomy*. Springer-Verlag, Berlin, Heidelberg, New York, Toyko.

DORMER, K.J. 1960. The truth about pollination in *Arum*. *The New Phytologist*. 59: 98–301.

DU TOIT, A.L. 1954. *The geology of South Africa*. Third edition. Oliver & Boyd, Edinburgh, London.

ELLIS, R.P. 1990. Tannin-like substances in grass leaves. *Memoirs of the botanical survey of South Africa* 59. National Botanical Institute, South Africa.

ENGLER, A. 1884. Beiträge zur kenntnis der Araceae V. 12. Über den Entwicklungsgang in der Familie der Araceen und über die Blütenmorphologie derselben. *Botanische Jahrbücher für Systematik* 5: 141–188, 287–336. (quoted in Grayum 1990).

——— 1915. Araceae-Philodendroideae-Anubiaceae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, Peltandreae. *Das Pflanzenreich Regni vegetabilis conspectus* IV: 61–69.

——— 1920. Araceae pars generalis et index familiae generalis. In: *Das Pflanzenreich* 74 (IV). 23A edted by Engler, A. pp. 1–71. (quoted in Grayum 1990).

ESTES, J.R., AMOS, B.B. & SULLIVAN, J.R. 1983. Pollination from two perspectives: the agricultural and biological sciences. In: *Handbook of experimental biology*. (ed.) Jones, C.E. & Little, R.J., Scientific and Academic Editions, New York, 536–554.

EVANARI, M. 1989. The history of research on white-green variegated plants. *The Botanical Review* 55: 106–139.

FAHN, 1974. *Plant anatomy*. Third Edition. Pergamon Press, Oxford, New York, Toronto, Sydney and Braunschweig.

FEDER, N. & O'BRIEN, T.P. 1968. Plant microtechnique: some principles and new methods. *American Journal of Botany* 55: 123–142.

FRENCH, J.C. 1987a. Systematic occurrence of sclerotic hypodermis in roots of Araceae. *American Journal of Botany*. 74: 891–903.

——— 1987b. Systematic survey of resin canals in roots of Araceae. *Botanical Gazette* 148: 360–371.

——— 1988. Systematic occurrence of anastomosing laticifers in Araceae. *Botanical Gazette* 149: 71–81.

——— & TOMLINSON, P.B. 1981a. Vascular patterns in stems of Araceae: Subfamily Pothoideae. *American Journal of Botany* 68: 713–729.

——— & ——— 1981b. Vascular patterns in stems of Araceae: Subfamily Monsteroideae. *American Journal of Botany* 68: 1115–1129.

——— & ——— 1981c. Vascular patterns in stems of Araceae: Subfamilies Calloideae and Lasioideae. *Botanical Gazette* 142: 366–381.

——— & ——— 1981d. Vascular patterns in stems of Araceae: Subfamily Philodendroideae. *Botanical Gazette* 142: 520–563.

——— & ——— 1983. Vascular patterns in stems of Araceae: Subfamilies Colocasioideae, Aroideae and Pistioideae. *American Journal of Botany* 70: 756–771.

FOX, F.W. AND YOUNG, M.E.N. 1982. *Food from the veld: edible wild plants of southern Africa.* Delta Books, Johannesburg and Cape Town.

GELFAND, M., MAVI, S., DRUMMOND, R.B. & NDEMERA, B. 1985. *The traditional medical practitioner in Zimbabwe: his principles of practice and pharmacopoeia.* Mambo Press, Zimbabwe.

GIBBONS, B. 1984. How flowers work: a guide to plant biology. Blandford Press, United Kingdom.

GORI, D.F. 1983. Post-pollination phenomena and adaptive floral changes. In: *Handbook of experimental biology.* (ed.) Jones, C.E. & Little, R.J., Scientific and Academic Editions, New York, 31–45.

GOTTSBERGER, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Plant systematics and evolution*, Suppl. 1: 211–226.

GRAYUM, M.H. 1986. Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. *Pollen & Spore: Form and Function*: 313–327.

——— 1990. Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Gardens* 77: 628–697.

GUILLARMOD, A.J. 1971. *Flora of Lesotho.* Verlag Von J. Cramer.

GREUTER, W., BURDET, H.M., CHALONER, W.G., DEMOULIN, V., GROLLE, R., HAWKSWORTH, D.L., NICOLSON, D.H., SILVA, P.C., STAFLEU, F.A., VOSS, E.G. & MCNEILL, J. (ed). 1988. *International code of botanical nomenclature*, adopted by the Fourteenth International Botanical Congress, Berlin, July-August 1987. *Regnum Veg* 118.

HATCH, M.D. & MILLERD, A. 1957. Respiration of the spadix from the aroid *Zantedeschia aethiopica* Spreng. *Australian Journal of Biological Sciences* 10: 310–319.

HEGNAUER, R. 1987. Phytochemistry and chemotaxonomy of the Araceae. *Aroideana* 10: 17–19.

HEYWOOD, V.H. 1993. *Flowering plants of the world.* B.T. Batsford Ltd, London.

HICKEY, C.J. 1979. A revised classification of the architecture of dicotyledonous leaves. In Metcalfe, C.R. & Chalk, L. (eds.). *Anatomy of the dicotyledons.* Second edition. Clarendon Press, Oxford.

HOTTA, M. 1971. Study of the family Araceae: general remarks. *Japanese Journal of Botany* 20: 269–310.

HUTCHINSON, J. 1973. *The families of flowering plants.* Clarendon Press, London.

JACOBSEN, N. 1985. Order Arales. In: Dahlgren, R.M.T., Clifford, H.T. & Yeo, P.F. *The families of the monocotyledons: structure, evolution and taxonomy.* Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.

JACKSON, W.P.U. 1986. The Cape white arum lily, *Zantedeschia aethiopica. Veld & Flora* 72: 44–45.

KITE, G.C. 1995. The floral odour of *Arum maculatum. Biochemical Systematics and Ecology* 23: 343–354.

LETTY, C. 1962. *Wild flowers of the Transvaal.* Hortors Ltd, Johannesburg.

——— 1973. The genus *Zantedeschia. Bothalia* 11: 5–26.

MABBERLEY, D.J. 1987. *The plant book: a portable dictionary of the higher plants.* Cambridge University Press, Cambridge.

MANENTI, G. 1975. The structure of variegated leaves of *Acer negundo* L. a light and electron microscope study. *Israeli Journal of Botany* 24: 61–70.

MARCHANT, C.J. 1971. Chromosome variation in Araceae: II. Richardieae to Colocasieae. *Kew Bulletin* 25: 47–56.

MAYO, S.J.; BOGNER, J. & BOYCE, P.C. (in press) The genera of Araceae. Royal Botabic Gardens, Kew.

MEEUSE, B.J.D. & MORRIS, S. 1984. *The sex liife of flowers.* Faber & Faber, London, Boston.

———, SCHNEIDER, E.L., HESS, C.M., KIRKWOOD, K. & PATT, J.M. 1984. Activation and possible role of the "food-bodies" of *Sauromatum* (Araceae). *Acta Botanica Neerlandica* 33: 483–496.

METCALFE, C.R. 1971. *Anatomy of the monocotyledons V. Cyperaceae*. Clarendon Press, Oxford.

——— & CHALK, L. 1950. *Anatomy of the dicotyledons*, Edition. 1. Clarendon Press, Oxford.

MOODIE, G.E.E. 1976. Heat production and pollination in Araceae. *Canadian Journal of Botany* 54: 545–546.

MULLER, T. 1993. Statistics update. *Calla News* 9: 37–38.

NICOLSON, D.H. 1960. A brief review of classifications in the Araceae. *Baileya* 8: 62–67.

——— 1982. Translation of Engler's classification of Araceae with updating. *Aroideana* 5: 67–88.

PERRY, P.L. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447–451.

PETERSEN, G. 1989. Cytology and systematics of Araceae. *Nordic Journal of Botany* 9: 119–166.

RADFORD, A.E. 1986. *Fundamentals of plant systematics*. Harper & Row Publishers, Inc., New York.

RASCHKE, K. 1960. Heat transfer between the plant and the environment. *Annual Review of Plant Physiology* 11: 111–126.

RAVEN, P.H. & AXELROD, D.I. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanic Garden*. 539–673.

REES, A.R. 1980. Research on monocotyledons of horticultural importance: and introduction. In: Brickell, C.D., Cutler, D.F. & Gregory, M. *Petaloid monocotyledons: horticultural and botanical research*. Academic Press, London, New York.

RICHARDS, A.J. 1986. *Plant breeding systems*. George Allen & Unwin (Ltd), London.

ROBACKER, D.C., MEEUSE, B.J.D. & ERICKSON, E.H. 1988. Floral aroma: how far will plants go to attract pollinators? *Bioscience* 38: 390–398.

RUDALL, P. 1994. Anatomy and systematics of Iridaceae. *Botanical Journal of the Linnean Society* 114: 1–21.

RUTHERFORD, M.C. & WESTFALL, R.H. 1986. *Biomes of southern Africa: an objective categorisation*. Botanical Research Institute, South Africa.

SACHS, M.M. & HO, T.H.D. 1986. Alteration of gene expression during environmental stress in plants. *Annual Review of Plant Physiology* 37: 363–376.

SCHOTT, H.W. 1860. *Prodromus Systematis Aroidearum*. Vindobanae. (quoted in Nicolson 1960).

SIMPSON, B.B. & NEFF, J. L. 1983. Evolution and diversity of floral rewards. In: *Handbook of experimental biology*. (ed.) Jones, C.E. & Little, R.J., Scientific and Academic Editions, New York, 142–159.

SINGH, Y., VAN WYK, A.E. & BAIJNATH, H. 1994. Leaf anatomy of the genus *Zantedeschia* (Araceae). *Proceedings of the Electron Microscope Society of southern Africa* 24: 57.

———, ——— & ——— 1995. Know your arums: a comparative guide to the members of the genus *Zantedeschia*. *Veld & Flora* 81: 54–55.

STACE, C.A. 1980. *Plant taxonomy and biosystematics*. Edward Arnold, London, Melbourne, U.S.A.

STEBBINS, G.L. 1974. *Flowering plants: evolution above the species level*. Edward Arnold, London.

STERN, W.L., MORRIS, M.W. & JUDD, W.S. 1993. Comparative vegetative anatomy and systematics of Spiranthoideae (Orchidaceae). *Botanical Journal of the Linnean Society* 113: 167–197.

TOMLINSON, T. B. 1969. *Anatomy of the Monocotyledons III. Commelinales-Zingiberales*. Clarendon Press, Oxford.

TRAUB, H.P. 1948. The genus *Zantedeschia*. *Plant Life* 4: 3–32.

VAN JAARSVELD, E.J. 1987. The succulent riches of South Africa and Namibia. *Aloe* 24: 46–92.

——— 1989. A revision of the genus *Gasteria* (Asphodelaceae). MSc. thesis, University of Natal, Pietermaritzburg.

VOGEL, S. 1990. *The role of scent glands in pollination: on the structure and function of osmosphores*. Smithsonian Institution Libraries & The National Science Foundation, Washington, D.C.

WATT, J.M. & BREYER-BRANDWIJK, M.G. 1962. *The medicinal and poisonous plants of southern and eastern Africa*. E. & S. Livingston Ltd., Edinburgh & London.

WEBERLING, F. 1989. *Morphology of flowers and inflorescences.* Cambridge University Press, Cambridge.

WHITTAKER, R.H. & FEENY, P.P. 1971. Allelochemics: chemical interactions between species. *Science* 171: 157–171.

WILLIAMS, M. 1994. Leaf anatomical investigation into *Philodendron* Schott (Araceae). MSc. thesis, University of Reading, Reading. 42pp. (Listed in *The Kew record of taxonomic literature relating to vascular plants* 1994.)

WRIGHT, S. 1940. Breeding structure of populations in relation to evolution. *American Naturalist* 74: 232–248. (quoted in Stebbins 1974).

WYATT, R. 1983. Pollinator-plant interactions and the evolution of breeding systems. In: Real, L. (ed.) *Pollination biology.* Academic Press, London, Orlando, pp. 51–95.

YAO, J.L. 1992. Interspecific hybridisation and molecular characterisation of hybrids in the genus *Zantedeschia.* Extracts from PhD thesis, Massey University, Palmerston North, New Zealand.

———, ROWLAND, R.E. & COHEN, D. 1994. Karyotype studies in the genus *Zantedeschia* (Araceae). *South African Journal of Botany* 60: 4–7.

SUMMARY

CONTRIBUTIONS TO THE SYSTEMATICS OF THE GENUS *ZANTEDESCHIA* SPRENG. (ARACEAE)

by

YASHICA SINGH

Supervisor: Prof. A.E. van Wyk
Co-Supervisor: Prof. H. Baijnath (UDW)

in the faculty of Biological and Agricultural Sciences
Department of Botany, University of Pretoria, Pretoria

MAGISTER SCIENTIAE

July 1996

In this systematic account of the genus *Zantedeschia*, data from morphology, anatomy, pollination biology and phytogeography are intergrated. Notes are also provided on the nomenclatural history and economic value of the genus. The possible functional significance of attributes such as maculations and staminodes, and primitive and advanced states of characters are speculated upon. Finally, a taxonomic treatment of the genus for the *Flora of Southern Africa* is provided, including keys and descriptions to all taxa.

Leaf and spathe attributes and post pollination changes were found to be of particular importance to the taxonomy of the genus. Geographical distribution patterns proved to be useful in confirming the identity of taxa, especially those endemic to restricted localities in South Africa.

On the basis of its distinct morphology and on its restricted distribution, *Z. albomaculata* (Hook.) Baill. subsp. *valida* Letty has been raised to specific level as *Z. valida* (Letty) Y.Singh. Eight species and two subspecies are recognised in this study and they include *Z. aethiopica* (L.) Spreng., *Z. albomaculata* subsp. *albomaculata*, *Z. albomaculata* subsp. *macrocarpa* (Engl.) Letty, *Z. elliotiana* (Watson) Engl., *Z. jucunda* Letty, *Z. odorata* P.L.Perry, *Z. pentlandii* (Watson) Wittm., *Z. rehmannii* Engl. and *Z. valida*. Two sections are proposed: Section *Zantedeschia* containing *Z. aethiopica* and *Z. odorata*, and Section *Aestivus* incorporating the remaining species.

OPSOMMING

BYDRAE TOT DIE SISTEMATIEK VAN DIE GENUS *ZANTEDESCHIA* SPRENG. (ARACEAE)

deur

YASHICA SINGH

Studieleier: Prof. A.E. van Wyk
Mede-leier: Prof. H. Baijnath (UDW)

in die Fakulteit Biologiese en Landbouwetenskappe
Departement Plantkunde, Universiteit van Pretoria, Pretoria

MAGISTER SCIENTIAE

Julie 1996

In hierdie sistematiese verslag oor die genus *Zantedeschia* word data uit die morfologie, anatomie, bestuiwingsbiologie en fitogeografie geïntegreer. Notas oor die nomenklatoriese geskiedenis en ekonomiese waarde van die genus word ook verskaf. Daar word gespekuleer oor die funksionele betekenis van kenmerke soos vlekke en staminodiums en oor die primitiewe en gevorderde stand van kenmerke. Laastens word 'n taksonomiese behandeling van die genus vir die *Flora of southern Africa* verskaf, met sleutels tot en beskrywings van alle taksons.

Daar is bevind dat kenmerke van die blaar en bloeiskede en veranderinge wat ná bestuiwing plaasvind, van besondere belang in die taksonomie van die genus is. Geografiese verspreidingspatrone was nuttig om die identiteit van taksons te bevestig, veral dié wat endemies aan beperkte lokaliteite in Suid-Afrika is.

Op grond van sy duidelik onderskeidende morfologie en beperkte verspreiding, is *Z. albomaculata* (Hook.) subsp. *valida* Letty to spesierang verhef as *Z. valida* (Letty) Y.Singh. Agt spesies en twee subspesies word in hierdie studie erken: *Z. aethiopica* (L.) Spreng., *Z. albomaculata* subsp. *albomaculata*, *Z. albomaculata* subsp. *macrocarpa* (Engl.) Letty, *Z. elliotiana* (Watson) Engl., *Z. jucunda* Letty, *Z. odorata* P.L.Perry, *Z. pentlandii* (Watson) Wittm., *Z. rehmannii* Engl. en *Z. valida*. Twee seksies word voorgestel: Seksie *Zantedeschia* wat *Z. aethiopica* en *Z. odorata* bevat en Seksie *Aestivus* wat die oorblywende spesies insluit.

ACKNOWLEDGEMENTS

Thanks are gratefully due to many persons and institutions who have assisted in various aspects of this study.

Professors A.E. van Wyk and H. Baijnath for their guidance, constructive criticism and assistance with field work and photography.

The University of Pretoria and the National Botanical Institute for partial financial support. The University of Durban-Westville for laboratory space and some facilities.

The Curators of the Geo-Potts Herbarium (University of the Orange Free State), Malolotja Reserve Herbarium (SWZ), National Herbarium (PRE), National Herbarium of Zimbabwe (SRGH) and National University of Lesotho Herbarium (ROML) for the loan of herbarium material.

The New Zealand Calla Council for the use of their colour guide 1993.

Mr Niven Anghar, Ms Nicolette Carstens, Mr Graham Duncan, Mrs Emsie du Plessis, Mr Joe Ganga, Mr Martin Potgieter, Dr Dee Patterson-Jones, Ms Adela Romanowski, Dr Elsie Steyn, Mrs Muriel van Staden and Mr Deon Viljoen who kindly rendered technical assistance. Mrs Estelle Potgieter, Librarian at the Mary Gunn Library, for her prompt response to literature requests. Mrs E.P. van Wyk for her assistance in a number ways. Mr Ashley Nicholas for help with the cladistics analysis.

Mr & Mrs Jaap Grobbelaar (Mpumalanga), Neil & Niva McGregory (Glen Lyon Farm, Nieuwoudtville), Ian & Pam Michelle-Innes (Farm Blanerne, Northern KwaZulu-Natal), Hans & Christa van Rooyen (Umpukane, Clocolan, Free State) for their hospitality during field work. Christa van Rooyen and Nancy Gardiner are thanked for the loan of photographs/slides of *Zantedeschia* 'pink marshmallow' and 'green Goddess' respectively.

Ms Rosemary Williams, Curator of the Natal Herbarium, for her considerate and supportive disposition.

My parents for their understanding, patience and encouragement.

CURRICULUM VITAE

Yashica Singh was born in Durban on 26 December 1965. She matriculated at the Reservoir Hills Secondary School. On completion of her BSc Degree in 1987, at the University of Durban-Westville (UDW), her career in Botany began. She worked as a Laboratory Assistant in the Department of Botany, at UDW. Whilst in employment, Yashica completed an Honours Degree in Botany (UDW) and a Diploma in Higher Education (UNISA). One of her projects for the honours course was a taxonomic study of the genus *Amaranthus* L. in Natal. It was at this stage that her interest in systematics developed. Since 1994, Yashica is employed as Scientific Officer at the Natal Herbarium (National Botanical Institute). Some of the larger families she identifies and curates include: Araceae, Iridaceae, Amaryllidaceae and Hypoxidaceae. Her interest in petaloid monocots has been further strengthened during this study.

APPENDIX 1

Southern African Aroids [*]

[Please note that inspite of the claimed difficulty in assigning *Z. odorata* to a section in this publication, subsequent analysis of characters has shown that it is better placed in Section *Zantedeschia* (see pp. 109–110).]

---

[*] published in *Proceedings of the VI International Aroid Conference*: 53. Kunming, China.

S1.14 SOUTHERN AFRICAN AROIDS

Singh, Y.[1], Van Wyk, A.E.[2], Baijnath, H.[3]
[1]Natal Herbarium, National Botanical Institute, Botanic Gardens, Durban, 4001 South Africa
[2]HGWJ Schweickerdt Herbarium, Department of Botany, University of Pretoria, 0001 South Africa
[3]Ward Herbarium, Department of Botany, University of Durban–Westville, Private Bag X54001, Durban 4001 South Africa

Abstract

In Africa, the family Araceae is represented by 15 genera, 13 of which are endemic to Africa. Five varied genera (number of species in southern Africa / total number of species) occur in southern Africa namely, *Amorphophallus* Blume (1 / 90), *Gonatopus* Hook. f. ex Engl. (2 / 5) , *Stylochiton* Lepr. (1 / 15), *Zamioculcas* Schott (1 / 1) and *Zantedeschia* Spreng. (7 / 7). In this paper an overview of the data available on characters of systematic significance to the southern African aroids is presented, with particular emphasis on the largest and predominantly southern African genus *Zantedeschia*.

Of all southern African aroids, *Zantedeschia* has become popular among plant lovers in America, Europe, Japan and New Zealang. It is their rich foliage that is often white spotted, and their colourful ornamental spathes that have drawn the attention of plant breeders world– wide. The sale of *Zantedeschia* cut flowers and tubers yields a high revenue to countries like New Zealand and the United States.

In this study, the morphology, anatomy, biogeography, and pollination biology of *Zantedeschia* has been extensively investigated. A taxonomic consideration of the genus indicates that the species are related to each other in various character combinations. Thus, a phylogenetic inference is perplexing. Nevertheless, from an integrated comparative study, certain homologies were recognised, upon which an interspecific phylogenetic relationship is postulated.

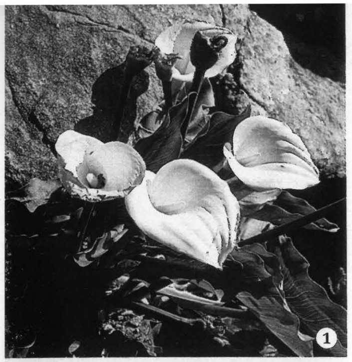
On the basis of mainly exomorphological characters, Letty (1973) informally grouped the species into two sections namely the typical section containing only one species, *Z. aethiopica* (L.) Spreng. and a section containing the remaining species. The present study not only builds on these differences but also highlights similarities between *Z. aethiopica* and the remaining species. The recently described species *Z. odorata* P. L. Perry exhibits characters of both sections. It is therefore difficult to assign *Z. odorata* to any of these sections. This paper purports that the establishment of the two sections is dispensable.

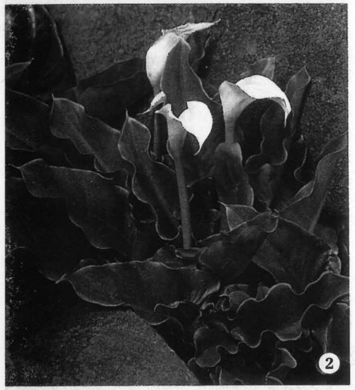
APPENDIX 2

Know your arums: an easy guide to identify members of the genus *Zantedeschia* [*]

---

[*] published in *Veld & Flora* 81: 54–55.





KNOW YOUR ARUMS

An easy guide to identify members of the genus *Zantedeschia*.

by Y. Singh, Natal Herbarium, National Botanical Institute; A.E. van Wyk, HGWJ Schweickerdt Herbarium, Department of Botany, University of Pretoria; and H. Baijnath, Ward Herbarium, Department of Botany, University of Durban-Westville

The genus *Zantedeschia* (family: Araceae), although native to Africa, is well-known to plant lovers throughout the world. Commonly known as arums or callas, their rich foliage, often spotted with white, and their colourful, ornamental spathes (see glossary) has drawn the attention of plant breeders world-wide. The foliage and spathe colours vary considerably depending on the species. They are extremely popular as pot plants because of the multitude of cultivars and hybrids available.

In many parts of the world the sale of arums yields a high revenue. In 1992 New Zealand exported over NZ$3 million worth of flowers and NZ$2 million worth of tubers to 27 countries: Japan, Germany, Switzerland, the Netherlands and the USA accounting for 95% of these exports.

Identifying arums

A key for the identification of the genus *Zantedeschia* was provided by Cythna Letty in 1973, but is difficult to use when flowers are absent, which is often the case for, apart from *Z. aethiopica* and *Z. albomaculata*, these plants rarely flower in cultivation. This key equips the non-scientist with a simple guide to identify the seven species of *Zantedeschia* using vegetative and floral characteristics, allowing easy comparison of the species. Sports are not uncommon within this genus; for example, the spathe or spadix may be double or even triple, and spathes of *Z. aethiopica* are sometimes blotchy green in colour. Although the key is aimed primarily at the wild taxa, it should also be applicable to most sports and cultivars.

Acknowledgments

Grateful appreciation is expressed to Dr Funnell for his interest and co-operation. Special thanks to Mrs I. Oliver for the slide of *Z. odorata* and to Mrs N. Gardiner for the slide of *Z. rehmannii*.

Further reading

Ball, V. (1986). A promising new pot plant. *Grower Talks*, November, 48-51.

Letty, C. (1973). The genus *Zantedeschia*. *Bothalia* **11** (1&2), 5-26.

Muller, T. (1993). New Zealand callas grown for the world's great floral artists: statistics update. *Calla News* **9**, 37-38.

Perry, P.L. (1989). A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* **55** (4), 447-451.

TIPS ON GROWING *ZANTEDESCHIA*

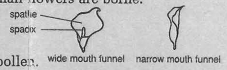
from Graham Duncan, Kirstenbosch

As *Zantedeschia aethiopica* occurs in both summer and winter rainfall areas, it can be dormant in either winter (summer rainfall areas) or summer (winter rainfall areas), or it can be evergreen if it receives water throughout the year. All the other species, with the exception of *Z. odorata* (from Nieuwoudtville and therefore winter-growing) are summer-growing and are dormant in winter. All the summer-growing species **must** be dry in winter, and *Z. odorata* **must** be dry in summer. Arums like rich soil, full sun , and liberal watering when in growth and flowering. Porcupines love arum rhizomes, and hawk-moth caterpillars love *Zantedeschia* leaves.

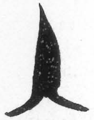
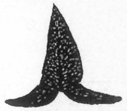
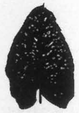
If grown in a container, water each day once leaves show, and until flowering is over. Reduce watering gradually and allow a dormant period after the leaves turn yellow.

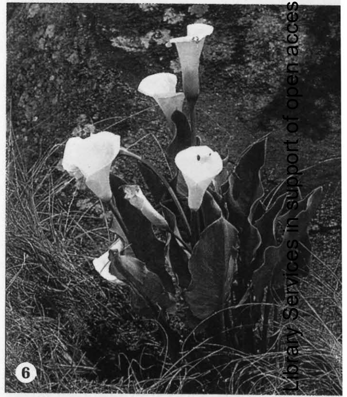
The Garden Shop at Kirstenbosch has *Zantedeschia aethiopica* plants for sale, some with speckled leaves and, occasionally, some with green flowers. Tel: (021) 762 1621.

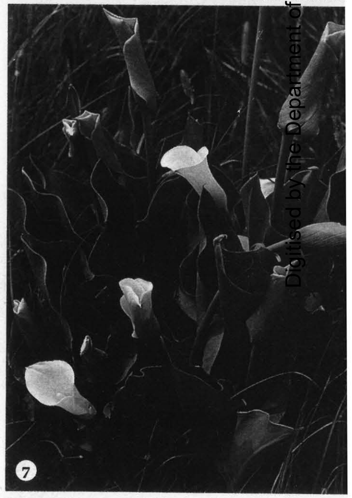
GLOSSARY

berry	a simple fleshy fruit without a stony layer, usually containing many seeds, e.g. tomato.	
cordate	heart-shaped, having the notched end at the base and pointed end at the apex.	
deciduous	referring to plants that drop their leaves at the end of each growing season.	
evergreen	referring to plants that bear leaves throughout the year.	
hastate	shaped like an arrow head but with the basal lobes turned outward.	
lanceolate	lance-shaped, over three times longer than broad, widened above the base and tapering upward.	
maculate	spotted.	
mucilaginous	slimy.	
oblong	blunt at each end, having nearly parallel sides and two to four times as long as broad.	
orbicular	circular in outline.	
ovate	egg-shaped in outline with the axis widest below the middle.	
spadix	a finger-like fleshy axis on which many small flowers are borne.	
spathe	large, often coloured bract (modified leaf) which encloses part of the spadix, often referred to as the 'flower'.	 spathe spadix wide mouth funnel narrow mouth funnel
staminode	a sterile stamen which does not produce pollen.	
tuber	a swollen underground stem which stores food, e.g. potato.	

CHARACTERISTICS OF THE DIFFERENT SPECIES OF *ZANTEDESCHIA*

SPECIES	***Z. aethiopica***	***Z. odorata***	***Z. albomaculata***			***Z. rehmannii***	***Z. jucunda***	***Z. pentlandii***	***Z. elliottiana***
			subsp. *albomaculata*	**subsp. *macrocarpa***	**subsp. *valida***				
DISTRIBUTION	Cape, Natal, Transvaal, Lesotho	Cape	Cape, Natal, Transvaal, Lesotho, OFS, Swaziland, Zimbabwe, Zambia Angola, Malawi	Natal, Transvaal. OFS, Swaziland	Natal	Natal, Transvaal, OFS, Swaziland	Transvaal	Transvaal	Known only from cultivated material
HABIT	Generally evergreen	Deciduous	Deciduous	Deciduous	Deciduous	Deciduous	Deciduous	Deciduous	Deciduous
UNDEGROUND PARTS	Tuber	Tuber	Tuber	Tuber	Tuber	Tuber	Tuber	Tuber	Tuber
FLOWERING TIME	August to January occasionally February to July	Late July to August	October to February	November to February	October to March	November to December	November to December	November to December	November to December
LEAF SHAPE	 Broadly ovate-cordate	 Ovate-cordate	 Oblong-hastate to ovate-hastate base very variable	 Triangular-hastate	 Ovate-cordate to orbicular-cordate	 Lanceolate	 Triangular-hastate	 Oblong-hastate	 Orbicular-cordate to ovate-cordate
MACULATION	Usually immaculate, occasionally maculate	Immaculate	Immaculate or conspicuously maculate	Sparsely maculate, occasionally immaculate	Immaculate	Immaculate	Intensely maculate	Immaculate, rarely maculate	Maculate
SPATHE SHAPE	Wide mouth funnel	Wide mouth funnel	Narrow mouth funnel	Narrow mouth funnel	Wide mouth funnel	Narrow mouth funnel	Wide mouth funnel	Wide mouth funnel	Wide mouth funnel
SPATHE COLOUR	White, sometimes with a purplish tinge on the outside	White	White, ivory, cream, rarely pale yellow or coral pink	Cream or straw	Ivory to cream	Various shades of red to dark maroon, white	Deep yellow	Lemon-chrome yellow	Golden yellow
PURPLE BLOTCH AT BASE OF SPATHE	Absent	Absent	Usually present	Usually present	Usually present	Absent	Present	Present	Present
STAMINODES AMONG OVARIES	Present	Present	Absent	Absent only 2 seen in 1 specimen	Absent,	Absent	Absent	Absent	Absent
SCENT	Very slight, easily missed	Freesia-like	None	None	None	None	None	None	None
BERRY AT RIPENING	Orange, soft and mucilaginous	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground	Green and firm disintegrates on ground
PEDUNCLE FORM WHEN BERRY IS MATURE	Erect	Bends towards the ground	Bends towards the ground	Bends towards the ground	Bends towards the ground	Bends towards the ground	Bends towards the ground	Bends towards the ground	Bends towards the ground
SPATHE COLOUR WHEN FRUIT ARE MATURE	Only lower portion of spathe turns green, upper portion withers	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green	Entire spathe turns green





1: *Zantedeschia aethiopica*, 2: *Z. odorata*, 3: *Z. rehmannii*, 4: *Z. jucunda*, 5: *Z. elliottiana*, 6: *Z. pentlandii*, 7: *Z. albomaculata* subsp. *macrocarpa*.

APPENDIX 3

Leaf anatomy of the genus *Zantedeschia* (Araceae) [*]

---

[*] published in *Proceedings of the Electron Microscopy Society of Southern Africa*: 57.

LEAF ANATOMY OF THE GENUS *ZANTEDESCHIA* (ARACEAE)

Y. Singh *; A.E. Van Wyk + & H. Baijnath ++

* Natal Herbarium, National Botanical Institute, Durban
+ HGWJ Schweickerdt Herbarium, Department of Botany, University of Pretoria, Pretoria
++ Ward Herbarium, Department of Botany, University of Durban-Westville, Durban

The araceous genus *Zantedeschia* is commonly known as arum or calla lily. Although native to Africa (especially South Africa) the genus has become well known to plant lovers world-wide for its rich foliage and beautiful ornamental spathes of varying colours.

Although most systems of classification of this family emphasise floral morphology[1], information from vegetative anatomy proved to be useful in separating subfamilies[2]. Virtually all anatomical surveys of vegetative organs of Araceae are broad[3], subsequently, no published data on a single genus is available. The purpose of this presentation is to detail leaf anatomical characters of all species of *Zantedeschia* from observations with light (LM) and scanning electron microscopy (SEM). A further objective is to consider the systematic implications of these characters.

Leaf surface structures were examined from leaf scrapes (LM) and SEM. Wax embedding and GMA techniques for LM were used for the study of internal leaf structure.

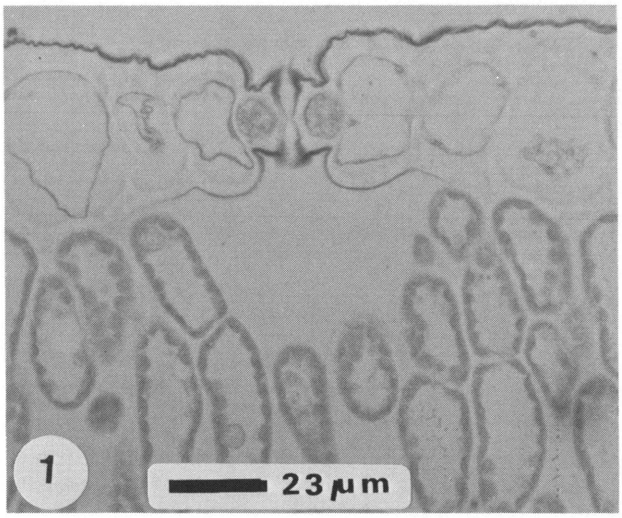
Leaves of *Z. elliotiana* and *Z. jucunda* are white spotted. *Z. aethiopica*, *Z. albomaculata*. and *Z. pentlandii* may also produce leaves with such spots. Non-spotted leaves were compared with green areas of spotted leaves. In addition, spots of different species were compared. For the non-spotted areas, ad- and abaxial surfaces are fairly uniform in regard to cellular details and ornamentation. Cuticular striations are pronounced on both surfaces. Striae regularly traverse across the position of the anticlinal walls. Epidermal cells are polygonal in shape (4-6 sided) and are uniformly distributed. Leaves are amphistomatic with the frequency of stomata being the same on both leaf surfaces. Transverse sections of the lamina indicated the presence of a thin cuticle that extends around the guard cells (Fig. 1). The mesophyll comprises aerenchyma cells with large air spaces. The adaxial part consists of 1-2 layers of well-developed palisade cells whereas the abaxial part is characterised by layers of collenchyma cells.

Shapes and dimensions of epidermal cells in the spots are similar to those of the non-spotted areas. However, surface details relating to the degree of striation and to the nature of the position of the anticlinal wall, provide characters of diagnostic value (Fig. 2). Transverse sections through the spot indicated the absence of a well-developed palisade layer, chloroplasts and collenchyma cells. It also confirmed the absence of stomata in these zones.

Although anatomical data for the species of *Zantedeschia* indicates homogeneity within the genus, there are a few differences of taxonomic importance. It is possible to identify some species by using a combination of leaf anatomical characters.

References

1. Bogner, J. and Nicholson, D.H. (1991) Willdenowia. 21, 35.
2. Engler, A. (1905-1920) Das Pflanzenreich. IV.
3. Hotta, M. (1971) Jap. Journ. Bot. 20(4) 269.



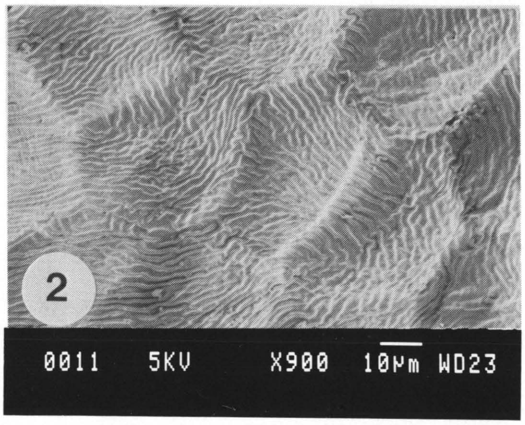


Fig. 1. LM of T/S of non-spotted zone of *Z. elliotiana*.
Fig. 2 SEM of adaxial surface of spot of *Z. aethiopica*.

APPENDIX 4

Floral biology of *Zantedeschia aethiopica* (L.) Spreng. (Araceae) [*]

Materials and Methods

Results and Discussion

---

[*] published in *South African Journal of Botany* 62: 146—150

S. Afr. J. Bot. 1996, 62(3): 146–150

Floral biology of *Zantedeschia aethiopica* (L.) Spreng. (Araceae)

Y. Singh,* A.E. van Wyk[1] and H. Baijnath[2]

Natal Herbarium, National Botanical Institute, Botanic Gardens Road, Durban, 4001 Republic of South Africa

[1]H.G.W.J. Schweickerdt Herbarium, Department of Botany, University of Pretoria, Pretoria, 0001 Republic of South Africa

[2]Ward Herbarium, Department of Botany, University of Durban-Westville, Durban, 4000 Republic of South Africa

Received 28 August 1995; revised 18 February 1996

Floral morphology, stages in floral development and insect visitation in *Z. aethiopica* are reported. Floral development can be divided into five phases: pre-female, female, male, fruit development and fruit ripening. Plants are self-incompatible and separation of sexes is achieved by marked protogyny. *Z. aethiopica* is the only member of the genus in which the basal part of the spathe turns green during fruit maturation while the apical part withers away. This species is further unique in that the berries turn orange, soft and mucilaginous on ripening. Both *Z. aethiopica* and *Z. odorata* have staminodes present amongst the ovaries and a faint scent is evident. Several insects, especially beetles, were seen visiting the inflorescence. Observations on *Z. aethiopica* are compared with other members of the genus, notably *Z. albomaculata* subsp. *albomaculata*.

Keywords: Araceae, beetle pollination, flower morphology, pollen, *Zantedeschia aethiopica*.

*To whom correspondence should be addressed.

Introduction

The genus *Zantedeschia* Spreng. is endemic to southern Africa and comprises seven species: *Z. aethiopica* (L.) Spreng., *Z. albomaculata* (Hook.) Baill., *Z. rehmannii* Engl., *Z. pentlandii* (Watson) Wittm., *Z. elliotiana* (Watson) Engl., *Z. jucunda* Letty and *Z. odorata* P.L.Perry. *Z. albomaculata* has three subspecies, the typical one, as well as *Z. albomaculata* subsp. *macrocarpa* (Engl.) Letty and *Z. albomaculata* subsp. *valida* Letty. Letty (1973) grouped the species into two informal sections, namely the typical section containing only one species, *Z. aethiopica*, and a section containing the remaining species. According to her, *Z. aethiopica* differs from the latter group in that the plants do not die down in winter, female flowers are intercalated with staminodes, peduncles remain upright during fruiting, and fruits turn orange, soften and become mucilaginous on ripening. This species is also the only one in which the upper portion of the spathe eventually withers and turns brown, and the lower portion turns green during fruiting. The recently described *Z. odorata* (Perry 1989) displays characters of both sections.

Apart from a few casual observations reported by Marloth (1915) and Jackson (1986), no detailed study on the floral biology and pollination of *Zantedeschia* has yet been undertaken. Furthermore, although pollinators have been recorded for many araceous genera (Grayum 1986), those of the southern African aroids have received no attention.

Z. aethiopica is perhaps the best known member of the genus. It is a popular horticultural subject with many cultivars that are grown all over the world. This species was chosen for the study because it is common and readily available. Where possible, observations were also made on *Z. albomaculata* subsp. *albomaculata* for comparison. The objectives of this study were to describe the various stages in floral development, to suggest possible sites of fragrance emission, to consider the role of scent in attracting insects and to assess the possible role of different insect visitors.

Materials and Methods

Field observations

Field observations on natural populations were made at three sites in Natal: Nottingham Road (2929BD), Cato Ridge (2930DA) and Merebank (2930DD). Sites were visited during the main flowering period (August to January) in 1992/3, 1993/4 and 1994/5. Activity of various insect visitors was observed. Additional observations were made on plants during collecting trips in Mpumalanga and the Western Cape Province.

Morphology of reproductive structures

Spathes were collected from different populations throughout South Africa and preserved in formalin-acetic acid-alcohol (FAA) at a ratio of 1:1:18. Spadices and flowers were examined using a Wild stereomicroscope. An assessment of stamens and pistils was undertaken for 15 inflorescences from a single population at Nottingham Road. Dried, unacetolysed pollen grains were studied using a scanning electron microscope (SEM), following standard procedures.

Stages of floral development

Plants collected from the wild were cultivated in a greenhouse. Different stages of floral development observed in these plants were photographed under a Wild Autophotomat MPS 55 photomicroscope. Inflorescences of these plants were also used to record the maturation of sexes and development of fruit.

Breeding behaviour

In the greenhouse, inflorescences of *Z. aethiopica* and *Z. albomaculata* subsp. *albomaculata* were bagged to test for self-incompatibility. Fine mesh nylon bags of 150 × 200 mm were placed over the inflorescences on emergence.

Collecting of insects

Spathes containing insects were collected in the field and stored in honey jars. In the laboratory, insects were killed and preserved by freezing. This method ensured that pollen remained on the bodies of the insects. The outer surface of insect bodies was examined for the presence of pollen, under a dissecting microscope. Pollen grains of members of the genus are white and are therefore easily visible on the usually dark bodies of the insects. In addition, insects were randomly collected from different inflorescences in a population. Insects were identified at the Durban Natural Science Museum.

Determination of scent

Using fresh material, the spathe, male and female portions of the inflorescence were separated and placed individually in glass bottles which were sealed. After 10 and 30 min, three persons not familiar

Table 1 Ratio of ovaries to anthers per spadix in *Z. aethiopica*

Inflorescence	Number of ovaries	Number of anthers	Ovaries: anthers
1	62	1392	1:22
2	83	1242	1:15
3	94	928	1:10
4	70	1200	1:17
5	59	1062	1:18
6	71	422	1:6
7	78	823	1:11
8	67	1092	1:16
9	69	966	1:14
10	48	1148	1:24
11	79	1450	1:18
12	63	956	1:15
13	71	1051	1:15
14	75	1104	1:15
15	97	1495	1:15
Mean	72.40	1088.73	1:15

with scent in this plant were asked to smell each bottle and to record the presence of a scent. To locate presumptive osmophoric tissue, freshly collected whole spathes were stained in a 1:1 000 neutral red:water solution, following the procedure used by Stern *et al.* (1986), except that the staining period was extended to one hour, rather than 20 min. After a rinse in tap water, the spathe and spadix were carefully examined for any possible floral patterns. In addition to the neutral red test, longitudinal sections of anthers and staminodes were examined under oil immersion with an Olympus compound microscope, to determine the presence of osmophores.

Results and Discussion

Morphology of reproductive structures

As is characteristic of the family Araceae, flowers of *Zantedeschia* are arranged on a fleshy axis (spadix) enclosed in a large, leaf-like bract, the spathe. The upper portion of the spadix is covered by a densely crowded mass of stamens, while the female flowers form a well-developed zone at the base. Male flowers are made up of one to three sessile anthers. Since it was not possible to resolve the exact number of stamens per male flower, the total number of anthers on the spadix was counted. Table 1 indicates the numbers of ovaries and anthers for 15 inflorescences.

Anthers range from about 400 to almost 1 500 and the ovaries from about 40 to almost 100 per spadix. From Table 1 it is clear that the ratio of anthers to ovaries is very variable. On average, the anthers are about 15 times more than the ovaries. The anthers are free and each is characterized by two terminal pores. Ovaries are ovoid in shape with a truncate stigma and 3-locular with 1–4 ovules per locule. The morphology of the reproductive structures is rather similar for all species, except that in *Z. aethiopica* and *Z. odorata*, staminodes are interspersed amongst the ovaries. Each ovary is surrounded by three spathulate staminodes (Figure 1). Although apparently without function, their presence is taxonomically useful in separating these two species from the remaining members of the genus.

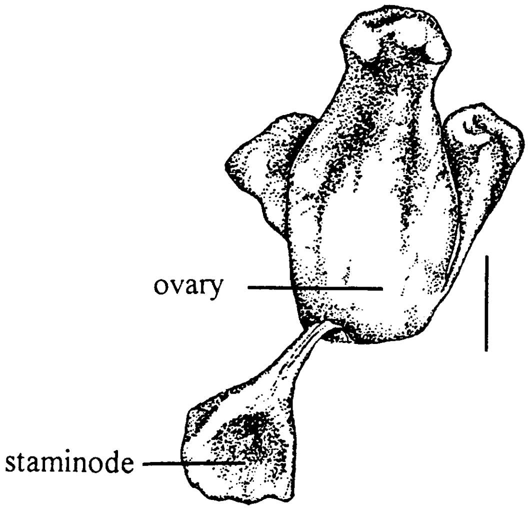


Figure 1 Female flower of *Z. aethiopica* surrounded by three staminodes. Scale bar = 1 mm.

Flowering behaviour

The development of flowers can be divided into the following five sequential phases (Figure 2a–e):

Pre-female phase. Spathe is tightly rolled. This stage lasts for about three days from the day the emerging spathe becomes visible. The stigmas are non-receptive and the anthers immature.

Female phase. Spathe begins to unwind. This phase, which lasts for about six days, can be discerned by well-developed glistening stigmatic areas, indicating their receptivity (Figure 3, arrows). A faint scent is emitted from the inflorescence. The flowers are markedly protogynous, with anthers still immature.

Male phase. Spathe is fully opened. All the anthers on the spadix dehisce simultaneously (Figure 4). Anthesis lasts for about 10 days. A faint scent is still present at this stage. The stigmatic surface degenerates, signified by a browning of the stigmas (Figure 5, arrow).

Fruit development. During this period of about 30 days the berries enlarge to reach a size of about 13 × 10 mm. By this stage, the staminodes have shrivelled and are squashed among the expanding berries. As the berries mature, the infructescence expands vertically and laterally. The upper portion of the spathe begins to wither, whereas the lower portion turns green (Figure 2d).

Fruit ripening. The fruit ripen sequentially from apex to base (Figure 2e). When all fruits are fully ripe, the infructescence is bright orange.

Breeding behaviour

Bagging experiments indicated that spontaneous selfing does not occur in *Z. aethiopica*, unlike in *Z. albomaculata* subsp. *albomaculata*, where selfing resulted in seed set. Solitary bagged inflorescences of *Z. aethiopica* simply withered away, while those of *Z. albomaculata* produced fruit. *Z. aethiopica* clearly requires cross-pollination for seed set. It is unfortunate that selfing could not be tested for the remaining species as these failed to flower under greenhouse conditions.

Pollen morphology and extrusion

Pollen exine sculpturing is psilate in *Zantedeschia*. Grayum (1986) found a positive correlation between psilate pollen and beetle pollination in the Araceae. He further suggests that pollen is attached onto the smooth hard-bodied insects such as beetles through the agency of sticky secretions of the stigma or of the

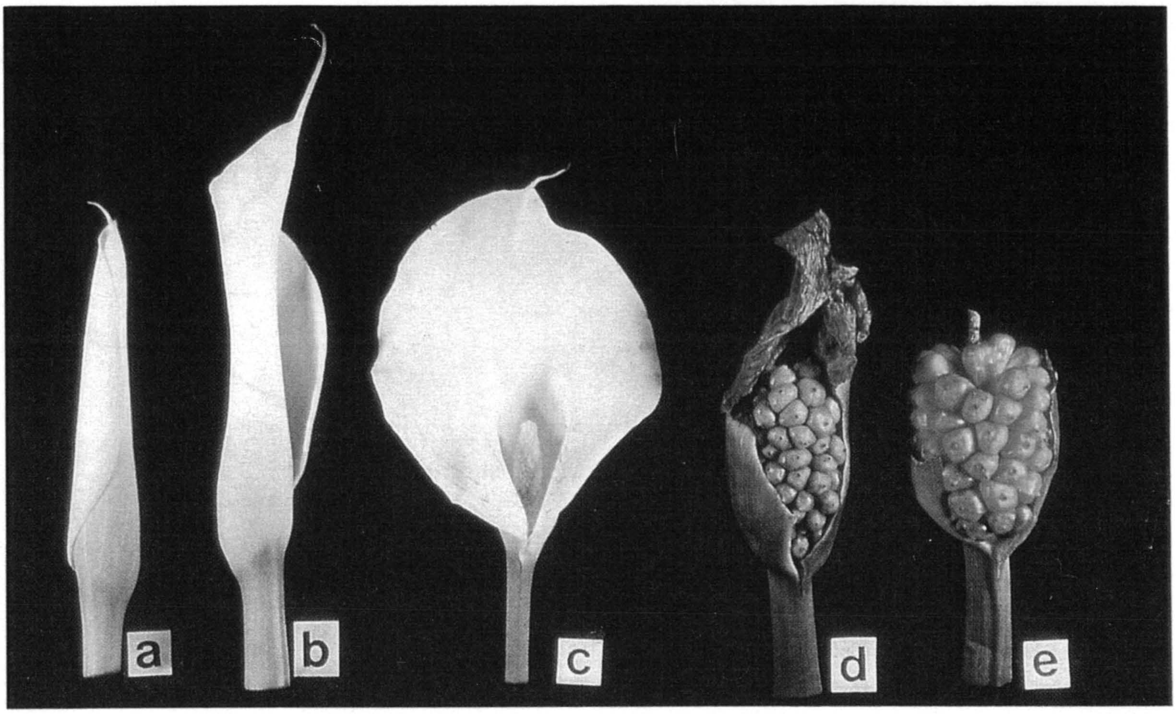
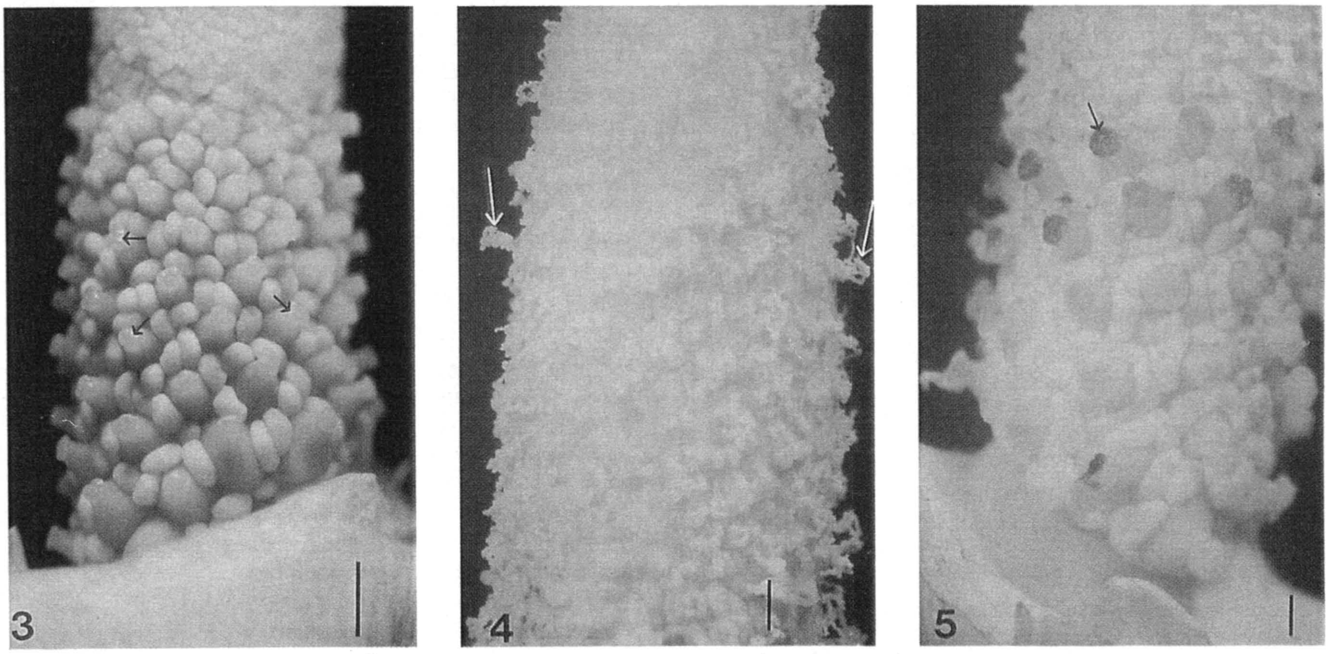


Figure 2 Phases of floral development in *Z. aethiopica*. a. Pre-female phase. b. Female phase. c. Male phase. d. Fruit development. e. Fruit ripening.

inner spathe surface as in *Dieffenbachia* Schott. In *Zantedeschia*, pollen grains are extruded through the anther pores in fine long threads (Figure 4, arrows), held together by a sticky substance. Whether pollen is also held together electrostatically is unknown. Presumably, the release of pollen in threads requires only one end of the thread to attach itself to the insect body for the entire thread to be transported. Under field conditions, these strings of pollen grains rarely accumulate, as they are soon removed by insects. However, under greenhouse conditions, pollen grains accumulate on the spadix, eventually falling to the base of the spathe. In *Z. albomaculata* subsp. *albomaculata*, in the absence of vectors, pollen has been observed to fall in large masses onto the stigmas.

The mechanism for the release of pollen in flowering plants is achieved by shrinkage of the endothecial layer as the cells lose water (Fahn 1974). In general, the inner periclinal walls of the



Figures 3–5 3, Female portion of spadix during the female phase in *Z. aethiopica* (spathe removed). Female flowers interspersed with staminodes. Note the glistening stigmas. Scale bar = 3 mm. 4, Male portion of spadix during the male phase in *Z. aethiopica* (spathe removed). All anthers have dehisced simultaneously, releasing the white pollen in fine threads (arrow). Scale bar = 1.5 mm. 5, Female portion of the spadix during the male phase, showing the browning of the stigmatic surfaces in *Z. aethiopica* (spathe removed). Scale bar = 2 mm.

endothecial cells or fibrous layer are thickened and this forces the anther slits to open during dehydration (Fahn 1974). Squeezing of pollen grains through pores in *Z. aethiopica* and other poricidal members of the Araceae is due to the thickening being on the outer rather than the inner periclinal walls of the endothecial cells (Weberling 1989). The inverse position of the thickening probably creates an inward pressure during water loss, thereby compressing the pollen sac, which releases the pollen in threads through the pore.

A range of insects was collected from the inflorescences of *Z. aethiopica*, including mainly beetles of the genera *Anoplochilus* MacLeay and *Leucocelis* Burmeister (Family Scarabaeidae). The bodies of all insects were covered with pollen. The species therefore, does not appear to have a single specific pollinator. Psilate pollen has been associated with beetle pollination (Grayum 1986) and since beetles were the predominant group of insects collected from spathes, *Z. aethiopica* is considered to be beetle pollinated. The beetles appear to enter the spathe at the female stage, and remain there until after anthesis, clustered mainly around the female portion of the spadix. It could not be confirmed whether the beetles were feeding on the stigmatic fluid. The regular presence of mating pairs indicates that the base of the spathe provides a suitable niche for mating. Observations suggest that arachnids and other insects (e.g. bees and flies) merely seek shelter or trap their food in the spathes, thereby accidentally effecting pollination.

Scent production

Marloth (1915) recorded the presence of scent in the spathes of *Z. aethiopica*. Perry (1989), on the other hand, reported its absence in *Z. aethiopica*, but its presence in *Z. odorata*, hence the choice of specific epithet. Vogel (1990) expressed the opinion that there is no discernible smell in the inflorescences of *Zantedeschia*, and if present, it serves no function. This study confirmed that the inflorescence of *Z. aethiopica* produces a faint scent which can easily be missed if not captured at the correct floral stage. All three persons asked to verify which part of the inflorescence produced an odour indicated the presence of a scent in the female zone, which suggests that either the staminodes or pistils are sites for osmophores.

Osmophores are common in the Araceae. They have been reported in the male flowers (*Philodendron* Schott), the flowers (*Spathiphyllum* Schott), the spathe (*Cryptocoryne* Fisch. ex Wydl.)·and the appendix of the spadix (*Amorphophallus* Blume ex Decne.) (Vogel 1990). Staminodes and fertile anthers in *Homalomena cordata* (Houtt.) Schott, a member of the same subfamily as *Zantedeschia*, were found to have the histological composition of osmophores (Eyde *et al.* 1967). Although, tissues of the spathe and spadix did not stain with neutral red, longitudinal sections through the anther (Figure 6a) and staminode (Figure 6b) of *Z. aethiopica* indicated a structure similar to that in *H. cordata*. Since scent in *Zantedeschia* is restricted to staminode-bearing species, it appears likely that the staminodes are responsible for scent emission. However, similarity in the histological composition of anthers and staminodes, as well as in anthers of all species, reduces the possibility of staminodes being involved in scent production. A survey of the histological composition of pistils in the scented and non-scented species would provide evidence as to whether the pistils are responsible for scent production. The question that arises is by what means are insects attracted to spathes of the non-scent producing species of *Zantedeschia*? Should the latter species prove to be self-compatible, then this state and the lack of detectable scent may be correlated.

Gottsberger (1977) reported that beetles visiting flowers may feed on pollen, nectar or flower organs like petals, tepals, stamens and carpels, and thereby cause considerable damage to flowers. In the scented species of *Zantedeschia*, staminodes may also provide protection against herbivores. The lateral walls of anthers and staminodes were found to be lined with several tannin cells. The ovaries however, lack tannin. Secondary substances such as tannins have evolved in response to natural selection for defence against herbivores and insects (Whittaker & Feeny 1971). Therefore, it may be assumed that tannins in staminodes of *Z. aethiopica* and *Z. odorata* act as antifeedants to beetles, thereby protecting the ovaries. The base of the spathe is cool and moist and therefore an ideal environment for fungal growth. Whittaker & Feeny (1971) have quoted several publications where it was found that tannins also inhibit fungal growth. Hence, tannins in the floral structures of *Zantedeschia* may protect the plants against animals and fungi.

Spathe greening

Once the ovules have been fertilized, the white spathe begins to turn green. Greening of the spathe occurs in all species of *Zantedeschia*. However, in *Z. aethiopica* only the lower portion of the spathe turns green, whereas the upper portion withers away to display the orange berries to dispersal agents. Fruit exposure is not necessary in the remaining species as seed dispersal is achieved by mere disintegration of the infructescence. Hence in these species the entire spathe turns green. Spathe greening is induced by endogenous cytokinins produced by the fruit and translocated to the spathe (Chaves das Neves & Pais 1980).

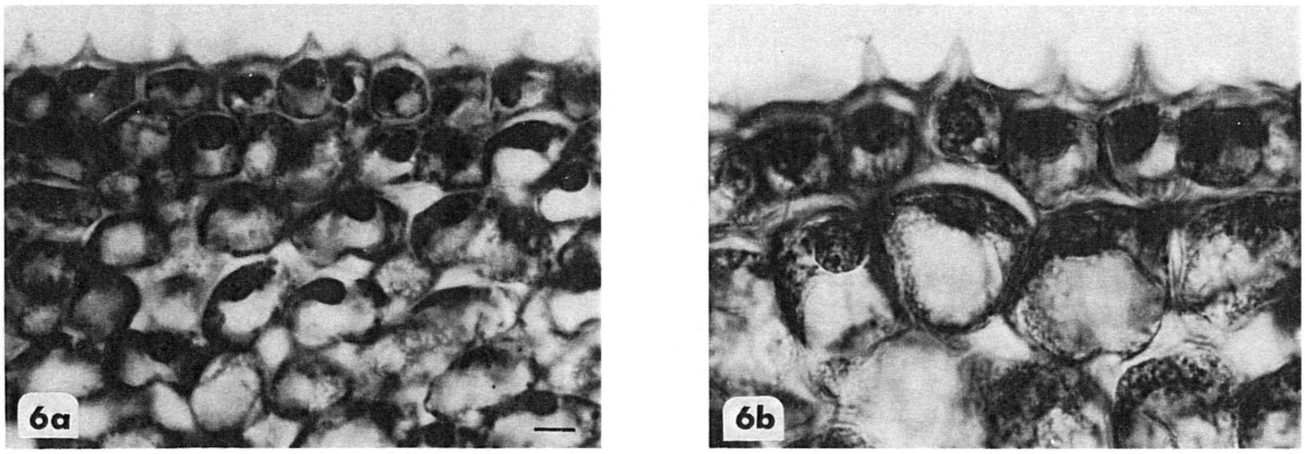


Figure 6 Papillate epidermal cells as in *Homalomena cordata*. a. L.S. anther. Scale bar = 12 μm. b. L.S. staminode. under oil immersion.

These authors have further identified the cytokinin 6-(o-hydrobenzylamino)-9-B-D-ribofuranosylpurines as the spathe-greening factor in *Z. aethiopica.*

Fruits

The orange coloration of the ripe berries, softening of the pericarp, erect peduncle and the withering away of the upper portion of the spathe to expose the berries in *Z. aethiopica* all play a role in attracting dispersers. In this study no continuous field observations were conducted to detect the seed-dispersal agent (if any) of this species. However, casual observations suggest that the berries are eaten by birds. To confirm this, and to determine which bird species feed on the berries, more extended field observations are required.

Conclusions

The present results provide essential information on the breeding behaviour of *Z. aethiopica.* The data correlates beetles with pollination, staminodes with possible scent production and/or defence, fragrance emission with self-incompatibility and berry phenology with bird dispersal. In addition, these observations provide characters useful for separating species and contribute to a better understanding of relationships within *Zantedeschia.*

Acknowledgements

This project was funded in part by the University of Pretoria and the National Botanical Institute. We thank A. Anandraj, S. Makwakwa and S. Soobramoney for technical assistance and A. Heeres of the Durban Natural Science Museum for the identification of insects.

Referencs

CHAVES DAS NEVES, H.J. & PAIS, M.S. 1980. Identification of a spathe regreening factor in *Zantedeschia aethiopica. Biochem. biophys. Res. Commun.* 95: 1387–1392.

EYDE, R.H., NICHOLSON, D.H. & SHERWIN, P. 1967. A survey of floral anatomy in Araceae. *Am. J. Bot.* 54: 47–497.

FAHN, A. 1974. Plant anatomy, 2nd edn. Pergamon Press, Oxford.

GOTTSBERGER, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Pl. syst. evolut.* Suppl. 1: 211–226.

GRAYUM, M.H. 1986. Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. In: Pollen and spores: form and function. The Linnean Society of London.

JACKSON, W.P.U. 1986. The Cape white arum lily, *Zantedeschia aethiopica. Veld Flora* 72: 44–45.

LETTY, C. 1973. The genus *Zantedeschia. Bothalia* 11: 5–26.

MARLOTH, R.A. 1915. Araceae. The Flora of South Africa, Vol. IV, pp. 51–54.

PERRY, P.L. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *S. Afr. J. Bot.* 55: 447–451.

STERN, W.L., CURRY, K.J. & WHITTEN, W.M. 1986. Staining fragrance glands in orchid flowers. *Bull. Torrey Bot. Club* 113: 288–297.

VOGEL, S. 1990. The role of scent glands in pollination: on the structure and function of osmophores. Smithsonian Institution Libraries & The National Science Foundation, Washington, D.C.

WEBERLING, F. 1989. Morphology of flowers and inflorescences. Cambridge University Press, Cambridge.

WHITTAKER, R.H. & FEENY, P.P. 1971. Allelochemics: chemical interactions between species. *Science* 171: 757–770.

APPENDIX 5

Taxonomic notes on the genus *Zantedeschia* Spreng. (Araceae) in southern Africa [*]

Results and Discussion

---

[*] under review - *South African Journal of Botany*

Taxonomic notes on the genus *Zantedeschia* Spreng. (Araceae) in southern Africa

Y. Singh*, A.E. van Wyk + & H. Baijnath ++

* Natal Herbarium, National Botanical Institute, Botanic Gardens Road, Durban, 4001 Republic of South Africa

\+ H.G.W.J. Schweickerdt Herbarium, Department of Botany, University of Pretoria, Pretoria, 0001 Republic of South Africa

++ Ward Herbarium, Department of Botany, University of Durban-Westville, Durban, 4000 Republic of South Africa

Received: ; revised:

A taxonomic re-assessment of *Zantedeschia* revealed that *Z. albomaculata* subsp. *valida* is markedly distinct from *Z. albomaculata* subsp. *albomaculata* and *Z. albomaculata* subsp. *macrocarpa*. Differences in morphology proved to be sufficient to exclude it from the Z. *albomaculata* complex, and to recognise it at specific level as *Z. valida*. The history of the classification of *Z. albomaculata* is briefly reviewed. This study further supports the delimitation of species into two sections: *Zantedeschia* and *Aestivus*. A key to sections, species and subspecies,based on macromorphology and geographical distribution, is presented.

Keywords: *Aestivus*, Araceae, distribution, macromorphology, taxonomy, *Zantedeschia*

Introduction

Zantedeschia Spreng. (Arum or Calla lilies), a relatively small genus of eight species, forms the tribe Zantedeschieae in the subfamily Philodendroideae (sensu Bogner & Nicolson 1991). The genus is confined to southern Africa, including Angola, Zambia, Malawi, Zimbabwe and Tanzania.

Showy and decorative hybrids and varieties of *Zantedeschia* have drawn much interest among plant breeders abroad, where tubers, cut flowers and container plants form the basis of a lucrative export industry in the U.S.A., the Netherlands and New Zealand.

---

* To whom correspondence should be addressed.

The previous revision of *Zantedeschia* was by Letty (1973) who recognised six species. She divided the species into two informal sections with *Z. aethiopica* as the sole member of the typical section and the remaining species were assigned to a second section, for which she did not suggest a name. Furthermore, Letty (1973) recognised three subspecies of *Z. albomaculata*, viz. *Z. albomaculata* (Hook.) Baill. subsp. *albomaculata*, *Z. albomaculata* subsp. *macrocarpa* (Engl.) Letty and *Z. albomaculata* subsp. *valida* Letty. In the present treatment, the cordate bases of the leaf lamina and the funnel-shaped spathes of subspecies *valida* are considered to be evidently anomalous in the *Z. albomaculata* group, and it is on this basis that this subspecies is raised to species level. In addition, the two sections implied by Letty, are formally described as *Zantedeschia* and *Aestivus*.

Materials and Methods

The present study is based on extensive observations of plants in the field and in cultivation. Plants obtained from several wild populations throughout South Africa were transplanted and kept in cultivation under greenhouse conditions to ensure adequate material for a thorough morphological investigation. Voucher herbarium specimens are deposited in the Natal Herbarium (Durban; NH). In addition, collections from the National Herbarium (Pretoria; PRE), Malolotja Nature Reserve Herbarium (Swaziland; SWZ), National University of Lesotho Herbarium (Lesotho; ROML) and National Herbarium & Botanic Gardens (Zimbabwe; SRGH), were studied.

Results and Discussion

Z. albomaculata complex

In 1859, *Z. albomaculata* was described by W.J. Hooker as *Richardia albo-maculata* Hook. The name was based on a plant with spotted leaves and a deep purple throat at the base of the spathe, introduced from Natal, by Messrs Backhouse, of York (England) (Watson 1892). Subsequently *Calla oculata* Lindl. (1859), *Richardia hastata* Hook. (1860), *R. angustiloba* Schott (1865), *R. melanoleuca* Hook. (1869) and *Zantedeschia macrocarpa* Engl. (1883) were described as separate species; all based on rather similar-looking material. In Engler's revision of the genus in 1915, *Z. albomaculata*, *Z. angustiloba*, *Z. macrocarpa*, *Z. melanoleuca* and *Z. oculata* (Lindl.) Engl. were among the eight species recognised. Engler treated *Z. hastata* Hook. as a synonym of *Z. oculata*. Traub (1948) upheld these species, but regarded *Z. oculata* as a synonym of *Z. hastata*. Letty (1973) proposed three subspecies of *Z. albomaculata* based on leaf lamina shape. She considered *Z. albomaculata*, *Z. angustiloba*, *Z. hastata*, *Z. melanoleuca* and *Z. oculata* as synonyms of *Z. albomaculata* subsp. *albomaculata* and reduced *Z. macrocarpa* to *Z. albomaculata* subsp. *macrocarpa*. Letty, further described a new subspecies, *Z. albomaculata* subsp. *valida* from KwaZulu-Natal.

Diagnostic characters

Characters useful in defining species of *Zantedeschia* include lamina shape, degree of maculation, spathe shape and colour, presence or absence of staminodes among ovaries, fruit coloration on ripening and geographic distribution (Singh *et al.* 1996).

Select morphological characters and distribution of *Z. valida* and the subspecies of *Z. albomaculata* are compared in Table 1 (Figures 1–3). Leaf laminae of *Z. albomaculata* are oblong-ovate to triangular-hastate whereas in *Z. valida*, laminae are ovate to orbicular with cordate bases. In *Z. albomaculata* subsp. *albomaculata*, leaf laminae may be immaculate or densely maculate, those of *Z. albomaculata* subsp. *macrocarpa* are sparsely maculate or occasionally immaculate while in *Z. valida*, laminae are rarely maculate. Since all three taxa may produce maculate laminae, the presence of maculation is an unreliable character for separating these taxa.

Table 1 Comparison of select morphological characters in *Z. valida* and the subspecies of *Z. albomaculata*

Characters	***Z. albomaculata***		***Z. valida***
	subsp. *albomaculata*	**subsp. *macrocarpa***	**(= *Z. albomaculata* subsp. *valida*)**
	Figure 1	Figure 2	Figure 3
Leaf lamina shape	oblong to ovate-hastate	triangular-hastate	ovate to orbicular-cordate
Degree of lamina maculation	immaculate or densely maculate	sparsely maculate or occasionally immaculate	immaculate or rarely maculate
Spathe shape	cylindrical, limb recurving, tapering to apex	cylindrical, limb upright, truncate at apex	funnel-shaped, limb spreading, truncate at apex
Spathe colour	white, ivory, cream, pale yellow or coral pink	cream	white
Distribution	Widespread in eastern parts of South Africa, also in Lesotho, Swaziland, Zambia, Zimbabwe, Angola, Malawi and Tanzania	South Africa and Swaziland	South Africa, confined to a restricted area in KwaZulu-Natal

Spathes of *Z. albomaculata* are cylindrical (Figure 4a) whereas those of *Z. valida* are funnel-shaped (Figure 4b). Spathe colour of the typical subspecies varies from white, ivory, cream, pale yellow to coral pink. Spathes of *Z. albomaculata* subsp. *macrocarpa* are cream and those of *Z. valida* are white.

Z. albomaculata subsp. *albomaculata* is widespread in the eastern parts of South Africa and also occurs in Lesotho, Swaziland, Zambia, Zimbabwe, Angola, Malawi and Tanzania. Subspecies *macrocarpa* occurs in South Africa and Swaziland. *Z. valida* is confined to a restricted area in KwaZulu-Natal in South Africa (Figure 5). Morphological distinction of *Z. valida* is supported by its geographical isolation, being restricted to the area bordered by the Biggarsberg (2829BB), Giant's Castle (2929AD) and Collin's Pass (2829BA) in KwaZulu-Natal.

Z. albomaculata subsp. *macrocarpa* differs from *Z. albomaculata* subsp. *albomaculata* in having triangular-hastate and sparsely maculate leaves, cream-coloured spathes that are truncate at the apex and relatively few large berries. This study confirms the observations by Letty (1973) that in a few instances, lamina or spathe shape of *Z. albomaculata* subsp. *albomaculata* approaches that of *Z. albomaculata* subsp. *macrocarpa* and vice versa, with some specimens having a combination of characters from both subspecies. Recognition of these two taxa at subspecific level is therefore retained. Suspected hybridisation between the two subspecies may explain specimens displaying characters of both subspecies.

Zantedeschia valida (Letty) Y. Singh, *stat. nov.*

Zantedeschia albomaculata (Hook.) Baill. subsp. *valida* Letty, Bothalia 11: 25 (1973). Type: Natal (2829 BD), farm Blanerne, 29 km N of Ladysmith, *Letty 492* (holotype PRE!).

Section **Zantedeschia**

Diagnostic characters as in key.

This section conforms to the typical section informally suggested by Letty (1973) and includes *Z. aethiopica* and *Z. odorata*.

Section **Aestivus** *Y. Singh* sect. nov.

Tuber discoideum; spatha intus basin versus cum vel sine macula purpurea; ovariae plerumque sine staminodis (si praesentia nunc solum in zona transitionis inter antheras et ovaria); tota spatha viridescit dum baccae maturant; non odorata; plantae crescunt in regione pluviae aestivae Austro-africana.

Typus: *Z. jucunda* Letty

Key to sections, species and subspecies of *Zantedeschia*

1a Tuber rhizomatous; spathe interior without a purple-coloured blotch at base; ovary surrounded by 3 spathulate staminodes; lower portion of spathe turns green while upper portion withers away during berry maturation; inflorescence scented; summer and/or winter rainfall regions of southern Africa [**i.** Section **Zantedeschia**] 2

2a Spathe funnel-shaped; spadix 50–75mm long, 5–7mm wide; peduncle erect during fruiting; berries turn orange and soft when ripe; widespread in South Africa .... ***Z. aethiopica***

2b Spathe cylindrical; spadix 25–35mm long, 5–10mm wide; peduncle bending to the ground during fruiting; berries remain green and firm when ripe; restricted to the Nieuwoudtville District in the Western Cape .... ***Z. odorata***

1b Tuber discoid; spathe interior with or without a purple-coloured blotch at base; ovaries usually lacking staminodes (if present, restricted to ovaries in zone between male and female); entire spathe turns green during berry maturation; inflorescence non-scented; summer rainfall region of southern Africa [**ii.** Section **Aestivus**] 3

3a Spathe funnel-shaped, interior with a purple-coloured blotch at base 4

3b Spathe cylindrical, interior with or without a purple-coloured blotch at base 7

4a Spathe white; leaf lamina ovate to orbicular cordate .... ***Z. valida***

4b Spathe yellow; leaf lamina variously shaped 5

5a Leaf lamina usually immaculate, oblong-hastate, glaucous green ...... ***Z. pentlandii***

5b Leaf lamina always maculate, triangular-hastate to ovate-orbicular, deep green 6

6a Leaf lamina triangular-hastate .... ***Z. jucunda***

6b Leaf lamina ovate-orbicular .... ***Z. elliotiana***

7a Leaf lamina narrowly lanceolate, cuneate at base .... ***Z. rehmannii***

7b Leaf lamina oblong, ovate or triangular-hastate 8

8a Leaf lamina oblong to ovate-hastate; spathe tapering to the apex .... ***Z. albomaculata* subsp. *albomaculata***

8b Leaf lamina triangular-hastate; spathe truncate at the apex .... ***Z. albomaculata* subsp. *macrocarpa***

Acknowledgements

This study was funded in part by the University of Pretoria and the National Botanical Institute. Mr and Mrs Mitchell-Innes are thanked for their hospitality during field work. We would like to thank the Directors and staff of SWZ, ROML and SRGH for the loan of herbarium specimens and Dr H. Glen (PRE) for the Latin translation.

References

BOGNER, J. & NICOLSON, D.H. 1991. A revised classification of Araceae with dichotomous keys. *Willdenowia* 21: 35–50.

ENGLER, H.G.A. 1883. *Botanische Jahrbücher für Systematik.* 4: 63.

ENGLER, H.G.A. 1915. Tribus V. *Zantedeschieae. Das Pflanzenreich* IV: 61– 69.

HOOKER, W.J. 1859. *Curtis's Bot. Mag.* t.5140.

HOOKER, W.J. 1860. *Curtis's Bot. Mag.* t.5176.

HOOKER, J.D. 1869. *Curtis's Bot. Mag.* t. 5765.

LINDLEY, J. 1859. *Gard. Chronicle.* 40: 788.

LETTY, C. 1973. The genus *Zantedeschia. Bothalia* 11: 5–26.

SCHOTT, H.W. 1865. *Richardia angustiloba* Schott. *Journal of Botany* 3: 35.

SINGH, Y., VAN WYK, A.E. & BAIJNATH, H. 1995. Know your arums: a comparative guide to the members of the genus *Zantedeschia. Veld & Flora* 81: 54–55.

TRAUB, H.P. 1948. The genus *Zantedeschia. Plant Life* 4: 9–32.

WATSON, W. 1892. Richardias. *Gard. Chron.* 12: 23–124.

Figure 1 *Z. albomaculata* subsp. *albomaculata*

Figure 2 *Z. albomaculata* subsp. *macrocarpa*

Figure 3 *Z. valida*

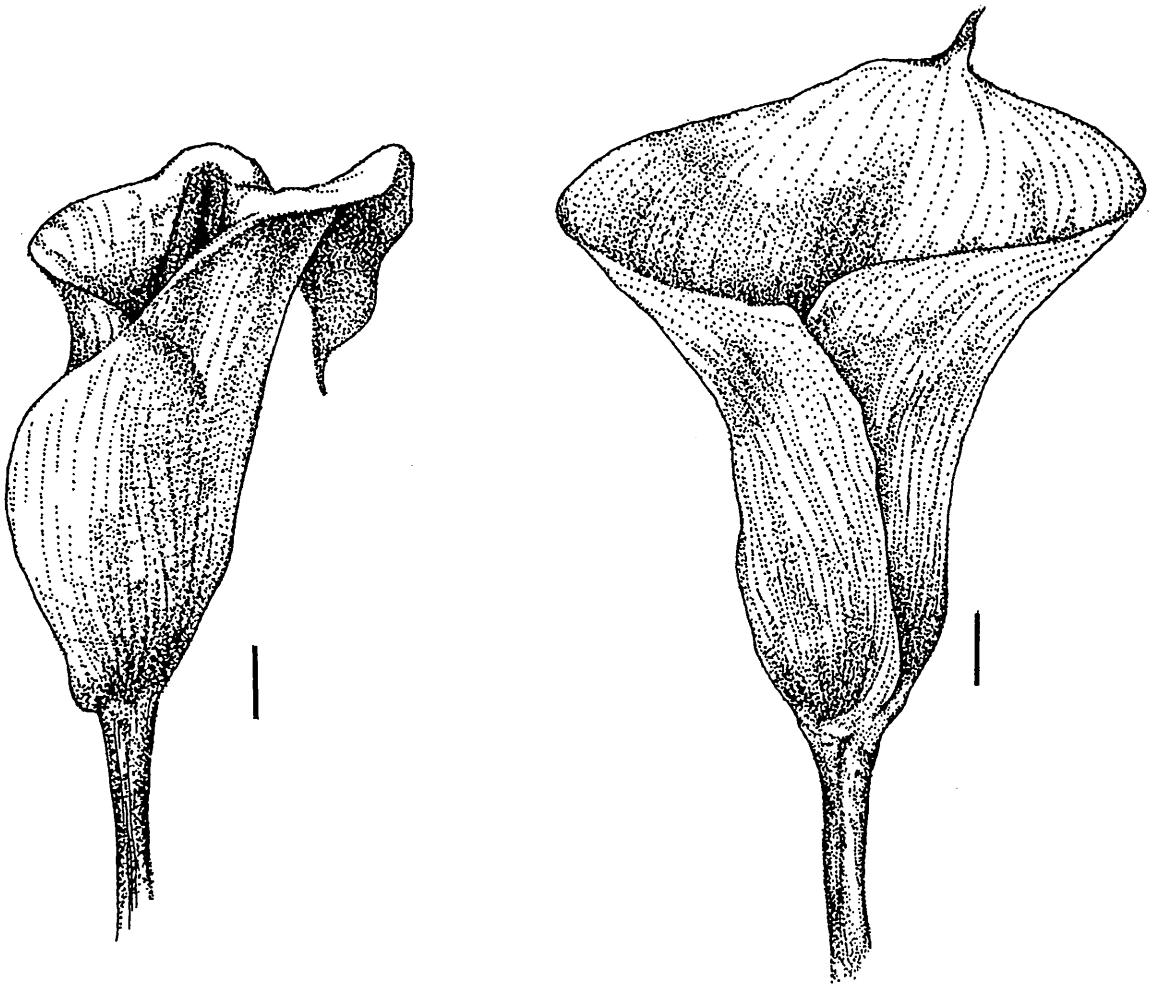


Figure 4 Spathe shapes. 4a. *Z. albomaculata* subsp. *albomaculata*, cylindrical. Scale bar = 8 mm. 4b. *Z. valida*, funnel-shaped. Scale bar = 8 mm.

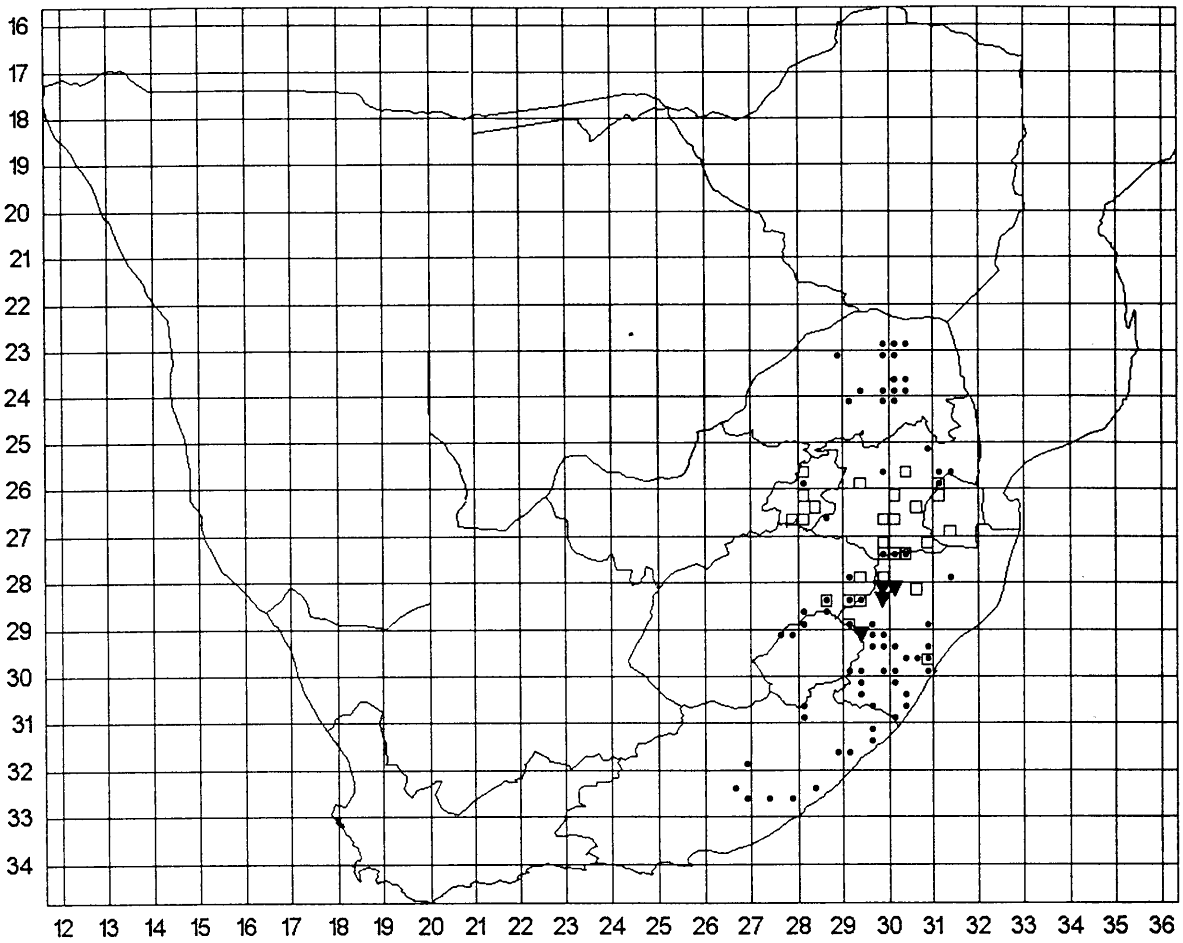


Figure 5 Distribution of *Z. albomaculata* and *Z. valida* in southern Africa.

● *Z. albomaculata* subsp. *albomaculata* □ *Z. albomaculata* subsp. *macrocarpa*
▼ *Z. valida*