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CONTRIBUTIONS TO THE SYSTEMATICS OF SELECTED GENERA OF THE ALOOIDEAE (ASPHODELACEAE)

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Contributions to the systematics of selected genera of the Alooideae (Asphodelaceae)

by

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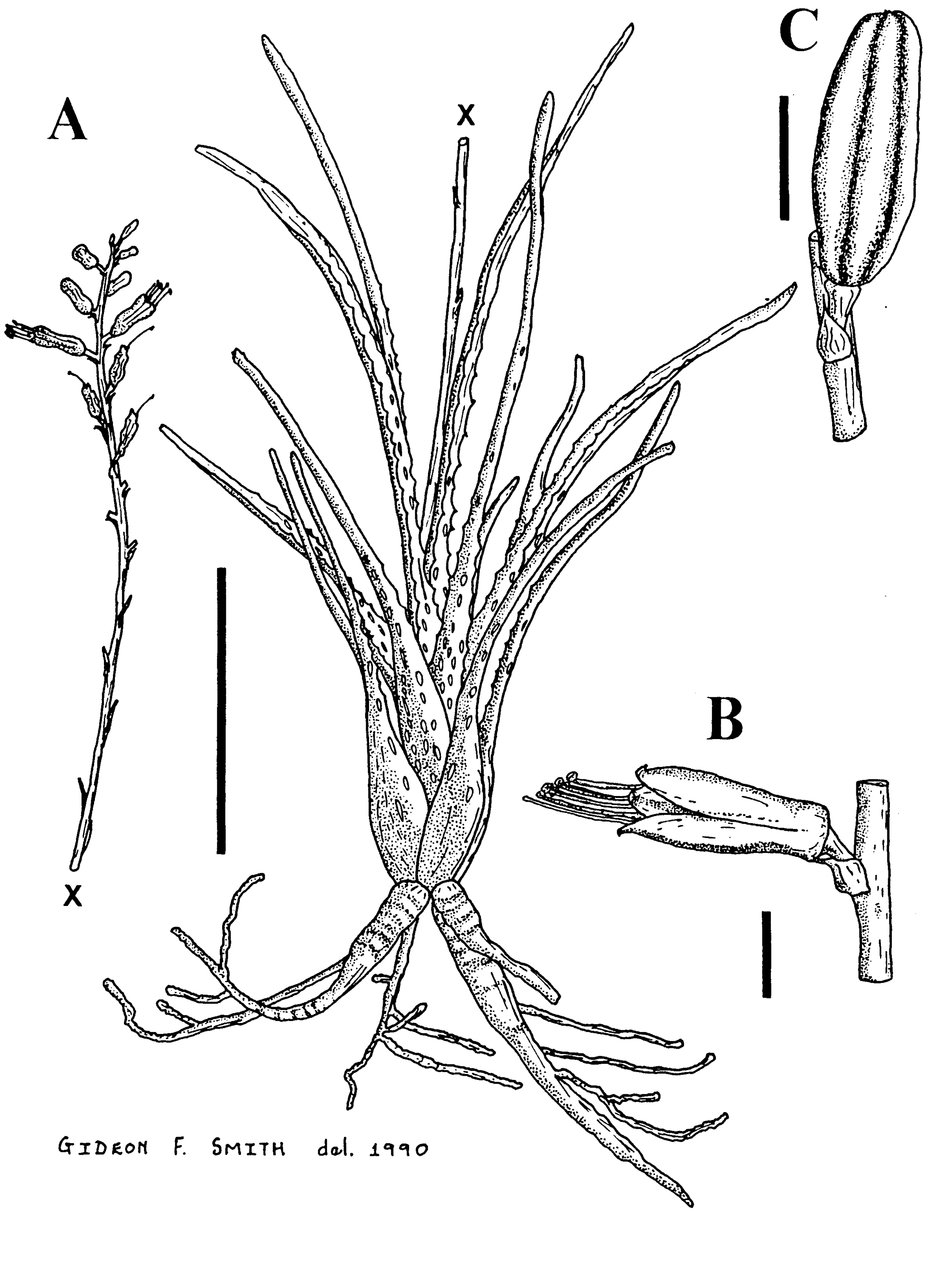
"And the Lord God took the man, and put him into the garden of Eden to dress it and to keep it."

Genesis 2: 15 of the *Holy Bible.*

"Most people who enter taxonomy do so not for fame and fortune. Rather, they are entranced by the diversity of the natural world around them and wish to make it an integral part of their lives. Most have a natural proclivity to group or classify objects of nature into units and to further group them into hierarchies, that is, to speculate upon relationships. Certainly the taxonomists without these inclinations is probably in the wrong field. The tedium of measuring and recording voluminous data and keeping track of what at times seems to be endless specimen citations are not the attractions of the discipline. Rather, it is the satisfaction of examining plants and, after study, seeing how they group themselves into natural units. In the field, while collecting a plant which appears to be taxonomically isolated, I have often asked myself what that plant has to tell me that neither I nor previous generations of taxonomists have understood about its relationships. Sometimes an answer is vouchsafed. It is at those moments, when what I had not previously understood suddenly becomes clear, that the hours of laboratory work are justified."

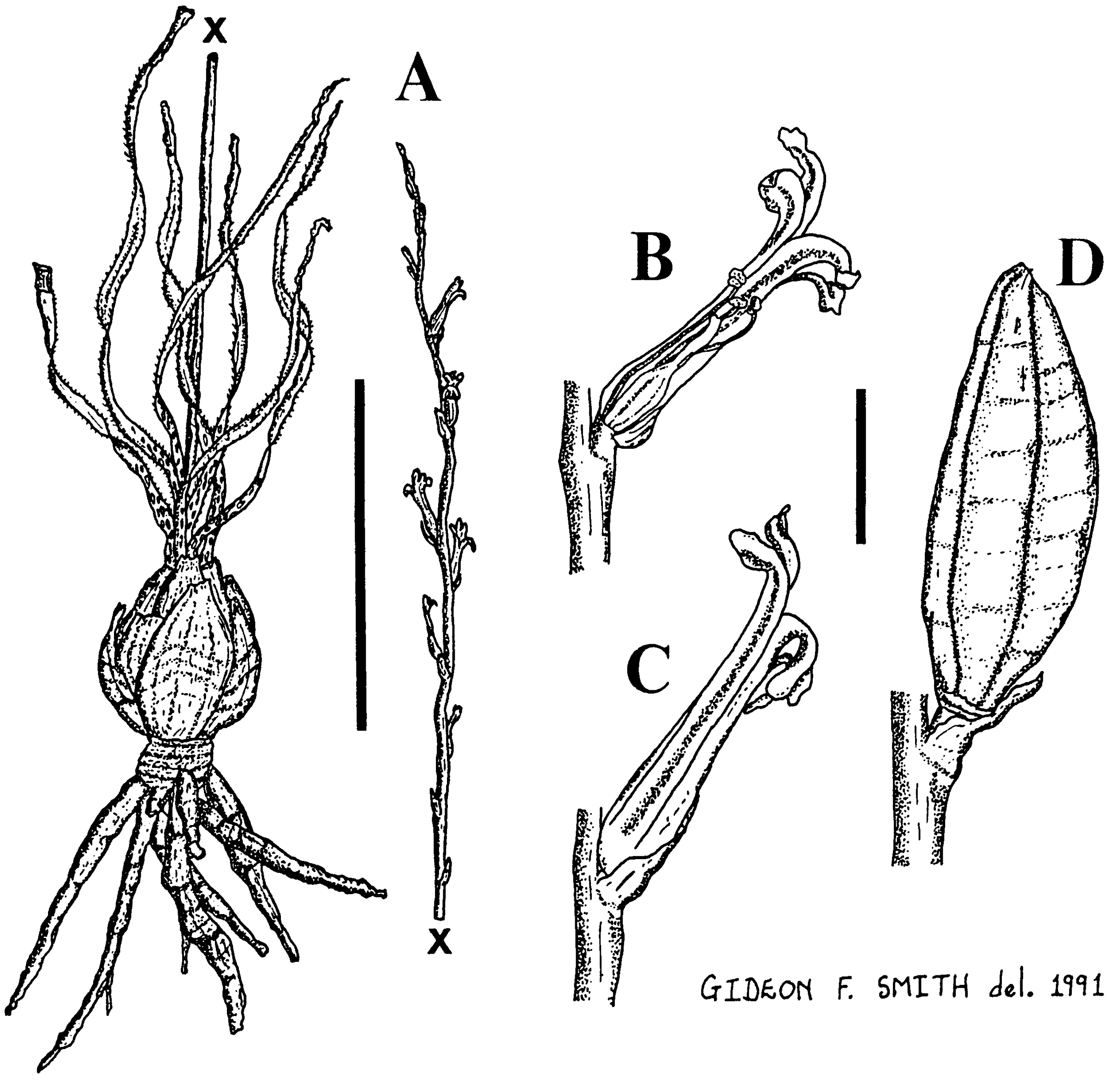
BUCK, W.R. 1986. Traditional methods in taxonomy: a personal approbation. *Taxon* 35: 306-308.

DEDICATED TO MY WIFE EL-MARIé AND DAUGHTERS JANINE AND TANYA WHO HAVE ALWAYS FOUND TIME TO LISTEN. THEY HAVE REMAINED A CONSTANT REMINDER THAT THERE IS MUCH MORE TO LIFE THAN UNIVERSITY.



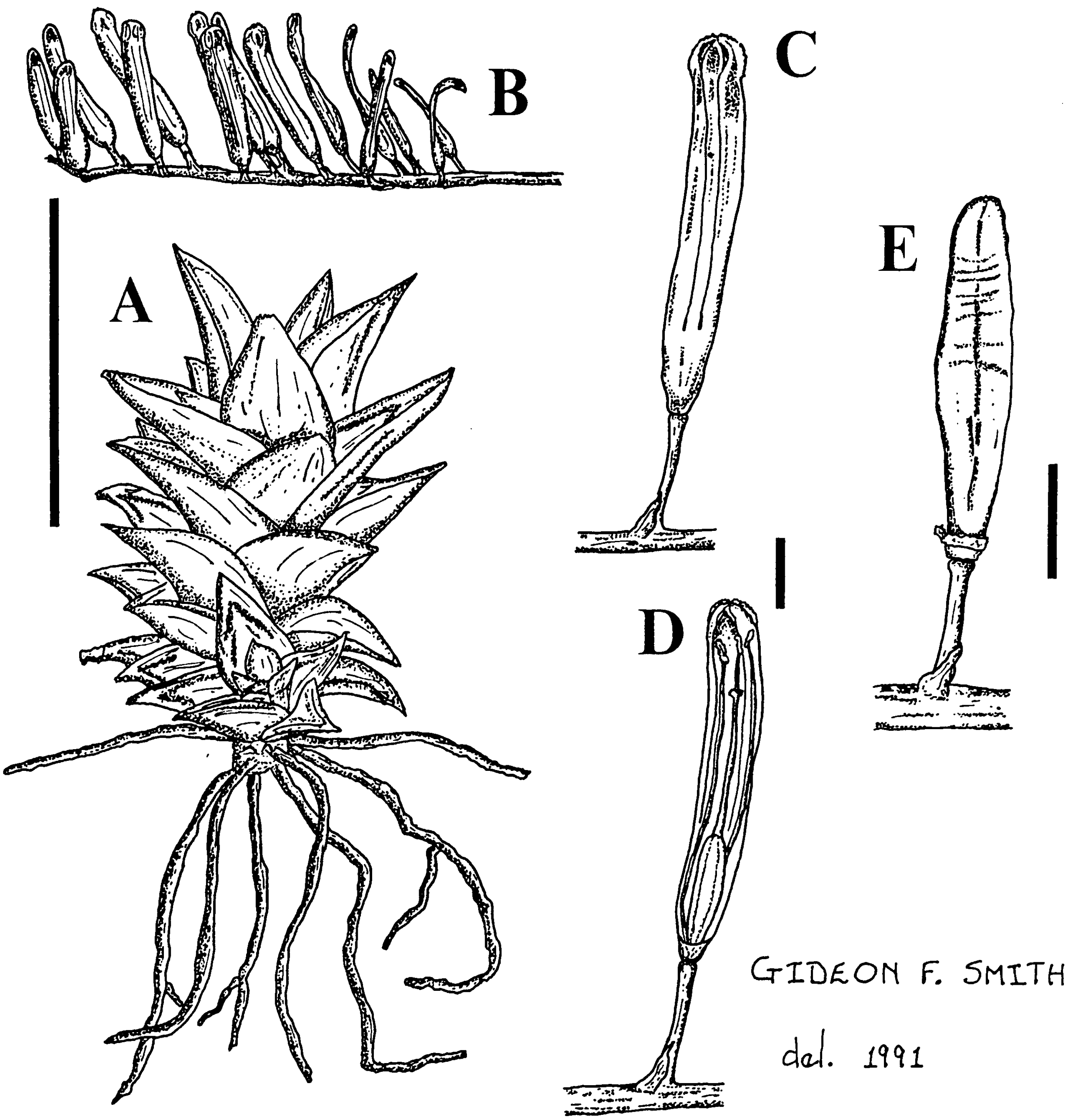
Aloe bowiea Schult. & J.H. Schult.

A. Habit; B. Single flower in lateral view, showing the position of the peduncle and bract; C. Fruit, trilocular capsule. All drawings were made from live material of *Smith 4* (PUC). Scale line = 50 mm in Figure A and 5 mm in Figures B & C.



Chortolirion angolense (Bak.) Berger

A. Habit; B. Longitudinal section of flower (three stamens removed); C. Lateral view of flower, showing the position of the peduncle and bract; D. Fruit, acuminate capsule. All drawings were made from live material of *Smith 14* (PUC). Scale line = 50 mm in Figure A and 5 mm in Figures B – D.



Poellnitzia rubriflora (L.Bol.) Uitewaal

A. Habit; B. Terminal portion of raceme; C. Lateral view of flower, showing the position of the peduncle and bract; D. Longitudinal section of flower (three stamens removed); E. Fruit, trilocular capsule. All drawings were made from live material of *Smith 174* (PUC). Scale line = 50 mm in Figures A & B and 5 mm in Figures C – E.

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"... all taxonomists are fully aware of our present acute lack of scientific knowledge of plants and their geographical distribution, resulting inevitably in very unsatisfactory systems of classification."

W. Robyns: 1964

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CHAPTER 1

INTRODUCTION

1.1 BACKGROUND

In a reclassification of the inclusive family Liliaceae, Dahlgren *et al.* (1985) reinstated the family Asphodelaceae, as well as several other segregate families. Within the Asphodelaceae two subfamilies, namely Asphodeloideae and Alooideae are recognized. The Alooideae constitutes a natural assemblage of more or less succulent-leaved taxa which were previously placed in the Aloineae, one of 28 tribes recognized by Hutchinson (1959) in the family Liliaceae *sensu lato*. Although 27 genus names are available for taxa included in the subfamily Alooideae, only seven genera are widely recognised (Table 1.1). It is fundamentally an Old World group with most genera occurring in sub-Saharan Africa. The genus *Aloe* L. is also found on the Arabian Peninsula, Madagscar and Socotra, while *Lomatophyllum* Willd. has been reported from the Aldabra Islands, Madagascar and Mauritius. The greatest concentration of genera and of species is in southern Africa, that is, roughly, the region south of the Kunene, Okavango and Zambezi Rivers.

Table 1.1 Synonymy of genera of the Alooideae *sensu* Dahlgren *et al.* (1985)

No.	Genera recognized in present study	Recent taxonomic treatment	Synonyms
1.	*Aloe* Linnaeus: 319 (1753).	Reynolds (1966, 1982)	*Catevala* Medikus: 67 (1786) *pro parte*; *Kumara* Medikus: 69 (1786); *Rhipidodendrum* Willdenow: 164 (1811); *Pachidendron* Haworth: 35 (1821); *Bowiea* Haworth: 299 (1824) *non* J.D. Hooker: t. 5619 (1867); *Agriodendron* Endlicher: 144 (1836); *Papilista* Rafinesque: 137 (1840); *Succosaria* Rafinesque: 137 (1840); *Busipho* Salisbury: 76 (1866); *Ptyas* Salisbury: 76 (1866); *Chamaealoe* Berger: 43 (1905); *Leptaloe* Stapf: t. 9300 (1933); *Aloinella* Lemée 27 (1939) *non* Cardot: 76 (1909); *Guillauminia* Bertrand: 41 (1956).
2.	*Gasteria* Duval: 6 (1809).	Van Jaarsveld (1989)	*Atevala* Rafinesque: 136 (1840).
3.	*Haworthia* Duval: 7 (1809) nom. cons.	Bayer (1982)	*Catevala* Medikus: 67 (1786) *pro parte; Apicra* Willdenow: 167 (1811) *non* Haworth: 61 (1819); *Kumaria* Rafinesque: 137 (1840); *Tulista* Rafinesque: 137 (1840).
4.	*Lomatophyllum* Willdenow: 166 (1811).	Jacobsen (1986)	*Phylloma* Ker: t. 1585 (1813).
5.	*Chortolirion* Berger: 72 (1908).	Smith (1985)	—
6.	*Poellnitzia* Uitewaal: 61 (1940).	Smith (1985)	—
7.	*Astroloba* Uitewaal: 53 (1947).	Roberts Reinecke (1965)	*Apicra* Haworth: 61 (1819) *non* Willdenow: 167 (1811).

The genera of Alooideae differ from other Asphodelaceae in their conspicuous succulent leaf consistency, crescentiform or cymbiform leaf outline in cross-section and the markedly bimodal karyotype consisting of 2n = 14 chromosomes. In this regard *Bulbine* Wolf and *Kniphofia* Moench appear to be prolematical, particularly since some of the species of *Bulbine* have karyotypes and morphologies similar to that of certain taxa of Alooideae (cf. Spies & Hardy (1983) on *B. latifolia* (L.f.) Schult. & J.H. Schult. and Rowley (1954a) on *Bulbine* in general]. However, *Bulbine* can be clearly distinguished from genera of the Alooideae on the basis of its open, yellow (only very rarely white or orange) flowers, free perianth segments, bearded filaments, lack of nectar production and the annual nature of some of its species (for example *B. alata* Baijnath). Furthermore, *Bulbine* has an African-Australian distribution whereas the Alooideae is absent from Australia. Mainly for these reasons *Bulbine* was not considered to be a constituent of the Alooideae. In contrast to representatives of *Bulbine* and the Alooideae, leaf succulence is absent in *Kniphofia*, the leaf outline (cross-section) is V-shaped and it has a chromosome base number of 6. However, synapomorphous characters suggesting monophyly of *Kniphofia* and the Alooideae are the tubular flowers and fusion of the perianth segments. I regard these characters as sufficient evidence to justify the choice of *Kniphofia* as outgroup (sister group) for the Alooideae, in cladistic terminology. Pending formal publication of the latter point of view (Smith & Van Wyk in press), the subfamilial concept of the Alooideae *sensu* Dahlgren *et al.* (1985) is upheld (discussed in detail in Chapter 2).

Numerous difficulties are encountered when dealing with taxonomic literature and herbarium specimens pertaining to succulent plants in general, the Alooideae being no exception. Especially in the 18th and 19th centuries species were described from single plants grown under artificial conditions in private collections thousands of kilometers from their natural habitats. In cultivation succulent plants often become etiolated and chlorotic and may bear only a slight resemblance to plants in the field. Furthermore, authors of new species had no idea of the variability of these taxa in their natural habitats (Smith 1948; Schelpe 1958).

Succulent plants easily survived long sea journeys to botanical gardens in Europe and the relative ease with which specimens can be rooted made them popular horticultural objects. Many of the early botanical explorers sent to the Cape of Good Hope to collect plants for, amongst others, Kew Gardens, had a special interest in succulent plants, resulting in a steady stream of such specimens reaching Europe (Gunn & Codd 1981; Smith & Van Wyk 1989a).

However, succulent plants make poor herbarium specimens (Chudovska 1979a, b; Fuller & Barbe 1981; Leuenberger 1982; Baker *et al.* 1985; Logan 1986) and (type) specimens were usually not prepared. Bradley (1716-1727), in the first ever publication devoted entirely to succulents, used this difficulty with which herbarium specimens are made of succulents as a criterion for distinguishing them from other plants (see also Higgins 1940; Rowley 1952, 1954b, 1977, 1983; Thomas 1952; Butterfield 1968; Stafleu & Cowan 1976). Succulent plants also tend to grow in a press, Marloth (1925) mentioning *Crassula barbata* Thunb. which sprouted and flowered after having been pressed for nine months. Unfortunately new species, such as *Haworthia venteri* Von Poelln. and *H. paradoxa* Von Poelln. were described from specimens which elongated during the sea voyage from the Cape to Europe (Von Poellnitz 1939; Smith 1948).

Scientific communication amongst succulent plant enthusiasts working on the same taxa was often unsatisfactory, resulting in multiple names being given to the same taxon or one name being published for different taxa, *Apicra* Haw. *non* Willd. being a good example. Species descriptions usually consisted of brief Latin diagnoses only, which, if unaccompanied by accurate illustrations, could be applied to a suite of species. Furthermore, much of the early work on aloeoid taxa was done by amateur collectors with little or no botanical background and no knowledge of the growing conditions of the plants in habitat. However, it is noteworthy that botanical training by no means guarantees success as a taxonomist specialising in the subfamily Alooideae, the often peculiar works of Prof. Dr. Flavio Resende (e.g. Resende 1943) being good examples. In contrast, the works on *Aloe* of amateurs such as Dr G. W. Reynolds (Anonymous 1967; D'Ewes 1967) and Mr L.C. Leach (Smith 1990 and references therein) are of excellent quality. Clearly, the difference between Reynolds and Leach and other, earlier amateurs interested in aloeoid taxonomy, is that they had field experience of the plants and based their studies on populations and not individuals. As Bayer (1972) justifiably surmises "... 'many the ship of a prospective taxonomist has been ship-wrecked on the rocks of the Liliaceae'. ".....

No matter how carefully a private collection of succulent plants are kept, living material can never replace herbarium specimens as a primary source of taxonomic information. Although Rowley (1951) claims that at least some of Adrian Hardy Haworth's (1768--1833) original material have survived to the present day, these plants can hardly be authenticated in terms of either original ownership or their status as having been the material originally described. All the *Haworthia* material, including some original Haworth clonotypes, which John Thomas Bates (1884 - 1966), an avid English succulent plant collector, possessed was lost during the First World War (Roan 1948; Rowley 1985). Although this collection which Bates subsequently reconstructed is currently administered scientifically it no doubt differs considerably in content from Bates' original collection (Roberts 1983). It is also likely that during the previous century only small quantities of what eventually proved to be new species was available and authors of plant names were reluctant to press the only specimen of a new element available to them. With no idea of variability along a habitat range authors of names of succulent plants must also have thought it easy to eventually link published names to natural populations. This is off course often impossible. Furthermore, not even the deposition of a herbarium specimen is always sufficient to assure the correct application of a published name, the confused interpretation of the name *H. pearsonii* C.H. Wright which was published as recently as 1907 being a good example (Scott 1980; Bayer 1982).

As Bayer (1982) and Heath (1989, 1990) has clearly shown with regard to the application of the name "*Haworthia pumila*" to the largest known species of *Haworthia*, confusion usually reigns where Linnaeus and other early taxonomists working on succulent plants did not give a clear lead (Scott 1978; Tjaden 1985; Wijnands 1985). In most of the genera included in the Alooideae nomenclatural and taxonomic confusion still exist, Bayer (1982), for example, recognizing 68 species in *Haworthia* while Scott (1985) upholds 88 species in the same genus. A comparison of two major monographs on *Aloe* which appeared shortly apart, namely that of Groenewald (1941) and Reynolds (1950) also illustrates how different researchers could draw vastly different conclusions with regard to species concepts and the correct application of previously published names in the same Alooideae genus.

The value of early taxonomic work on the Alooideae is often difficult to assess since it might be valuable in one group but valueless in another. Some of the publications of these early workers were also not as valuable as other publications by the same author. Remarking on Salm-Dyck's *Catalogue raisonné des Espèces de' Aloes* which appeared in 1817, Reynolds (1950) concluded that "The taxonomist and Aloe student would have been spared many puzzles had this work never been published." In contrast Schelpe (1958) claims that Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi*" which appeared periodically between 1836 and 1863 "... is undoubtedly the most valuable single publication to the modern student of *Gasteria*."

1.2 AIM OF THE STUDY

With the exception of *Gasteria* (Van Jaarsveld 1989) and *Astroloba* (Roberts Reinecke 1965), critical monographic revisions of the genera of Alooideae based on extensive field work have not been attempted recently. Baker (1880, 1896) and Berger (1908), who wrote monographs on large sections of the Liliaceae, could not possibly approach the problem of ambiguous generic and species concepts critically and many of their taxonomic judgements proved to be unsound and are rejected today. Although having been studied sporadically by botanists for more than two centuries most genera of the Alooideae remain little-known (see Chapter 2 for a detailed discussion). Furthermore, since no major genetic or systematic studies have been carried out on many of the smaller aloeoid genera, our knowledge of intrageneric variation and intergeneric relationships still is incomplete.

Aspects of the taxonomy and systematics of the genera *Chamaealoe* Berger, *Chortolirion* Berger and *Poellnitzia* Uitewaal form the basis of the present study. Of the genera which are major sources of confusion in the Alooideae, these three shine as firsts among equals. Furthermore, no comprehensive treatment exists which will allow easy access to their literature by anyone but a specialist on the group.

Botanists attempting to order the (often not too) complex variation encountered within the latter genera created confusion with ambiguous designations and multiple names for the same taxon. Species were transferred from one genus to another at an alarming rate without supporting evidence being presented. Thus, taxonomic problems were merely transferred to new genera and only added to the burgeoning synonymy and reigning confusion. Revisionary studies were often based on conjecture and speculation and did not lead to a better understanding of the Alooideae as a whole. Furthermore, important papers were overlooked during previous taxonomic treatments, yielding them incomplete and of limited value. Clearly, the taxonomic status of *Chamaealoe*, *Chortolirion* and *Poellnitzia* is, to say the least, confusing. Therefore one of the main objectives of the study was to provide synoptic accounts of these genera for the *Flora of southern Africa* research programme (*FSA*). The latter research programme is maintained by the National Botanical Institue, Pretoria, and was initiated more than twenty five years ago. One of its primary aims is to arrive at an inventory of all the plants, indigenous and naturalized, occurring south of, but excluding, Angola, Zambia, Zimbabwe and Mocambique (Anonymous 1991). To complement the study of macromorphological variation it was decided to explore some alternative sources of taxonomic evidence as a possible aid towards solving difficulties at the species and generic levels. In this regard this study extends the work on the taxonomy of the genus *Chamaealoe*, which was considered by the author in a B.Sc. project (1983), and the taxonomy of the genera *Chortolirion* and *Poellnitzia*, which the author presented as a B.Sc. (Hons.) scription (1985).

Soon after the initiation of the project it was realized that *Chamaeoloe* should be included in the synonymy of *Aloe*. This entity is therefore referred to as *A. bowiea* Schult. & J.H. Schult. throughout the study. It is a low-growing, rosulate, leaf succulent. Its leaves are linear-subulate and have small white spots scattered on the abaxial surfaces. The margins of the pale green leaves are armed with soft, white prickles. This rare and endangered plant is endemic to the eastern Cape Province. It is known only from two populations, one in the vicinity of Coega and the other near Kariega.

Chortolirion and *Poellnitzia* are retained as separate genera. *Chortolirion*, a perennial, deciduous herb with a subterranean bulb is widely distributed mainly in the summer rainfall region of southern Africa. With short, annual, succulent shoots arising from a perennial underground bulb, it presents a combination of a geophytic and succulent habit. *Chortolirion* is summer-growing and is ecologically adapted to grassland which is subject to seasonal burning and to extreme temperature fluctuations.

Poellnitzia is a low-growing caulescent, succulent herb with densely leaved stems up to 250 mm long. The ovate leaves are pungent-acuminate and up to 40 mm long. *Poellnitzia* has a restricted distribution in the south-western Cape Province. It is a floristic component of the Robertson Karoo which is one of the drier winter rainfall areas bordering the Fynbos Biome.

1.3 LAY-OUT OF DISSERTATION

This dissertation (*sensu* Schmid 1986) consists of a collection of contributions on several diverse aspects of *Aloe bowiea*, *Chortolirion* and *Poellnitzia* in southern Africa. All the studies were approached with the primary objective of a taxonomic revision in mind. Contributions are included either in the form of papers (reprints or copies thereof) which have been published regularly in various journals over a period of about three years, or in manuscript format (papers which have not yet appeared in print). Each chapter is furnished with an introduction. A list of publications to which reference has been made in these parts of the text, is presented at the end of each introduction. Brief introductions to the research undertaken, details of relevant materials and methods and literature references are presented in the individual contributions. Each paper also includes a comprehensive discussion of results presented. A synthesis of the principal findings of the work up to now is presented in the form of a cladistic analysis (Chapter 8). This includes a key to the genera of the Alooideae and is followed by a chapter on the diagnostic characters, typification and synonymy of *Aloe bowiea* (=*Chamaealoe*), *Chortolirion* and *Poellnitzia*. It should be stressed that for these taxa this work is the formal revision for the *FSA*.

The papers presented here differ considerably in style. These are primarily due to differences in lay-out and style required by the various journals. To have manuscripts accepted for publication, conformation to some idiosyncrasies of referees and editors was sometimes unavoidable. The papers contain a number of minor typographic errors. Most of the errors were corrected on the enclosed reprints. The dissertation is nevertheless provided with an Appendix for corrections and additional notes.

In each chapter the three genera included in the study are treated chronologically, based on the publication dates of the generic names. The sequence used throughout is *Aloe bowiea* [= *Chamaealoe* Berger (1905)], *Chortolirion* Berger (1908) and *Poellnitzia* Uitewaal (1940). Parts of chapters not intended for formal publication was prepared according to the "Instructions to authors" of the *South African Journal of Botany*, with the exception that journal titles were not abbreviated. The main reason for this is the difficulties encountered in locating and obtaining obscure publications referred to by means of cryptic literature references only. Thus, the titles of all journals cited in the introductions to the chapters are given in full. In this regard the proposals of Eggli (1985, 1987), Newton (1987) and Smith & Van Wyk (1989b, 1990) were followed.

For the sake of brevity authorities of names of genera of the Alooideae are not repeated in the introductory paragraphs of all the chapters. (Table 1.1. carries a complete list). Clearly, this does not apply to either published or yet to be published material, where inclusion of author citation at first mention of the name of a taxon is compulsory.

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CHAPTER 2

THE GENUS CONCEPT IN THE ALOOIDEAE

"Historically, taxonomists have attempted to establish various criteria by which generic boundaries can or should be established. Some have argued that genera, particularly segregate genera (i.e., genera that have been removed from large, often polymorphic genera of long historic standing), should be sharply delimited and include few or no intermediate species. ..... Others have suggested that genera are nothing more than convenient reference systems and rarely should be redefined, since existing classification systems are convenient enough. Still others have argued that the primary criterion for the recognition of genera, and other supraspecific taxa should be monophylesis, and the monophyletic groups are recognized on the basis of shared derived characters. Although these methods of defining genera differ in the philosophical foundations, they all are based upon an evaluation of characters and an assessment of phenetic and phylogenetic relationships that is derived from such character analyses."

D.A.L.H. Young: 1987

CONTENTS

CHAPTER 2

THE GENUS CONCEPT IN THE ALOOIDEAE

2.1 INTRODUCTION

2.1.1 Background

A broad-based, multidisciplinary study taking all the genera of the Alooideae into consideration with as many populations represented as possible, is likely to give insight into phylogenetic relationships among genera, species and populations. Whether or not the taxa that this study is primarily concerned with, *Aloe bowiea*, *Chortolirion* and *Poellnitzia*, are recognized as species of larger polymorphic genera, such as *Aloe*, *Astroloba* and *Haworthia*, or as warranting acceptance as segregate genera [*Bowiea sensu* Haworth (1824, 1827), *Chamaealoe sensu* Berger (1905) for *Aloe bowiea*] is largely a matter of taxonomic opinion. Clearly, before an interpretation of the results of modern biosystematic investigations [*sensu* Hagen (1983)] can be attempted, it is imperative that generic concepts as applied in a variety of taxonomic groups are analysed. For this reason the criteria and philosophical bases that taxonomists have used in the past for establishing the concept of the genus in general are briefly discussed.

2.1.2 The importance of the genus category in a hierarchical classification system

The hierarchy that taxonomists currently recognize and use for the classification of plants consists of 10 most commonly used, successively inclusive categories above (and including) the species level, and three main infraspecific ones. These ranks or levels are species, series, section, genus, tribe, family, order, class, division and kingdom. The three main infraspecific categories are subspecies, variety and form (Stace 1989). The concept of the genus, which concerns us here, was developed over a protracted period of time, the foundation of what we today regard as genera having been laid since the sixteenth century by a number of European botanists. The gradual realization that a formal system of classification is required to create order amongst the known plant taxa coincided with exploration in regions beyond Europe which resulted in a growing number of plants reaching European taxonomists (Jones & Luchsinger 1986; Lawrence 1951). For example, by the late 1600's John Ray (1627--1705), an English naturalist, produced a system of classification which dealt with nearly 18 000 species (Ray 1703). Although technically advanced, Ray's system was complicated and unmanageable due largely to the great number of species that it dealt with. In his works Ray laid the foundation of what was to become "natural classification", that is, grouping together plants that look alike

(Radford 1986).

As long as 130 years before the publication of Linnaeus' (1753) *Species plantarum*, Gaspard Bauhin (1560--1624), a Swiss botanist, distinguished nomenclaturally between species and genera (Bauhin 1623). Thus, to many of the plants that he described Bauhin gave a generic name and specific epithet. The Frenchman Joseph Pitton de Tournefort (1656--1708) is, however, universally regarded as the father of the genus concept. He treated the genus as the smallest practical unit of classification and considered species to be variants of the genus (Tournefort 1700; *cf.* Lawrence 1951). Several of Tournefort's generic names, such as *Populus* L. (Salicaceae), *Fagus* L. (Fagaceae), *Lathyrus* L. (Fabaceae) and *Verbena* L. (Verbenaceae), were accepted by Linnaeus (1753) and are therefore still used today. Thus, it appears as if the genus represents a category that can claim a real existence, since its origin can, on historical and philosophical grounds, be traced back to the pre-Linnaean folk taxonomy (Clayton 1972; Radford *et al.* 1974). The features of present-day classification systems, including aspects such as generic concepts, were not only determined by European botanists, but were also based on an analysis of mainly European flowering plants. This is clear from the fact that approximately two thirds of the genera that Linnaeus (1753) had discussed, were European (Walters 1961). Furthermore, during the 18th and 19th centuries, southern African succulent plant species were mostly described by European botanists who lacked appreciation of the variability of these plants in their natural habitat. This has resulted in the situation where, in genera such as *Gasteria*, many species names have been published which cannot be linked to natural populations (Schelpe 1958; Ginns 1975; Bayer 1980; Speirs 1986; Van Jaarsveld 1991).

In 1751 Linnaeus defined the genus as follows: "Genus omne est naturalis, in primordia tale creatum" (quoted by Löve 1963). He therefore regarded every genus as being a natural entity and that it was initially created as such (Jonsell 1978). To Linnaeus, the founder of modern botanical and zoological taxonomy, the genus was of central importance and he put this category in order of hierarchical importance second only to the species. It is, however, often impossible to determine to what extent the genus category represents a natural plant grouping and, in contrast, to what extent it is only an artificial arrangement conveniently created by man (Walters 1961; Clayton 1972). This is further illustrated by the fact that, at least in the tribe Stapelieae (family Asclepiadaceae), species were initially conveniently placed in what later proved to be the wrong genera, simply because a great deal of research would have been necessary to determine their true generic affinities (Bruyns 1984).

Clayton (1972) provides mathematical evidence suggesting that the frequency distribution of genera of different size (that is, number of species in a genus) within a family is remarkably constant for a selection of 19 families. It also became apparent that monotypic genera (those with only one species) occur more frequently in a family than that which is predicted by a logarithmic curve for that family (Clayton 1972). However, Clayton (1972) does not attribute this phenomenon to excessive and therefore artificial genus recognition by some taxonomists. It is rather an inherent quality of the present-day interpretation of the genus concept. The relative constancy of generic size distribution amongst the families which Clayton (1972) investigated also suggests that evolutionary processes [mutation, genetic recombination, natural selection, chance fixation of genes and reproductive isolation *sensu* Stebbins (1977)] have operated uniformly to produce similar patterns of species groups in the families. These groups are recognizable as genera (Clayton 1972). Especially in the case of aggregates of specialized plant taxa, for instance succulents (Jacobsen 1966; Kamstra 1973; Woodell 1973; Flach & Eller 1990; Eller & Flach 1990; Von Willert *et al.* 1990), it can be expected that evolutionary experimentation can lead to the suitable recognition of genera of different sizes within a given family (Bruyns 1984). Furthermore, few genera contain large numbers of species, Stace (1989) justifiably concluding that, in general, monotypic taxa are natural entities that should be recognized as such taxonomically. This phenomenon is, however, not the only one to lead to the establishment of small genera within a family. The subjective inclination to diminish the borders between genera and species in, amongst others, the Poaceae (grass family) has contributed to new genera being described at a much faster rate than species. Clayton (1972) justifiably questions the desirability of this gradual convergence of generic and species concepts.

Although the species concept was at first interpreted as an arbitrary level of morphological difference, it gradually became clear that plant taxa at this level of the hierarchy normally form part of a closed breeding system (Fearn & Chirnside 1967; Clayton 1983). However, a similar biological phenomenon that can serve as basis for our present interpretation of the genus concept has not yet been found. In its formal definition the genus remains an arbitrary and abstract level of morphological difference (Clayton 1972). In any analysis of the guide lines generally used for the recognition of genera, it should be clear that a genus can more easily be distinguished if there exist obvious morphological differences between it and other species aggregates (Rollins 1953; Clayton 1972). The absence of such differences in two closely related genera would rather point to the preferable acceptance of the one as an infrageneric taxon of the other. Clayton (1972) therefore suggests that generic patterns closely reflect patterns of evolution, that is, mutual similarities result from common descent.

2.1.3 Conclusion

One should, however, be wary of oversimplifying the interpretation through time [historical aspects of Walters (1986)] of the complexities of nature. For this reason Cronk (1989, 1990) has more recently suggested that ".... classifications are psychohistorical artifact and biological reality in roughly equal proportions." It is therefore obvious that if generic concepts are to have meaning, a historical, phylogenetic (evolutionary) and phenetic (hierarchical representation of similarity of form) approach to their study must be followed. There is not a single criterion which in itself can be regarded as unfailing for genus recognition [*cf.* Walker (1982, 1984) on stapeliad genera and Koutnik (1984) on *Chamaesyce* S.F. Gray of the Euphorbiaceae]. Thus, for practical considerations, the genus can be regarded as an inclusive category whose species have more characteristics in common with each other than with species of other genera within the same family (Jones & Luchsinger 1986). There should also be a clear break (a discontinuity) in variation between the members of a particular genus and the members of any other genus. Finally, past practice should be considered since a large change in classification and naming will create a barrier to communication and result in a loss of information (Jeffrey 1968).

The genus is not the only taxonomic category fraught with controversy. The species concept, too, does not comply with sets of prescribed rules (*cf.* Liden & Oxelman 1989). Levin (1979) effectively sums up the situation and concludes that the most useful species concept is a mental abstraction which arranges dissimilar groups in multidimensional character space. Furthermore, in a benchmark publication on the higher level flowering plant classification, Stevens (1984) has shown that it is not only the delimitation of concepts at the lower levels of the hierarchy which is unclear. Suprageneric categories are often subject to similar problems as species and generic concepts.

Classically *Aloe bowiea*, *Chortolirion* and *Poellnitzia* are interpreted as constituents of the Aloineae, one of 28 tribes of the family Liliaceae (Hutchinson 1959). More recently two extensively revised classification systems were published (Cronquist 1981; Dahlgren *et al.*. 1985) which not only differ from the system of Hutchinson (1959), but also from each other. The merits of these systems have been discussed elsewhere (Smith & Van Wyk in press; Chapter 2.2) and need not concern us here.

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2.2 AN ANNOTATED HISTORY OF GENERIC CONCEPTS AND TAXONOMIC RESEARCH IN THE ALOOIDEAE

2.2.1 Introduction

The taxonomic study of a group of plants, such as the subfamily Alooideae, Asphodelaceae, must necessarily include an analysis of the botanical way of thinking at the time of publication of its constituent generic names and their subsequent histories. Such an investigation gives insight into the circumstances prevalent when the names were proposed as well as their current relevance. This contribution presents an overview of the familial and infrafamilial classification of the aloeoid genera. As defined here the Alooideae includes *Aloe* L., *Astroloba* Uitewaal, *Chortolirion* Berger, *Gasteria* Duval, *Haworthia* Duval, *Lomatophyllum* Willdenow and *Poellnitzia* Uitewaal [see Chapter 1 and Smith & Van Wyk (in press) for the full generic synonymy]. Although some of the genera included in the subfamily are found elsewhere (mainly *Aloe* which ranges from the southern tip of Africa to the Arabian Peninsula and some of the islands, such as Socotra and Madagascar off the east African coast), it is fundamentally a southern African group.

2.2.2 Recent suprageneric classification of *Aloe* and its relatives

In recent years the Liliaceae, where the aloeoid genera have been traditionally classified, has been subjected to significant taxonomic reassessment in terms of its constituent infrafamilial taxa. The different interpretations of the circumscription of the Liliaceae by various taxonomists have resulted in, amongst others, the tribe Aloineae *sensu* Hutchinson (1959) being removed from the family. However, the circumscription of the Aloineae, one of 28 tribes recognized by Hutchinson (1959) in the Liliaceae, has undergone comparatively little change. The major controversies surrounding the taxonomy of the Aloineae have rather centred on genus and species concepts.

Apart from the obvious morphological and anatomical variation that many species belonging to these usually highly succulent plant genera display (Schelpe 1958; Reynolds 1966, 1982; Newton 1972; Cutler *et al.* 1980), remarkable cytogenetic uniformity exists within the tribe as a whole (Sharma & Mallick 1966; Brandham 1971, 1974; Riley & Majumdar 1979). Moreover, chromosomes are few enough and large enough to enable any deviation from the rule to be detected easily (Brandham 1976, 1977). The latter similarities, along with the probable monophyletic origin of this natural assemblage of genera, led Cronquist (1981) to remove them from the Liliaceae *sensu lato*. He reclassified the genera *Aloe* (including *Aloinella* Lemée *non* Cardot, *Chamaealoe* Berger, *Guillauminia* Bertrand and *Leptaloe* Stapf), *Gasteria*, *Haworthia* (including *Astroloba*, *Chortolirion* and *Poellnitzia*), *Kniphofia* Moench (including *Notosceptrum* Bentham) and *Lomatophyllum* in the family Aloeaceae Batsch, the latter being regarded as a derivative of the Liliaceae *sensu stricto* (Table 2.1). The relative ease with which most of the aloeoid genera interbreed most likely indicates that they are closely related. The absence of barriers to hybridization remains the most important evidence for phylogeny, especially since barriers may evolve rapidly even in closely related groups [see for example Riley & Majumdar (1979) on the aloeoid genera].

Table 2.1 Summary of the taxonomic treatments of the aloeoid genera of Cronquist (1981), Dahlgren & Clifford (1982) and Dahlgren *et al.* (1985), compared with the proposals of the present study. Only the genera *Bulbine, Kniphofia* and those traditionally included in the tribe Aloineae, family Liliaceae *sensu* Hutchinson (1959) are listed. Synonyms are not included.[- = genus not mentioned]

	Cronquist (1981)	**Dahlgren & Clifford (1982)**	**Dahlgren *et al.* (1985)**	**Proposals of present study**
Family	Aloeaceae	Asphodelaceae	Asphodelaceae	Asphodelaceae
Infrafamilial classification	-	Subfamily Asphodeloideae	Subfamily Alooideae	Subfamily Alooideae
Genera upheld	*Aloe*	*Aloe*	*Aloe*	*Aloe*
	-	*Astroloba*	*Astroloba*	*Astroloba*
	-	*Chamaealoe*	*Chamaealoe*	- [1]
	-	*Chortolirion*	-	*Chortolirion*
	Gasteria	*Gasteria*	*Gasteria*	*Gasteria*
	Haworthia	*Haworthia*	*Haworthia*	*Haworthia*
	Lomatophyllum	*Lomatophyllum*	*Lomatophyllum*	*Lomatophyllum*
	-	-	*Poellnitzia*	*Poellnitzia*
	-	*Bulbine*	-	- [2]
	Kniphofia	*Kniphofia*	-	*Kniphofia* [3]

[1] Included in the synonymy of *Aloe*.
[2] Retained in the subfamily Asphodeloideae.
[3] See Chapter 1.

The proposal of Cronquist (1981) was primarily based on the fact that the closely related Agavaceae is currently recognized as a separate family owing, amongst others, to its specialized growth habit. Since the Aloeaceae differ from the Liliaceae on essentially the same grounds, recognition of the Agavaceae as a family warrants the acceptance of the Aloeaceae as a lilioid segregate. Although the classification of at least *Yucca* Dill. *ex* L. (superior ovary) and *Agave* L. (inferior ovary) in the Agavaceae is supported by the common occurrence of a very distinctive bimodal karyotype consisting of five large chromosomes and 25 small ones, the karyology of other genera referred to the Agavaceae on habital grounds differ significantly from that of *Yucca* and *Agave*. Cronquist (1981) concluded that in the Agavaceae karyological characters "... does not correlate well enough with other features to be of critical taxonomic importance." In contrast, the Aloeaceae is characterised by a distinctive karyotype (2n = 14) which consists of four pairs of long chromosomes and three pairs of short chromosomes (see Chapter 6 for a detailed discussion).

It is noteworthy that Cronquist (1981) retains *Bulbine* Wolf in the Liliaceae. Several species of *Bulbine* have morphological and cytological characters in common with species which he included in the Aloeaceae (Rowley 1954, 1967). Furthermore, Reynolds (1950) recorded a plant 10 km north of Alice in the eastern Cape Province, which gave every indication of being a hybrid between *Aloe tenuior* Haworth var. *decidua* Reynolds and *Bulbine alooides* (L.) Willd. Whilst retaining *Bulbine* in the Liliaceae, Cronquist (1981) included *Kniphofia* along with the other aloeoid genera in the Aloeaceae. The latter genus is generally regarded as transitional between the Liliaceae and Aloeaceae. I support Cronquist's (1981) treatment since the exclusion of *Kniphofia* from the group of aloeoid genera would probably prove to be inconsistent with cladistic interpretation of the family Asphodelaceae [discussed in detail by Smith & Van Wyk (in press)].

Subsequently Dahlgren & Clifford (1982) included the genera traditionally classified in the tribe Aloineae, along with many others, in the type subfamily of the reinstated Asphodelaceae A.L. Jussieu. In their restructuring of the Liliaceae *sensu lato* they made use of characters derived from a wide range of disciplines and attempted an arrangement of all monocotyledonous families according to overall similarities obtained from comparative studies. Although Dahlgren & Clifford (1982) did not elaborate on the infrasubfamilial classification of the Asphodeloideae, they did mention that, within the latter taxon, the so-called *Aloe*-group forms a coherent unit. Thus, recognition of the aloeoid genera as a discreet entity within the Asphodelaceae would accord with the generally accepted requirement that supraspecific taxa should ideally be monophyletic.

Table 2.2 Chronology of genus name proliferation in the Alooideae *sensu* Dahlgren *et al.* (1985)

Major periods of systematic biology (Alston & Turner 1963; Merxmüller 1972)	**Historical phases of plant classification (Lawrence 1951)**	*Anno Domini*	**Reference**	**Genus names generally upheld[1]**	**Genus names not upheld**
	Artificial systems based on numerical classifications	1753	Linnaeus (1753)	*Aloe*	
			Medikus (1786)		*Catevala; Kumara*
		1800			
Micromorphic			Duval (1809)	*Gasteria; Haworthia*	
			Willdenow (1811)	*Lomatophyllum*	*Apicra* [2]*; Rhipidodendrum*
			Ker (1813)		*Phylloma*
			Haworth (1819)		*Apicra* [3]
			Haworth (1821)		*Pachidendron*
	Natural systems based on form relationships		Haworth (1824)		*Bowiea*
			Endlicher (1836)		*Agriodendron* [4]
			Rafinesque (1840)		*Atevala; Kumaria; Papilista; Succosaria; Tulista*
		1860			
			Salisbury (1866)		*Busipho; Ptyas*
Evolutionary					
		1880			
		1900			
			Berger (1905)		*Chamaealoe* [5]
			Berger (1908)	*Chortolirion*	
Cytogenetical	Systems based on phylogeny				
			Stapf (1933)		*Leptaloe*
			Lemée (1939)		*Aloinella*
			Uitewaal (1940)	*Poellnitzia*	
			Uitewaal (1947b)	*Astroloba*	
		1956	Bertrand (1956)		*Guillauminia*

[1] These seven genera are also recognized in the present study.

[2] *Apicra* Willd. is a superfluous name for *Haworthia* Duv.

[3] *Apicra* Haw. is a later homonym of *Apicra* Willd. and was applied to a group of species which is currently upheld as a separate genus. Although an attempt was made to conserve *Apicra* Haw. against *Apicra* Willd. (Stearn 1939a, b), the genus was later renamed *Astroloba* by Uitewaal (1947b).

[4] Endlicher (1836) attributed *Agriodendron* to Haworth. However, this name could not be located in any of Haworth's publications. Jackson (1895) justifiably cites Endlicher as author of the name *Agriodendron.*

[5] *Chamaealoe,* although published as a substitute name for *Bowiea* Haw., was superfluous at the time of publication. If Berger's (1905) generic concept is revived a new name would therefore have to be given to what has been called *Bowiea* Haw. *(nom. rej.)* and *Chamaealoe* Berger *(nom. illeg.).*

This point of view was amplified and brought to its full consequence when, in a later publication on structure, evolution and taxonomy of monocotyledons (Dahlgren *et al.* 1985), seven aloeoid genera were removed from the Asphodeloideae and placed in a separate subfamily, Alooideae. These genera show distinct phenetic similarities and the latter authors interpreted it as a monophyletic group derived from a common ancestor also shared with other Asphodelaceae. The eleven genera retained by Dahlgren & Clifford (1982) in the Asphodeloideae do not display the same marked African concentration as in the case of those transferred to the Alooideae, and probably represent a paraphyletic group.

Of the genera originally upheld in the *Aloe*-group of the Asphodeloideae (Dahlgren & Clifford 1982), only *Chortolirion* was not transferred to the Alooideae, probably as an oversight (Table 2.1). However, the genus *Poellnitzia* which they omitted from their initial comparative study (Dahlgren & Clifford 1982), was subsequently included in the Alooideae (Dahlgren *et al.* 1985; Perry 1985). In both publications the monotypic genus *Chamaealoe* is upheld (Table 2.1). In accordance with a recent proposal by Smith (1990), *Chamaealoe* Berger should be included in the synonymy of *Aloe*. Dahlgren & Clifford (1982) included the aloeoid genera in the Asphodeloideae along with, amongst others, the apparently related *Bulbine* and *Kniphofia*. In their subsequent rearrangement of the Asphodelaceae (Dahlgren *et al.* 1985) both these genera were retained in the subfamily Asphodeloideae while the aloeoid genera were classified in the Alooideae. This treatment therefore approximates that of Cronquist (1981), with the exception that he included *Kniphofia* along with the *Aloe*-group of genera in the Aloeaceae (Table 2.1).

2.2.3 The genus concept in the Alooideae

The chronology of genus name proliferation and the history of the aloeoid genus concept are summarized in Tables 2.2 and 2.3. The chronology (Table 2.2) is compared to the historical phases of plant classification and to the major periods of systematic biology. Although the latter phases and periods cannot be sharply delimited (Turner 1967), it is clear that early-19th century attempts by some European botanists to reflect natural affinities amongst plants in general resulted in the publication of 17 of the 27 genus names available for aloeoid taxa. However, the circumscription of only three of these genera are generally accepted.

The opening up of distant lands, such as the southern African interior, by, amongst others Masson, Burchell and Bowie (Smith & Van Wyk 1989), resulted in a steady stream of novel material reaching European botanical gardens. Botanists who had to deal with the wealth of new and undescribed specimens evidently did not know how to fit them into existing classifications and reverted to basing new genera on (what later often proved to be) non-diagnostic (floral and/or vegetative) structures or combinations of structures. However, in some circles the recognition of only a single genus, *Aloe*, for all the succulent-leaved, rosulate, asphodelaceous taxa persisted until at least the 1880's (Table 2.3). Clearly, a genus lies somewhere between these two extremes and, as Rowley (1976c) so aptly put it, "... the best we can hope to do is to avoid gross inconsistencies in our chosen unit." --- in this case the Alooideae.

Table 2.3 History of the aloeoid genus concept. Only the most important genus names and authorities are included

Authority				**Genera recognized**			
Linnaeus (1753)	*Aloe*						
Miller (1768)	*Aloe*						
Haworth (1804)	*Aloe*						
Duval (1809)	*Aloe*			*Gasteria*	*Haworthia*		
Schultes & Schultes (1829)	*Aloe*						
Endlicher (1836)[1]	*Aloe*					*Lomatophyllum*	
Salm-Dyck (1836-1863)	*Aloe*						
Baker (1880)	*Aloe*	*Apicra*[2]		*Gasteria*	*Haworthia*		
Bentham & Hooker (1883)	*Aloe*	*Apicra*[2]		*Gasteria*	*Haworthia*	*Lomatophyllum*	
Berger (1908)	*Aloe*	*Apicra*[2]	*Chortolirion*	*Gasteria*	*Haworthia*	*Lomatophyllum*	
Phillips (1926)	*Aloe*	*Apicra*[2]	*Chortolirion*	*Gasteria*	*Haworthia*	[3]	
Dyer (1976)	*Aloe*			*Gasteria*	*Haworthia*	[3]	
Present study	*Aloe*	*Astroloba*	*Chortolirion*	*Gasteria*	*Haworthia*	*Lomatophyllum*	*Poellnitzia*

[1] See Stearn (1947).
[2] *Astroloba* was then still known as *Apicra*. See Table 2.2 for the *Apicra* Willd. versus *Apicra* Haw. controversy.
[3] *Lomatophyllum* does not occur in the *Flora of southern Africa* region.

The taxonomic history of the Alooideae started out conservatively in 1753. Of the genera currently classified in this subfamily, Linnaeus (1753) recognized only one, namely *Aloe*, which he included in his Class Hexandria Order Monogynia. Up to the time that Linnaeus proposed his sexual classification system based primarily on the number, union and length of stamens, the few known aloeoid taxa, mainly *A. vera* (L.) Burm. f., possibly of Arabia (Newton 1979; Webb 1980; Bloomfield 1985;

Forster & Clifford 1986; Grindlay & Reynolds 1985), *A. perryi* Bak. of Socotra (Lavranos 1969; Horwood 1971) and the South African *A. maculata* All. (Dandy 1970), *A. arborescens* Mill., *A. brevifolia* Mill., *A. commixta* Berger, *A. ferox* Mill., *A. glauca* Mill., *A. humilis* (L.) Mill., *A. plicatilis* (L.) Mill., *A. succotrina* All. and *A. variegata* L. (Wijnands 1983; Reynolds 1950), were grouped on the basis of their characteristic succulent leaves (Bauhin 1651; Uitewaal 1947a; Rowley 1960, 1976d). Although Linnaeus did not intentionally utilize vegetative characters in his classification system, the latter line of thought did, to some degree, precipitate in his treatment of *Aloe*. This is clearly illustrated by the inclusion in *Aloe* of taxa currently classified in *Aloe*, *Astroloba*, *Gasteria*, *Haworthia* (Reynolds 1950; Bayer 1976), *Kniphofia* (Codd 1968) and *Sansevieria* (Brenan 1963; Wijnands 1973). In contrast to other early taxonomists, such as Bradley (1716-1727) who inexplicably confused the New World *Agave* and *Aloe*, Linnaeus (1753) aforded the former separate generic status. Recently research workers in the Alooideae, for example Reynolds (1950, 1966) and Holland (1978) on *Aloe sensu stricto* and Bayer (1976, 1982) on *Haworthia*, have attempted natural classifications for these genera. However, the age of artificial Alooideae classification has not yet passed, with Scott (1985) proposing an entirely artificial classification system for *Haworthia*, based mainly on vegetative characters.

Since the publication of the genus name *Aloe* (Linnaeus 1753), this taxon has been plagued by taxonomic confusion. Linnaeus preferred a broad circumscription of this genus and his use of a limited number of reproductive characters as criteria for classification did not provide conclusive evidence for generic circumscription in the Alooideae. Furthermore, Linnaeus made extensive use of infraspecific categories for classification, one of his species, *A. perfoliata*, being burdened by 16 varieties. Although Reynolds (1950) established the identity of ten of these varieties, some remain obscure and cannot with certainty be linked to field populations.

Attempts to subdivide *Aloe sensu* Linnaeus (1753) started some 30 years after this heterogeneous entity was proposed (Table 2.2). Although this initial attempt (Medikus 1786) to split *Aloe* into smaller, more homogeneous units was unsuccessful, the present-day circumscription of the four comparatively large aloeoid genera, *Aloe*, *Gasteria*, *Haworthia* and *Lomatophyllum* (Figures 2.1--2.3) dated from the early nineteenth century (Tables 2.2 & 2.3). However, the Alooideae does not consist of large genera only. Especially in the first half of the twentieth century genus names were proposed for several smaller units segregated from *Aloe*, *Haworthia* and *Astroloba*, the latter then being known as *Apicra* Haw. *non* Willd. (see footnote 3 of Table 2.2). This period coincided with the publication of the first plant classification systems based on phylogeny and probably represented attempts to display patterns of evolution within the aloeoid taxa. Of the genera proposed during this period, only *Chortolirion* and *Poellnitzia* are generally upheld, *Astroloba* having been recognized as a segregate of *Aloe* as early as 1880 [Table 2.3; Baker (1880)].

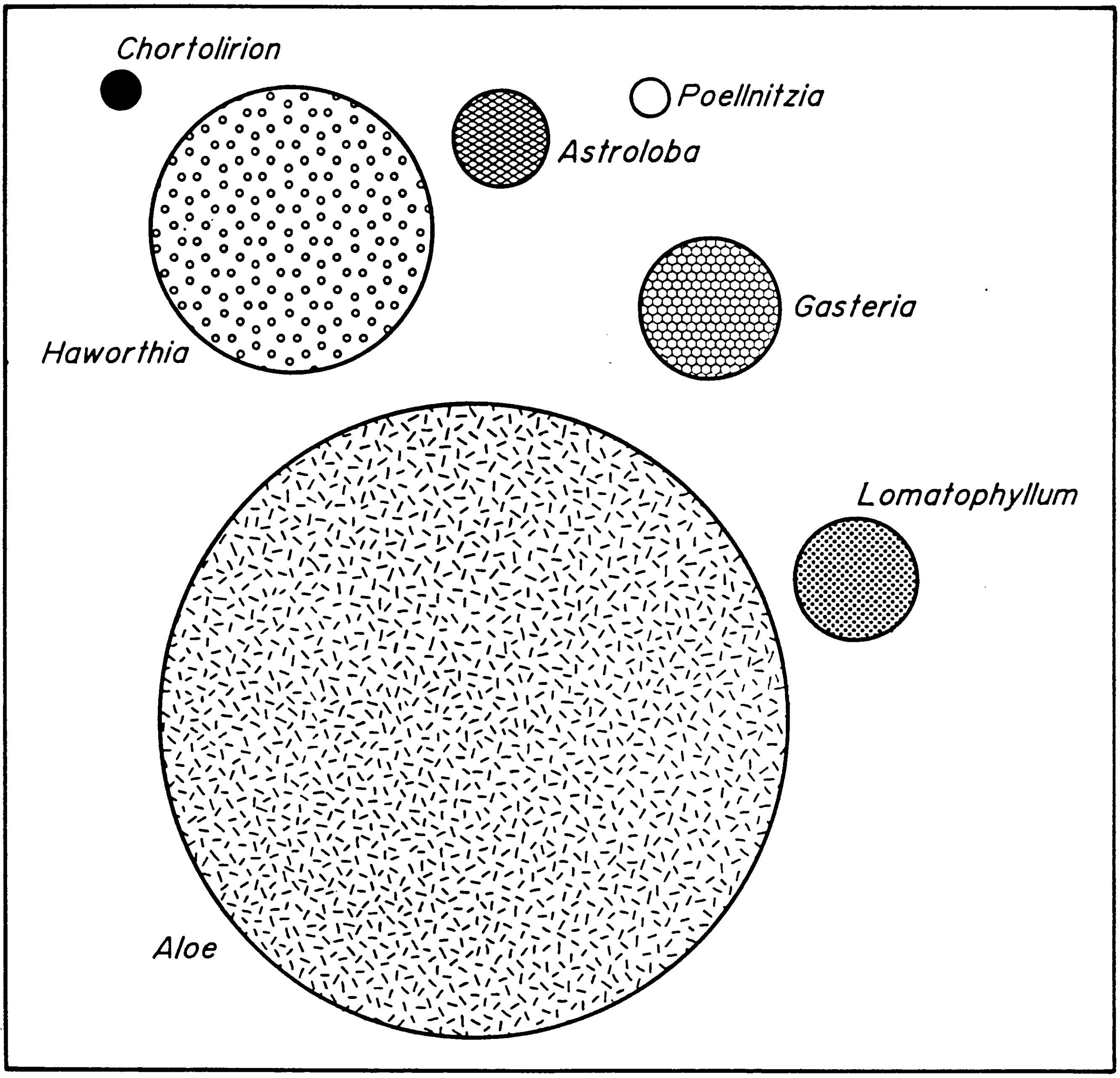

Figure 2.1 Genera of the Alooideae upheld in the present study. The area of each circle is proportional to the number of included species: *Aloe* 363 (Harding 1980); *Astroloba* 7 (Roberts Reinecke 1965); *Chortolirion* 1 (present study); *Gasteria* 16 (Van Jaarsveld 1991); *Haworthia* 68 (Bayer 1982); *Lomatophyllum* 12 (Jacobsen 1977); *Poellnitzia* 1 (present study). Diagram adapted from Rowley (1976a).

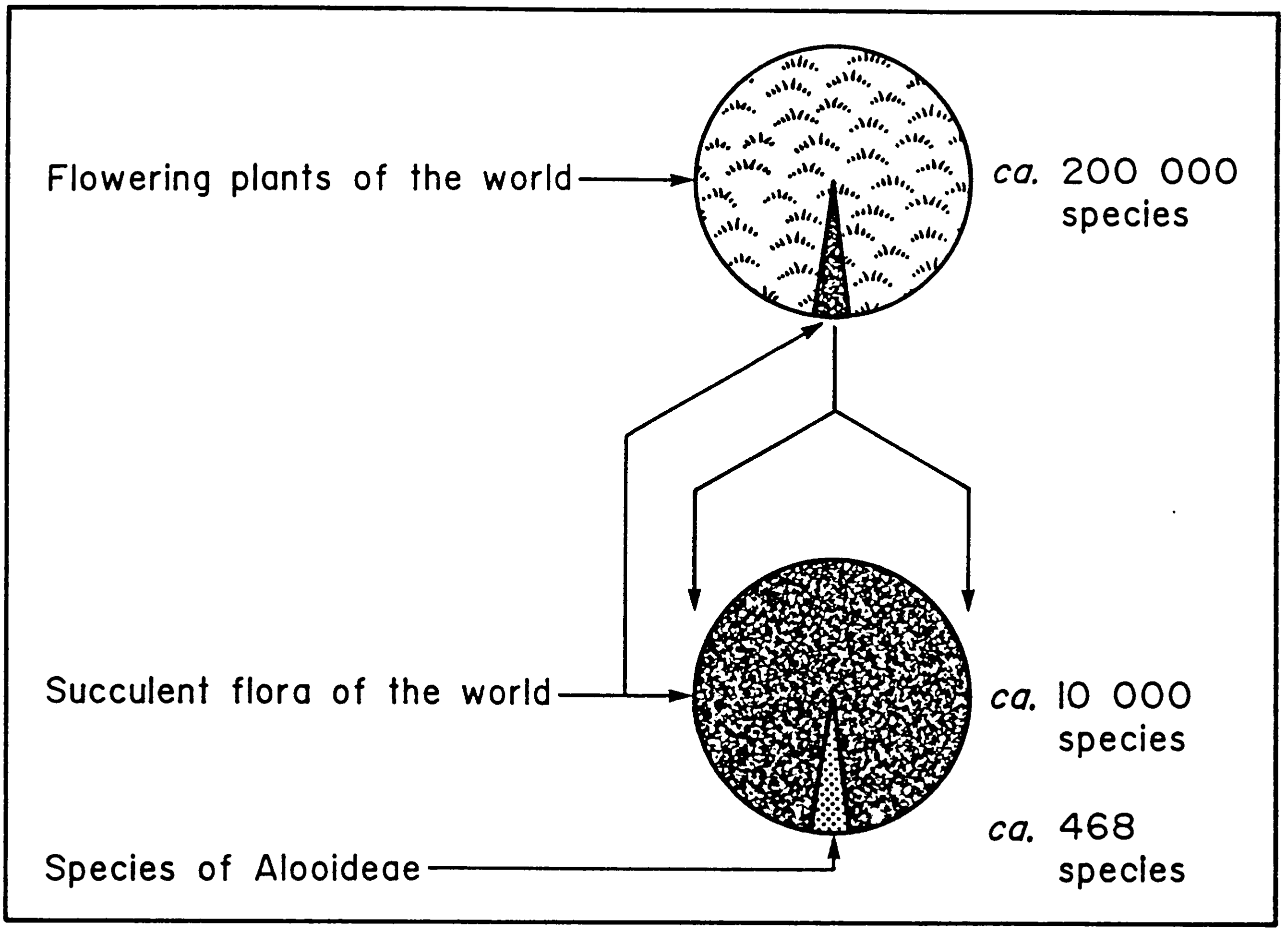

Figure 2.2 Pie chart of the Alooideae in relation to the flowering plants of the world [*ca.* 200 000 (Bell & Woodcock 1968)] and the world succulent flora [*ca.* 10 000 (Rowley 1978; Van Jaarsveld 1987)]. Adapted from Van Jaarsveld (1989).

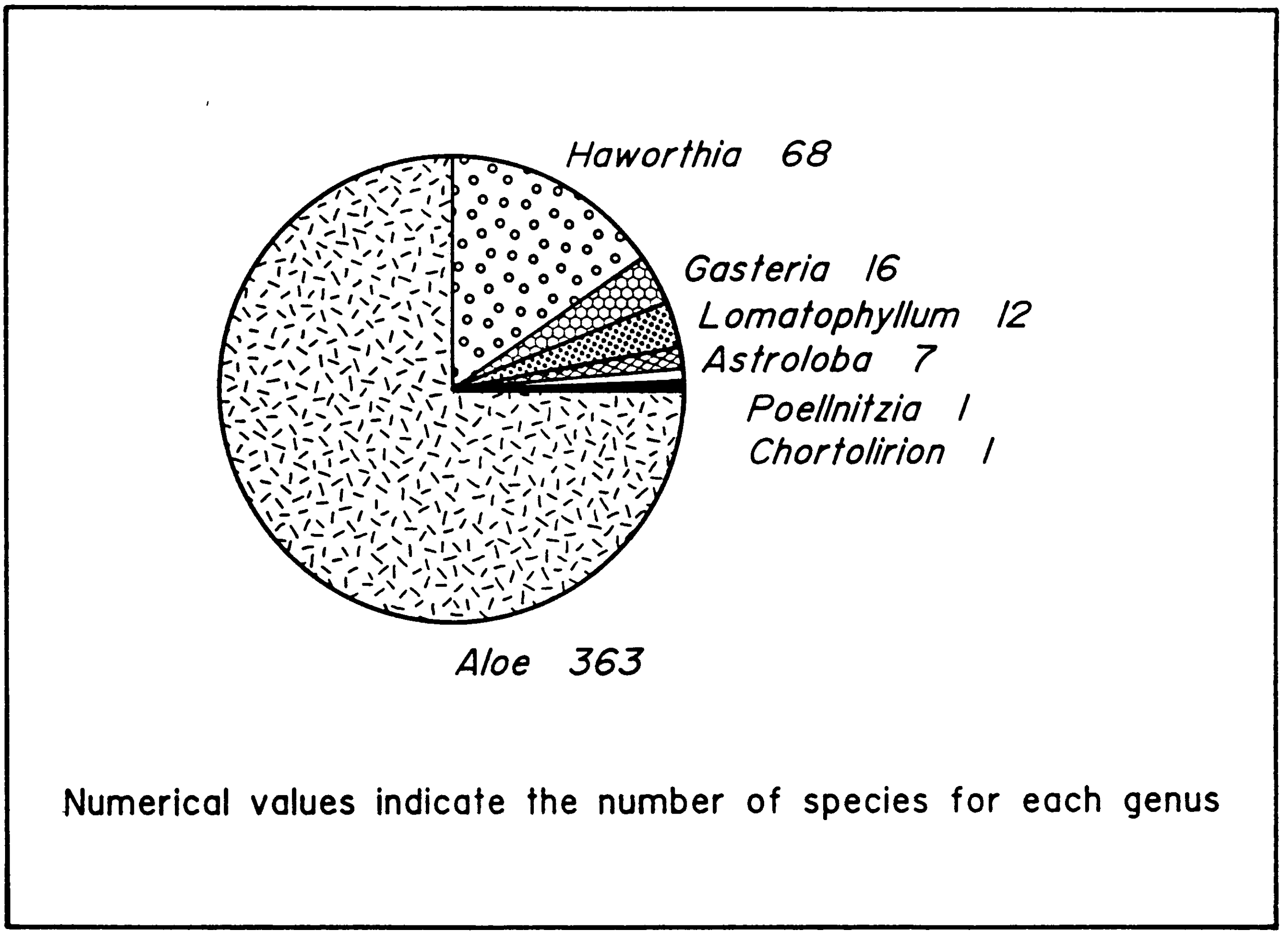

Figure 2.3 Pie chart of the Alooideae. See caption to Figure 2.1 for literature references. Adapted from Van Jaarsveld (1989).

2.2.4 Taxonomic notes on the genera of the Alooideae

Brief notes are given here on the aloeoid genera upheld in this study, with emphasis on recent taxonomic contributions. For additional information on the genera Smith & Van Wyk (in press) should be consulted.

2.2.4.1 Core aloeoid genera (*Aloe*, *Lomatophyllum*)

In the taxonomy of the Alooideae *Aloe* is of central importance. Not only is it the oldest genus in the subfamily, but of all the genera of the Alooideae it has been studied most extensively, both in terms of taxonomy and systematics. [For the taxonomy versus systematics controversy the argumentative contributions of Gilmartin (1986, 1987), La Duke (1987), Donoghue (1987) and Small (1989) should be consulted]. Furthermore, since it was the only genus recognized by Linnaeus (1753), all seven genera generally upheld in this monophyletic group are in effect segregates of *Aloe* (Table 2.3).

Although *Aloe* was monographed on a number of occasions in the nineteenth century, the botanical community and students of the genus owe most credit to Dr. G.W. Reynolds who travelled widely and studied *Aloe* intensively for more than thirty years on a continental scale. Thus, not only did he survey the southern African species of *Aloe* (Reynolds 1950), but expanded his research to include the tropical African and Madagascan species as well (Reynolds 1958, 1966). However, at the time of his death in 1967, many taxonomic problems remained unsolved and numerous newly discovered species awaited formal description. Many of the latter taxa were eventually published by Messrs. L.C. Leach and D.S. Hardy. Both had a working knowledge of Reynolds' methodology and were in a good position to add further to our knowledge of the genus. Presently the southern African representatives of *Aloe* are being revised by Dr. H.F. Glen and Mr. D.S. Hardy as part of the *Flora of southern Africa* research programme. Indications are that they will reduce substantially the number of species of *Aloe* worthy of recognition [see for example Glen & Hardy (1987)].

The second "typically" aloeoid genus, *Lomatophyllum*, is taxonomically very poorly known. Pending revision the genus is maintained separately from *Aloe*, due mainly to its baccate (and not capsular) fruit.

2.2.4.2 *Gasteria*

For many years species concepts in *Gasteria* were poorly defined. The genus was a taxonomists nightmare with more than 100 names available for some 20 discreet taxa. The revision of *Gasteria* by Mr. E.J. van Jaarsveld, to be published shortly (Van Jaarsveld 1991), should provide a clear picture of relationships amongst species and the phytogeography of the genus.

2.2.4.3 *Poellnitzia*

Prior to the present study *Poellnitzia* was either excluded from treatments of the Alooideae or simply shifted from genus to genus without adequate supporting evidence being offered. Cladistically there is little doubt about the generic status of *Poellnitzia*. It is one of the few Alooideae genera with a distinctive and unique apomorphy, namely the connivence of the tips of the perianth segments.

2.2.4.4 Haworthioid genera (*Astroloba*, *Chortolirion*, *Haworthia*)

This infrasubfamilial group is characterized by a combination of the following three characters: greenish-white flowers, flowers slanted upwards and a nectar sugar composition where glucose is present in much larger quantities than fructose. (Note that the first two characters are not unique to the haworthiod genera; they do, however, occur in all the species of this group and are very rare in the other aloeoid genera).

Since the recognition of *Haworthia* as a genus separate from *Aloe* by Duval (1809), it has been burdened by a profusion of species names often based on specimens of unknown or garden origin. Furthermore, most of the more than 160 species names available in the genus have been subdivided into numerous varieties and forms. Probably few of these warrant recognition at any rank in a hierarchical classification system. Although *Haworthia*, like *Aloe*, has been monographed on a number of occasions during the past 180 odd years, most of these "revisions" can be discarded as of limited value due to the fact that they reflect little more than horticultural fashion and had little or no connection with habitat collected material (Smith 1989). Recently one of the first overviews of *Haworthia* based on detailed field work was published by Bayer (1976, 1982).

The current uncertain state of the taxonomy of *Haworthia* is amply illustrated by the fact that Bayer (1982) recognised 68 species in this genus and Scott (1985) 88, while Gibbs Russell *et al.* (1985) listed 166 names for *Haworthia*, the latter work including *Chortolirion* Berger, *Astroloba* Uitew. and *Poellnitzia* Uitew. as constituents of *Haworthia*. More recently Bayer (1986) has expressed the view that a truly botanical dispensation could reduce to 33 the number of species of *Haworthia* worthy of recognition. The latter suggestion should, however, be seen in the correct perspective, some of the reasons for this confusing situation having been set out by Bayer (1978, 1986).

The second haworthioid genus, *Astroloba*, has recently been monographed by Roberts Reinecke (1965; unpublished) and Groen (1986, 1987a,b,c,d,e,f). *Astroloba* is a small genus consisting of seven (Roberts Reinecke) or four (Groen) species, depending on which revision is preferred [see Table 1 in Smith & Marx (1990)]. Characteristically species of *Astroloba* have 5-tiered, pungent-leaved, caulescent rosettes. At least in comparison to *Haworthia*, the flowers of *Astroloba* appear regular rather than bilabiate. Two species of *Astroloba*, *A. herrei* Uitewaal and *A. spiralis* (L.) Uitewaal, have flowers with marked inflation of the perianth tube (Bayer 1975). This character (unique apomorphy present in at least one species of the genus, in cladistic terminology) is absent from all other genera of the Alooideae.

The third and final haworthioid genus, *Chortolirion*, is treated in detail in the present study. It is a perennial, deciduous herb and is widely distributed in the summer rainfall region of southern Africa. The genus is morphologically quite distinct from *Haworthia*, especially with regard to the presence of an underground bulbous rootstock. Furthermore, *Chortolirion* is unique amongst haworthioid species in that it is the only grassland taxon of which the leaves are deciduous and die back to ground level after fires or frost.

2.2.5 Conclusions and key to the genera

From its modest beginning as a single, heterogeneous genus, *Aloe*, the number of both genera and species in the Alooideae have increased substantially. Apart from the 27 genus names which have been proposed for taxa of the subfamily at one time or another (Rowley 1976a,b), *Aloe* alone currently boasts approximately 360 species and some 50 infraspecific taxa (Harding 1980; Torrance 1988). However, the taxonomy of the Alooideae remains in flux as the existence of some genera is questioned and boundaries of others debated. This can primarily be attributed to the fact that, although being a genetically homogeneous group, the Alooideae displays unusual patterns of variation among populations and species and inconsistent intergradations among genera. It is my conviction, that the generic concepts as proposed in this study best reflect the current state of knowledge. Pending detailed taxonomic revisions of, particularly *Aloe*, *Haworthia* and *Lomatophyllum*, any reclassification of "groups of species" (*fide* Funk 1985) would be premature, and not in the best interest of nomenclatural stability.

As has been shown by Osborne *et al.* (1988) for the South African cycads, the aloes and aloe-like plants have deservedly been admired by botanists, horticulturists and laymen, especially in view of their aesthetical appeal and medicinal value. Increasing attention should now be paid to their taxonomy, micro- and macromorphology (vegetative and reproductive) and chemistry. In many cases this work is in its infancy and some of the avenues of research may yet cast additional light on the aloeoid genus concept.

The following key to *Kniphofia* and the aloeoid taxa traditionally included in the Alooideae is presented in support of my concept of these genera:

1. Leaves herbaceous, soft, non-succulent, immaculate, lacking distinct spines, in basal rosettes (apically in *Kniphofia northiae*) .... *Kniphofia*
1. Leaves thick, rigid, succulent, maculate, often margined with prickly teeth, in basal or apical rosettes or cauline:
    2. Fruit a berry .... *Lomatophyllum*
    2. Fruit a capsule:
        3. Capsule apically acuminate, underground parts bulbous ......*Chortolirion*
        3. Capsule apically rounded or obtuse, underground parts rhizomatous (if rarely bulbous then flowers > 10 mm long, regular):
            4. Perianth segments apically connivent .... *Poellnitzia*
            4. Perianth segments apically spreading or recurved:
                5. Flowers pendulous at anthesis, bulbous-based, perianth tube curved upwards .... *Gasteria*
                5. Flowers erect, suberect or spreading at anthesis, perianth tube straight or curved downwards:
                    6. Perianth bilabiate .... *Haworthia*
                    6. Perianth regular (if rarely bilabiate then flowers > 10 mm long, mouth upturned):
                        7. Flowers usually brightly coloured, smooth, fleshy, stamens as long as or longer than the perianth ......*Aloe*
                        7. Flowers dull coloured, occasionally with inflated tissue, flimsy, stamens included ....*Astroloba*

2.2.6 References

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CHAPTER 3

DISCOVERY AND TAXONOMIC HISTORY OF *ALOE BOWIEA, CHORTOLIRION* AND *POELLNITZIA*

"Any taxonomic study of a group of plants in a country like South Africa where the names and routes of the earliest explorers are known with greater or lesser accuracy, must necessarily include a study of these early explorations in order to deduce the date and circumstances of the discovery of the group in question, and its subsequent history."

H.F. Glen:.1975

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CHAPTER 3

DISCOVERY AND TAXONOMIC HISTORY OF *ALOE BOWIEA*, *CHORTOLIRION* AND *POELLNITZIA*

3.1 INTRODUCTION

3.1.1 Background

In southern Africa man's relation to succulent plants is doubtless far older than the modern history of this region. The impression that these plants made on early inhabitants of the country must have been far greater than on modern man and they were put to a large number of uses (Smith 1895; Dekenah 1951; Watt & Breyer-Brandwijk 1962; Bredenkamp & Van Vuuren 1987; Fox & Norwood Young 1988; Hutchings 1989a, b; Hutchings & Terblanche 1989; Roberts 1990). However, the history of the botanical exploration of southern Africa dates back to the early years of the seventeenth century, the first illustration of a terrestrial plant from this region (capitulum of *Protea neriifolia* R. Br.) having been published in 1605 (Palmer & Pitman 1972; Rourke 1980; Smith 1982). Some fifty years later the Lords XVII of the Vereenigde Oost-Indische Compagnie (V.O.I.C.) decided to establish a victualling station at the Cape of Good Hope. On 7 April 1652 the small fleet of three ships, the "Drommedaris", "Reyger" and "Goede Hoop" sailed into Table Bay under Jan van Riebeeck and within one month of arriving at the Cape work was started on the so-called Company's Garden (Gunn & Codd 1981; Anonymous no date). Due to the agricultural and botanical interests of a succession of commanders and governors residing at the Cape during the latter part of the seventeenth century, the Garden flourished and became the subject of favourable and glowing comment from visitors to the Cape (McCracken & McCracken 1988). Furthermore, a purposeful effort was made to collect and cultivate in the Company's Garden plants indigenous to southern Africa. Soon specimens of many of the novelties collected at the Cape were shipped to Europe where they caused a stir amongst the ranks of those who could afford heated greenhouses (Oliver 1980).

Since the southern Africa subcontinent hosts the richest and most diverse succulent flora in the world (Van Jaarsveld 1987; Smith & Van Wyk 1990), it was inevitable that many of the specimens which reached Europe from this region were succulents. An analysis of the botanical exploration of any region rich in succulents (North, Central and South America; South Africa) will clearly show that these plants have gone through different periods of popularity amongst European botanists and collectors. Following their large-scale introduction to Europe in the mid-1600's, these plants were immensely popular (Masson 1987). Interest in succulents increased steadily during the early eighteenth century (Stearn 1939), with the period between the Napoleonic Wars and the revolutionary years (late 1840's) marking another upsurge in the popularity of these plants. The prime collectors, however, were still members of aristocratic circles (Rayzer 1984; Subik 1989).

It is not surprising that plants with water storage tissue were popular with botanical collectors in southern Africa and cultivators in Europe. Firstly, these plants were able to survive readily the long periods that sea voyages took from South Africa to Europe during the seventeenth and eighteenth centuries. Secondly, succulents in general have always fascinated some botanical collectors and students of botany purely for the beauty in their oddity and the appeal of their strange and often bizarre morphologies. Shortly after the first succulent plants reached the educated and knowledge-hungry world of Europe, the demands for these unusual plants, both to grow and to have as dried specimens or paintings, increased considerably (Bradlow 1985). Remarking on the popularity of succulent plants in eighteenth century Europe (with reference to Richard Bradley [1688--1732], professor of botany at Cambridge), Haworth (1794) wrote the following (cf. also Rowley (1954)]:

> "In the days of Bradley, succulent plants, by the beauty and splendour of their various coloured flowers; by their numbers and variety; by their singularity, oddness and spangled gaiety; and by the great facility accompanying their cultivation, gained the admiration of most, ..."

As Europeans penetrated to the heart of the southern African subregion, new marvels were brought to light (McCracken & McCracken 1990). After the splendour and magnificence of the fynbos and tropical forests of the south-western and southern Cape, respectively, the explorers were faced with the stark beauty of the arid and apparently drab inland. It was in this region that *Aloe bowiea* and species of *Chortolirion* and *Poellnitzia* were discovered (Figure 3.1).

Two of the three taxa that this dissertation is primarily concerned with (*A. bowiea* and *Chortolirion*) occur comparatively far from the original European settlement at Table Bay. Consequently they were discovered relatively recently. *Poellnitzia*, however, grows naturally in the south-western Cape and, as Bayer (1982) remarked, it remains a mystery why it went undetected for more than 300 years after the botanical exploration of southern Africa had commenced. The history and chronology of the discovery and description of species of the three major genera of Alooideae have been covered admirably by Groenewald (1941) and Reynolds (1950) for *Aloe*, Van Jaarsveld (1989) for *Gasteria* and Bayer (1982) and Scott (1985) for *Haworthia*. For obvious reasons this information will not be repeated here. The bulk of Chapter 3 consists of notes on the taxonomy and discovery of *Aloe bowiea* (Smith 1991a) with biographical notes on James Bowie (Smith & Van Wyk 1989). Up to the present investigation very little had been known about Bowie who "... managed to survive the hazardous, dangerous and uncomfortable conditions of an early plant hunter's life, ..." (Lemmon 1968). The dates and circumstances of the discovery of *Chortolirion* (Smith 1991b) and *Poellnitzia* (Smith 1991c) are also enumerated in detail.

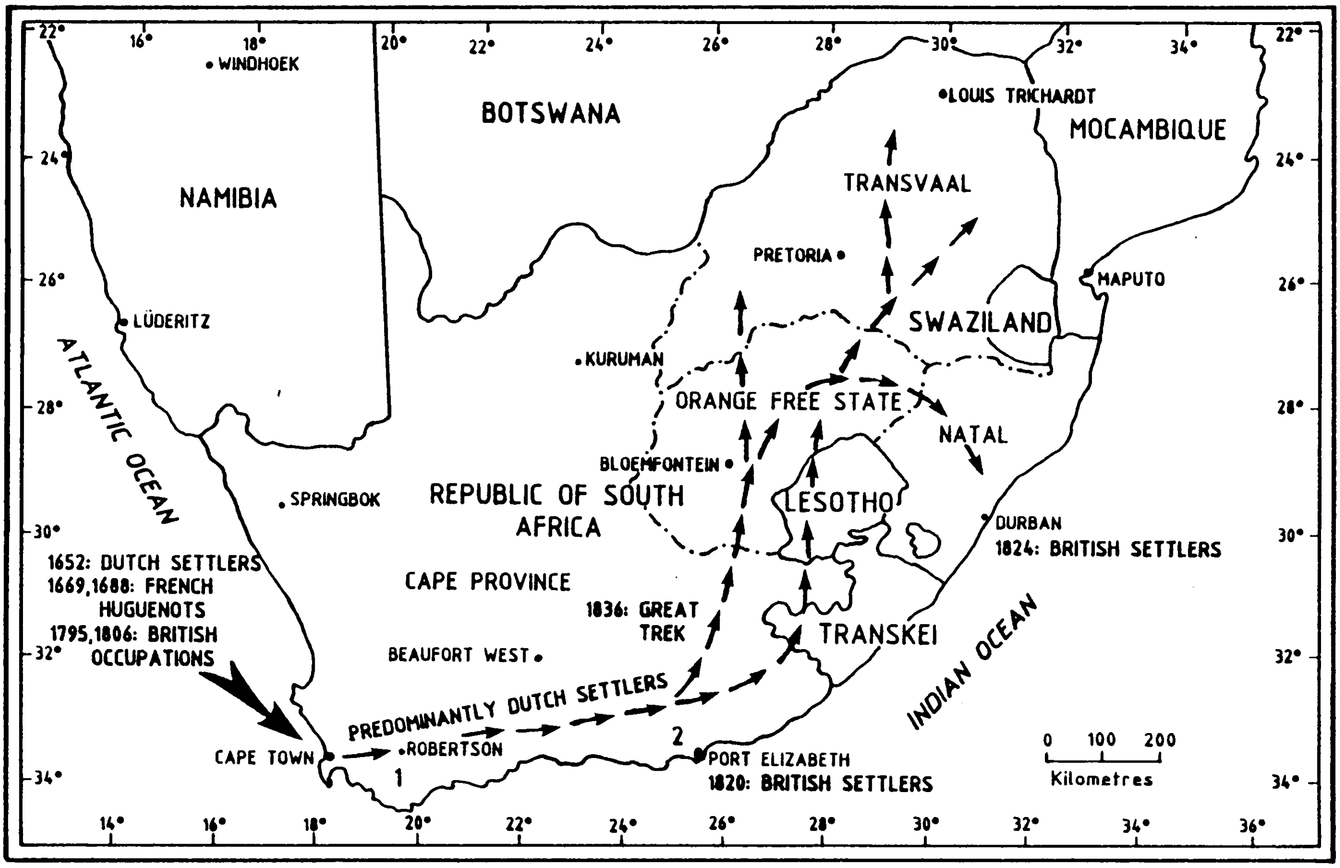

Figure 3.1 Chronology of European settlement in South Africa. 1, Locality of *Poellnitzia*; 2, locality of *Aloe bowiea*. *Chortolirion* occurs over much of central and southern Namibia, southern Botswana, Transvaal, Orange Free State, northern Natal and northern Cape.

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BIOGRAPHICAL NOTES ON JAMES BOWIE AND THE DISCOVERY OF *ALOE BOWIEA* SCHULT. & J. H. SCHULT. (ALOOIDEAE: ASPHODELACEAE)

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Summary

James Bowie served Kew as a plant collector in Brazil and at the Cape of Good Hope. From an examination of the itineraries of the four journeys he undertook to the southern African interior during his initial stay at the Cape it is possible to deduce the most likely type locality (vicinity of Algoa Bay) and approximate date of collection (30 December 1821–26 February 1822) of *Aloe bowiea* Schult. & J. H. Schult. Detailed grid references are provided and should enable systematists to pinpoint the localities in which Bowie collected. An enumeration is given of Bowie's publications on Cape plants.

Introduction

The Royal Botanic Gardens, Kew, will always be linked indissolubly to the history of the botanical exploration of southern Africa. Even before it became a national institution in 1841 (Anon., 1982; Field et al., 1987), numerous collectors employed by Kew visited the shores of the then Cape of Good Hope (Gunn and Codd, 1981). Especially towards the end of the eighteenth century an increasing interest in gardening and botany in Great Britain lead to a big demand for exotic plants. Many of the novelties that found their way into private collections and public gardens in Great Britain and Europe originated from South Africa.

The early volumes of the *Botanical Magazine* founded by William Curtis in 1787 (Kaden, 1982), contain numerous drawings and engravings of Cape plants and bear witness to the enthusiasm of early collectors. Two of the first British collectors sent on official collecting trips to South Africa by Kew were Francis Masson (1772–1775, 1786–1795) and James Bowie (1816–1823). However, very little is known about Bowie's collecting activities during his initial stay at the Cape. Although Bowie introduced many Cape plants into cultivation, Stafleu and Cowan (1976) do not mention his contributions towards the expansion of our knowledge of South Africa's indigenous flora.

This paper provides a more complete account of the localities where Bowie collected plants during his initial stay at the Cape (1 November 1816–20 May 1823) (Gunn and Codd, 1981) and enumerates his publications on Cape plants. Biographical notes on Bowie are also included. Any account of Bowie's collecting activities would necessitate reference to Francis Masson who preceded him as official collector of botanical specimens in southern Africa. Masson's travels have, however, been recorded in more detail elsewhere (Britten, 1884; MacOwan, 1887) and so his contributions towards the botanical exploration of the Cape of Good Hope are mentioned only briefly in this paper.

Based on the evidence resulting from this study we have been able to determine the possible type locality and date of collection of *Aloe bowiea* Schult. & J. H. Schult. (Alooideae: Asphodelaceae), a small, inconspicuous plant with a confused taxonomic history. Apart from its current acceptance as a species of *Aloe* (Obermeyer, 1973; Smith, 1983), it has also been considered a species of *Bowiea* Haworth (1824, 1827) non W. H. Harvey ex J. D. Hooker (Hooker, 1867) and as the only species in the genus *Chamaealoe* Berger (1905).

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Aloe bowiea has a very restricted distribution and is currently only known from two localities in the south-eastern Cape Province.

Francis Masson (August 1741–23 December 1805)

Francis Masson, one of the most celebrated of English plant collectors at the Cape, became a gardener and took up employment at the Royal Gardens at Kew some time before 1772. This institution was then still a private royal domain (MacOwan, 1887). At Kew Masson first worked as under-gardener and later accepted a position as collector of seed and living plants (MacOwan, 1887; Britten, 1920). The advantages of having a botanical collector residing at the Cape of Good Hope were realized by Sir Joseph Banks who persuaded King George III ("Farmer George") to act as patron of the proposed collecting trips to areas such as the Cape (Banks, 1985). Masson visited the Cape twice, his second and final visit coming to an end during March 1795 shortly before the first British occupation of the Cape colony (Gunn and Codd, 1981). As one of the first horticulturists to be employed as a collector of foreign material, Masson was unchallenged for his perseverance and enthusiasm. At that time the superiority of the plant collection kept at Kew was in great part ascribed to his endeavours (Baker, 1880; MacOwan, 1887; Britten, 1920).

Biographical Notes on James Bowie (ca. 1789–2 July 1869)

It was as the successor to Masson that James Bowie was sent to the Cape of Good Hope, almost 22 years after this great botanical collector had finally left the shores of southern Africa. Bowie was the son of a London seedsman who did business at the west end of what used to be Oxford Street in the early 1880's (MacOwan, 1887; Watson, 1897). In 1810, when nearly 21, Bowie also obtained employment at Kew and spent the next four years working there as a gardener. In 1814 Bowie and a colleague, Allan Cunningham, were sent on what was to be his first collecting trip abroad. They embarked for Rio de Janeiro and collected material in Brazil until 1816 (MacOwan, 1887; Hutchinson, 1946; Gunn and Codd, 1981). This visit lasted until 28 September 1816 (Hutchinson, 1946) and not 1817 as stated by Smith (1881), MacOwan (1887), and Watson (1897). Bowie was then ordered to the Cape of Good Hope as botanical collector and Cunningham, in a similar capacity, to New South Wales, Australia. Cunningham eventually discovered numerous Australian plants new to science and is commemorated in *Alania* Endlicher and, along with his brother Richard, in *Cunninghamia* R. Brown nom. cons. (Stafleu and Cowan, 1976).

On 28 September 1816 Bowie boarded the "Mulgrave Castle" and arrived at Table Bay on 1 November 1816. During the first 18 months of his initial stay at the Cape, Bowie concentrated his collecting activities to the vicinity of Cape Town. At this time he seems to have been engaged in the normal duties expected of a collector, cultivating and exporting to Kew plants of mainly horticultural interest (MacOwan, 1887; Rowley, 1960). Bowie apparently held his own collecting capabilities in high esteem since he stated in a letter dated November 1826 (quoted by MacOwan, 1887) that he collected and forwarded to Kew almost every plant from the Cape of Good Hope figured in Great Britain after 1817.

An account of the four journeys that Bowie eventually undertook during his initial stay at the Cape is provided in Tables 1–4. In listing the Bowie localities, the presentations of Hutchinson (1946) and Gunn and Codd (1981) have been followed. Hutchinson (1946) based his account of Bowie's travels on information obtained from G. H. Fourcade, a plant collector and Forest Officer at Knysna, stationed with the Superintendant of Woods and Forests for the Cape of Good Hope from 1882 to 1913. With regard to specific localities little can, however, be gleaned from the above sources. In many cases the only information available is a general locality or district. These names have been retained even though the present district limits differ from the limits accepted during the early part of the previous century. Where necessary the spelling was corrected to conform with current usage. Where possible the grid references of the respective localities are provided according to the system

Table 1. An account of the first inland journey (23 March 1818–14 January 1819) undertaken by James Bowie during his initial stay at the Cape.

Locality	Grid reference	Date
Left Cape Town.	3318 DC	23 March 1818
Explored from Caledon	3419 AB	
via Gouritz River (Gourits River),	3321/3421	
Great Brak River,	3422 AA	
George,	3322 DC	April–June 1818
Kayman's River (Kaaimans River),	3322 DC	
Zwart River (Swart River) and	3322 AA	
Goukamma to	3322 DD/3422 BB	
Knysna.	3423 AA	
Resided at Knysna and	3423 AA	July–November 1818
Plettenberg Bay,	3423 AB	
with an excursion to Avontuur.	3323 CA	29 September–1 October 1818
Returned to Cape Town via the	3318 DC	
coastal route.		14 January 1819

of Leistner and Morris (1976) and Raper (1987). The final item of information listed in Tables 1–4 is the dates on which Bowie visited the respective localities. In the tables extended periods during which Bowie visited certain localities but which cannot be specifically dated are indicated by bold bars.

Bowie began his first collecting trip into the interior of southern Africa on 23 March 1818. On this trip he explored from Cape Town and Caledon in the west to Knysna and Plettenberg Bay in the east, returning to Cape Town almost ten months later along the coastal route (Table 1). Bowie arrived at Cape Town on 14 January 1819 and probably spent the next three months despatching to Kew the material that he collected on this journey. During this and subsequent journeys Bowie made Plettenberg Bay his headquarters (Fourcade, 1944).

On 9 April 1819 Bowie departed from Cape Town on his second collecting trip. This trip again lasted almost ten months and took Bowie as far east as Knysna (Table 2) where Bowie stayed with George Rex (19 July or 29 August 1765–3 April 1839), a notary and pioneer of this town. The legend that Rex was the legitimate son of Prince George (later King George III) seems to be unfounded (Gunn and Codd, 1981). King George III did,

Table 2. An account of the second inland journey (9 April 1819–22 January 1820) undertaken by James Bowie during his initial stay at the Cape.

Locality	Grid reference	Date
Left Cape Town.	3318 DC	9 April 1819
Explored via the Berg River,	3218	
Roodezand,	3319	
Breede River,	3220–3420	
Caledon,	3419 AB	April–November 1819
Swellendam and	3420 AB	
Great Brak River to	3422 AA	
Knysna and	3423 AA	
Plettenberg Bay.	3423 AB	
Resided with George Rex at Knysna.	3423 AA	23 November 1819–9 January 1820
Arrived back at Cape Town in the	3318 DC	
company of George Rex.		22 January 1820

Table 3. An account of the third journey (early 1820–29 January 1821) undertaken by James Bowie during his initial stay at the Cape.

Locality	Grid reference	Date
Left Cape Town in the company of George Rex.	3318 DC	Early 1820
Resided at Knysna and	3423 AA	9 March–11 September 1820
Plettenberg Bay.	3423 AB	
Visited the Goukamma.	3322 DD/3422 BB	12 September 1820
Crossed the Long Kloof (Langkloof)	3322/3323	–
over Devil's Kop, George Division.	–	–
Crossed Keurbooms River and	3323	23 September 1820
proceeded to Avontuur,	3323 CA	26 September 1820
Uniondale Karoo,	3323 CA	27–29 September 1820
Kromme River,	3323 DD	9 October 1820
Gamtoos River,	3325 CC	–
Lowrie River,	–	–
Uitenhage,	3325 CD	28 October 1820
Algoa Bay,	3325 DD	5 November 1820
Addo,	3325	–
Bushmans River,	3325/3326	–
Kowie,	3326 BC/DB	6 December 1820
Blaauw Krantz River and	3326 BD	8 December 1820
Grahamstown.	3326 BC	
Returned to Algoa Bay.	3325 DD	21 December 1820
Sailed from Algoa Bay.	3325 DD	15 January 1821
Called at Plettenberg (Bay).	3423 AB	–
Arrived at Table Bay.	3318 CD	29 January 1821

however, act as patron of the overseas collecting trips of, amongst others, James Bowie. Rex was a hospitable man and he received many naturalists of that time at Knysna, Bowie in particular paying him frequent visits (Fourcade, 1944). He is commemorated in *Streptocarpus rexii* (Hook.) Lindl. which was collected by Bowie at Melkhoutkraal, one of Rex's farms at Knysna (Gunn and Codd, 1981). *Streptocarpus rexii* was the first species of this interesting genus to be discovered and was introduced into cultivation from the material sent to Kew by Bowie (Hilliard and Burtt, 1971). After having completed his second journey, Bowie arrived back at Cape Town on 22 January 1820 in the company of George Rex (Fourcade, 1944).

Although the exact date on which Bowie departed on his third journey which took him as far east as Bushmans River, Kowie and Grahamstown is not known, it must have been shortly after 22 January 1820 (Table 3). On 9 March 1820 he was already residing at Knysna, whilst it took him between three and seven months, respectively, to reach Rex on his first two journeys (Tables 1 and 2). One would thus have to assume that Bowie was now more familiar with the route from Cape Town to Knysna and that he did not stop to collect along the way. On this third journey George Rex accompanied Bowie from Cape Town to Knysna. This collecting trip, which lasted approximately one year, took Bowie further east than either of his first two journeys. After completing this journey he sailed from Algoa Bay on 15 January 1821, arriving on 29 January 1821 in Tabel Bay where he remained until 23 May 1821.

On his fourth journey Bowie seems to have been eager to explore from Algoa Bay eastward since he again sailed from Cape Town (24 May 1821) and arrived at Algoa Bay two weeks later on 5 June 1821. During this last collecting trip that Bowie undertook into the interior of southern Africa during his initial stay at the Cape, he explored the lesser known eastern

Table 4. An account of the fourth journey (24 May 1821–4 December 1822) undertaken by James Bowie during his initial stay at the Cape.

Locality	Grid reference	Date
Sailed from Cape Town.	3318 DC	24 May 1821
Arrived at Algoa Bay and proceeded to	3325 DD	5 June 1821
Uitenhage,	3325 CD	14–25 June 1821
Sundays River,	3325	26 June 1821
Bathurst,	3326 DB	4 July 1821
Great Fisch River (Great Fish River),	3125–3327	9 July 1821
Sundays River,	3325	21 July 1821
Uitenhage,	3325 CD	25 July–18 August 1821
Algoa Bay,	3325 DD	19–29 August 1821
Graaff Reinet (Graaff-Reinet),	3224 BA	14 September 1821
Erste Poort (Eerste Poort), Colesberg Division,	3024 DB	30 September 1821
Sundays River,	3325	25 October 1821
Graaff Reinet (Graaff-Reinet),	3224 BA	27 October–29 December 1821
Algoa Bay,	3325 DD	30 December 1821–18 January 1822
Uitenhage,	3325 CD	19 January–26 February 1822
Kowie River,	3326 BC/DB	15 March 1822
Uitenhage,	3325 CD	29 March 1822
Algoa Bay and	3325 DD	1–9 April 1822
Uitenhage.	3325 CD	10 April–6 May 1822
Returned to Knysna via Vanstadens (Van Stadens River),	3325 CC	—
Lowerie River,	—	—
Gamtoos River,	3325 CC	—
Kromme River,	3323 DD	—
Avontuur,	3323 CA	16 May 1822
Vlugt and	—	23 May 1822
Uplands (Knysna).	3323 CD	31 May 1822
Resided with George Rex at Knysna.	3423 AA	1 June–22 September 1822
Returned to Cape Town via Goukamma,	3322 DD/3422 BB	3–9 October 1822
Groen Vlei,	3422 BB	—
Zwart River (Swart River),	3322 AA	—
George,	3322 DC	12–20 October 1822
Great Brak River,	3422 AA	—
Caledon, where he met Dr. Thom, and	3419 AB	—
Genadendal.	3419 BA	27 October–27 November 1822
Arrived at Cape Town.	3318 DC	4 December 1822

and south-eastern parts of the Colony more thoroughly and also proceeded to the north-eastern Cape where he collected plants in the vicinity of Colesberg (Table 4). He again resided with George Rex at Knysna from 1 June 1822 to 22 September 1822 and eventually returned to Cape Town overland. On his return journey Bowie met Dr. George Thom (18 June 1789–11 May 1842), a missionary and minister of the Dutch Reformed Church at Caledon. Thom took a great interest in botany and sent specimens from South Africa to Prof. W. J. Hooker at the Glasgow University (Stirton, 1986).

Sir Joseph Banks, who initially convinced King George III to make funds available for the employment of collectors of foreign botanical material, died on 19 June 1820. Two years later a vote reducing by one half the sum available for such collectors was passed in the House of Commons (Smith, 1881). This meant that either Cunningham, an earlier exploring companion of Bowie in Brazil, had to be recalled from New South Wales, or that Bowie had to be recalled from the Cape. Apparently because of his intemperate habits and lack of perseverance in his collecting duties, it was decided that Bowie should be recalled. On 23 May 1823, six months after completing his fourth journey into the southern African interior, he sailed from Cape Town for England in the "Earl of Egremont". After briefly collecting at St. Helena, he arrived at London on 15 August 1823 (Hutchinson, 1946).

Bowie was now no longer employed by Kew and spent his days working on herbarium specimens collected during his visits abroad. At night he passed his time in public houses and there boasted of his adventures and encounters with wild animals at the Cape and in Brazil (Verduyn den Boer, 1929). These drinking bouts eventually resulted in Bowie becoming an alcoholic. He decided to settle in South Africa and to become a collector of objects of natural history. After four aimless years in England, Bowie finally sailed for the Cape in the "Jessie" in April 1827 (Ffolliot, 1981).

For the next 42 years Bowie, who never married, lead an unproductive life at the Cape. His attempts to take over the business of Villet and Son, who dealt in the export of natural history specimens, failed and his hope of becoming the curator of a botanic garden at the Cape was never realized (MacOwan, 1887; Gunn and Codd, 1981). Later he made an unsuccessful attempt to make a living from selling Cape bulbs and also failed to obtain land for establishing an experimental English nursery (Anon., 1970; Ffolliot, 1981).

By 1836, some nine years after having settled in Cape Town, he seems to have been employed as gardener and collector to Baron Carl von Ludwig of Ludwigs Garden in Kloof Street (Marloth, 1915; Stafleu and Cowan, 1983). This engagement lasted less than five years and, by 1841, he was again working independently and making a meagre living from horticultural tuition and inspection and from selling plants collected on field trips (Bowie, 1842). During the latter part of his life he was in poor health and, as an act of charity, was employed as a gardener by Ralph H. Arderne at his magnificent garden in Claremont, Cape Town (Gunn and Codd, 1981). James Bowie died on 2 July 1869 (not in 1853 as stated by Smith, 1881) and was buried in Cape Town. Specimens that Bowie collected at the Cape of Good Hope are kept at the British Museum (Natural History) and at Kew. Drawings of plants sent to England by Bowie are in the Kew collection (Hutchinson, 1946; Reynolds, 1982).

The Discovery of Aloe bowiea

Most of the novelties amongst the material which Bowie sent to Kew were described by Adrian Hardy Haworth (Stearn, 1939). Haworth (19 April 1768–24 August 1833), a contemporary of James Bowie, completed his training as a lawyer, but was more successful as a gardener-botanist. He was a leading authority on succulents and authored many publications on this subject. W. T. Stearn (1971) provides a more complete account of Haworth's contribution to our knowledge of succulent plants.

In October 1824 Haworth, who then resided at Queens Elm, Chelsea, described specimens of *Aloe bowiea* as *Bowiea africana.* In this article Haworth stated that the description was based on plants received shortly before from the Cape of Good Hope and that they were sent to Kew by "... Mr. Bowie, our gracious sovereign's most successful collector of succulent plants". However, the exact locality of the specimen(s) on which Haworth based the name *Bowiea africana* is not given. *Bowiea africana* is currently known as *Aloe bowiea* (Smith, 1983).

Almost 100 years after this species had been discovered, Schonland (1919) published a checklist of the phanerogamic flora of the divisions of Uitenhage and Port Elizabeth. According to Schonland (1919) Carl Peter Thunberg was the first botanist to have visited this region of southern Africa. However, in the subsequent list of collectors he does not mention Bowie as having collected in the south-eastern Cape and *A. bowiea* is not included in the checklist. Furthermore, this species has been overlooked by other investigators involved in floristic research in the south-eastern Cape (Ecklon, 1830; Britten, 1908; Drege, 1913). Also, *A. bowiea* is not included in systematic checklists available for areas in close proximity to localities where it is known to occur (Jessop and Jacot Guillarmod, 1969; Penzhorn and Olivier, 1974; Olivier, 1977, 1981, 1983; Lubke, 1983; Phillipson, 1987; Lubke and Van Wijk, 1988; Lubke et al., 1988; Van Wyk et al., 1988a, b). It can thus be safely assumed that this species is endemic to the eastern Cape and that it does not occur outside this region. Field investigations in the vicinity of Port Elizabeth and Uitenhage by one of us (G. F. Smith) confirmed that, in habitat, *A. bowiea* is represented by two populations only, a third colony having been extinguished recently. It is likely that Bowie visited these localities during his original collecting trips.

Of the four journeys which James Bowie undertook into the interior of South Africa during his initial stay at the Cape, only his third and fourth journeys took him as far afield as the south-eastern Cape. His third journey was, however, completed by 29 January 1821 (Table 3) and Obermeyer (1973) states that *A. bowiea* was first collected in 1822. At Kew there is also a plate of this species by Thomas Duncanson bearing the inscription "Received from Mr. Bowie in the year 1822 from the Cape of Good Hope" (Fig. 1). Duncanson served the Gardens for five years (1822–1826) and during this time he executed more than 300 drawings which now form part of the Kew collection. In 1826 he suffered a mental illness (Daniels, 1974). Since *A. bowiea* was collected and received at Kew in 1822 it could only have been collected on Bowie's fourth journey (Table 4). During the 1820's a sea voyage from the Cape to England took approximately two and one-half months so that Bowie had to have collected specimens of *A. bowiea* quite early in 1822 if it had to be established in cultivaton and had to attain the proportions as reflected in Duncanson's drawing. The most likely period during which Bowie collected *A. bowiea* thus seems to have been either 30 December 1821–18 January 1822 or 19 January 1822–26 February 1822. During these periods Bowie collected in the vicinity of Algoa Bay (Port Elizabeth) and Uitenhage, respectively (Table 4). Contrary to statements by Bond and Goldblatt (1984) and Court (1981) this species flowers mainly during the summer (southern hemisphere). Although *A. bowiea* bears an insignificant inflorescence it could have assisted in making a small and rare plant easier to locate.

In December 1826, two years after having described *A. bowiea* as *Bowiea africana*, Haworth submitted for publication a further article in which he described ten more succulents new to science (Haworth, 1827). Five of these species were sent by Bowie from South Africa. Haworth considered one of these plants to be a new species of *Bowiea* and named it *B. myriacantha*. James Bowie apparently claimed that in habitat the flowers of this species were always arranged in umbels. This was not the case for the specimens of *B. myriacantha* received at Kew and is an indication of Bowie's habit to provide inaccurate details of, if not their localities, then the morphologies of the plants he sent to Kew. *Bowiea myriacantha* was later transferred to *Aloe* L. and then to *Leptaloe* Stapf., but is currently accepted as a species of *Aloe* (Reynolds, 1982). Haworth (1827) also briefly amplified the description of *B. africana* with regard to leaf and floral morphology. Two years later this species, too, was transferred to *Aloe* (Schultes and Schultes, 1829) and, since the epithet

Fig. 1. Aloe bowiea Schult. & J. H. Schult. Reduced photograph of an unpublished painting by T. Duncanson at Kew, of Bowie's material. The inscription reads "Received from Mr. Bowie in the year

africana had already been occupied in *Aloe* (Reynolds, 1982) *B. africana* was renamed *Aloe bowiea.*

Eponymy

James Bowie was originally commemmorated in the genus *Bowiea* Haworth (1824). However, the latter generic name became a synonym for *Aloe* L. when Schultes and Schultes (1829) transferred the known species of *Bowiea* to *Aloe.* Although creating a later homonym for *Bowiea* Haworth, Hooker (1867) reinstated *Bowiea* for another liliaceous genus of small bulbous plants, the name *Bowiea* W. H. Harvey ex J. D. Hooker currently being conserved in favour of *Bowiea* Haworth (Voss et al., 1983). *Bowiea volubilis* W. H. Harvey ex J. D. Hooker was described from material sent to Kew by a Mr. Henry Hutton of Grahamstown who discovered this curiosity in the vicinity of the old Katberg convict station (MacOwan, 1887). Although Bowie only died in 1869, Hooker (1867) inexplicably states that *Bowiea* commemorates "... the late Mr. Bowie". More recently a second southern African species of *Bowiea* W. H. Harvey ex J. D. Hooker, *B. gariepensis* was described by Van Jaarsveld (1983, 1984).

Publications of James Bowie

According to Reynolds (1982) Bowie contributed numerous articles on a variety of botanical topics to the *South African Quarterly Journal* between 1829 and 1830. The following list of Bowie's publications is based on Bullock (1978) and Kerkham (1988). All Bowie's articles were published after his voluntary emmigration to South Africa in April 1827.

Bowie, J. 1829. *Indigenous plants, generally flowering in the months of October and November in the Cape District.* (Extracted from a communication read in the South African Institution, 30 September 1829.) P. 12. W. Bridekirk, Cape Town. The earliest guide to the Cape flora printed at the Cape.

———. 1830a. Sketches of the botany of South Africa. *S. African Quart. J.* 1: 27–36. (A list of 209 Cape plants.)

———. 1830b. On the species of *Aloe* and *Gasteria.* (Listed in the alphabetical index under "*Aloe,* genus, Botany".) *S. African Quart. J.* 1: 90–91. (Brief discussion of 3 *Aloe* species and 5 *Gasteria* species.)

———. 1830c. Remarks on the culture of exotic vegetables, adapted for the soil and climate of South Africa. *S. African Quart. J.* 1: 160–171, 293–304, 408–413. (A single article listed in the alphabetical index under Exotic vegetables.)

———. 1831a. A list of the most conspicuous plants blossoming in the month of June at Wynberg and its vicinity. *Cape of Good Hope Literary Gazette* 13: 160.

———. 1831b. A list of the most conspicuous plants blossoming in the month of July at Wynberg and its vicinity. *Cape of Good Hope Literary Gazette* 14: 172–173.

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———. 1842. Extracts of a letter from Mr. Bowie, late gardener to Baron Ludwig, of Ludwigsberg, Cape of Good Hope, to the Hon. W. H. Harvey. *J. Bot. (Hooker)* 1: 306–308.

Pritchard, S. F. 1836. *An alphabetical list of indigenous and exotic plants growing on the island of St. Helena.* Printed by G. J. Pike, 11 St. George Street. (This publication

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was corrected by Mr. James Bowie. Stafleu and Cowan [1983], however, lists Bowie as being a co-author.)

We have been unable to substantiate the existence of an article "Remarks on the advantages of having a Botanic Garden near Cape Town" by James Bowie which, according to Reynolds (1982), also appeared in the *South African Quarterly Journal.* Considering the numerous journeys that Bowie undertook into the interior of southern Africa, his written contribution towards our knowledge of the plants of this region is disappointing.

The Mary Gunn Library of the Botanical Research Institute, Pretoria, has in its possession six unique, unpublished volumes which give every indication of having comprised personal diaries and sketch and note books of James Bowie. With the exception of two volumes (A and E) they are undated and lack bibliographical notations. The pages of the volumes are unnumbered. The pagination given in brackets thus refers to the number of separate pages contained in the respective volumes. These volumes can be identified as follow:

A. "James Bowie London 1809". Contains pencil sketches of human faces and pen and ink drawings of miscellaneous plant species, some with descriptive notes. These drawings were probably made from cultivated specimens in England. This volume also contains what appear to be notes on historical events of the time (57 pp.).
B. No title. Undated. Contains notes on numerical notation and arithmetic and pen and ink and pencil sketches of miscellaneous plant species. These drawings were probably made from cultivated specimens in England (87 pp.).
C. No title. Ca. 1815. Contains pen and ink and pencil drawings of mostly unidentified plant species, and water-coloured sketches of, amongst others, an epiphytic orchid and *Gloriosa superba* L. It is evident from drawings of taxa such as Bromeliaceae that at least some of the sketches in this volume were made while Bowie collected in Brazil (92 pp.).
D. "Mr. James Bowie". Undated. Contains pencil and pen and ink drawings. Numerous drawings in this volume are of succulent Crassulaceae, Euphorbiaceae, Mesembryanthemaceae and Asclepiadaceae (76 pp.).
E. Numerical Catalogue of Plants. Botanic Garden Cape Town. 1850. A numerical list of plants collected by Bowie for cultivation. The numeration extends from 1 to 3010 but includes only about 900 entries. The origin of this volume is obscure and whether its entire contents is attributable to Bowie is doubtful (79 pp.).
F. Ensatae. Undated. Contains pen and ink and pencil drawings and water-colours of mainly Southern African Iridaceae. Brief generic and specific descriptions are supplied for some groups. Although this volume is undated the flimsy pages on which the drawings were made carry a watermark "J. Greene 1821" (217 pp.).

Discussion

James Bowie spent a total of almost 49 years in South Africa and during his initial stay (1816-1823) undertook four journeys into the interior. Although very little is known about his activities after his emmigration to the Cape Colony (1827) he no doubt travelled widely and was a member of many more botanical expeditions (Bowie, 1842). Apart from not having published much about his collecting trips and field experience in southern Africa, Bowie was notorious for providing insufficient and misleading details of the material which he collected, apparently for business reasons. An example is *Clivia nobilis* Lindl. (=*Imatophyllum aitoni* Hook.) which Bowie introduced into England at a time that Cape plants were in high fashion in Europe. He mentioned this species as having been collected from the Orange River, although its natural habitat is known to be in the vicinity of Grahamstown (Obermeyer, 1972; Duncan, 1985). This habit of Bowie has greatly detracted from the scientific value of his collections.

The taxonomic study of a group of plants such as the subfamily Asphodeloideae must necessarily include a study of the early botanical exploration in order to confirm the date and circumstances of the discovery and subsequent history of its constituent species. However, the only geographical information provided for the specimens of *Aloe bowiea* from which Duncanson prepared a plate, is that the plants were received from the Cape of Good Hope. Because of the limited distribution of this species it was possible to establish not only its most likely type locality but also its approximate date of discovery.

Some of the other *Aloe* spp. which Bowie introduced into England include: *A. aristata* Haw., *A. ciliaris* Haw., *A. gracilis* Haw. non Bak., *A. humilis* (L.) Mill., *A. microcantha* Haw., *A. mitriformis* Mill., *A. myriacantha* (Haw.) Schult. & J. H. Schult., *A. pluridens* Haw., *A. striatula* Haw., and *A. tenuior* Haw. Although it thus seems that at times Bowie was less than honest in ascribing localities to the plants that he collected in South Africa, he played a major role in the early botanical exploration of this country and contributed much to our knowledge of aloes and succulents in general.

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Additional notes on the taxonomic status and habitat of *Aloe bowiea* (Asphodelaceae: Alooideae)

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Abstract

Of the taxa which are major sources of taxonomic confusion in the subfamily Alooideae of the Asphodelaceae, *Aloe bowiea* Schult. & J.H. Schult. shines as a first amongst equals. For this species which was previously regarded as a constituent of *Bowiea* Haw. *non* Harv. *ex* Hook. and as the only species of *Chamaealoe* Berger, no comprehensive treatment exists which will allow easy access to the literature by anyone but a specialist on the group. This article attempts to bring together all the information known for *A. bowiea*. The taxonomic and nomenclatural histories of this species are reviewed in detail. A recent revision has shown that both *Bowiea africana* Haw. and *Chamaealoe africana* (Haw.) Berger should best be treated as synonyms of *A. bowiea*. The latter is a distinctive species of *Aloe* which does not warrant segregation at generic level. Its restricted geographical distribution in the eastern Cape Province, Republic of South Africa, is discussed with special reference to the phytogeography of the genus *Aloe* in this region.

Introduction

Aloe bowiea Schult. & J.H. Schult. (= *Bowiea africana* Haworth; = *Chamaealoe africana* (Haw.) Berger) of subfamily Alooideae, Asphodelaceae *sensu* Dahlgren *et al.* (1985), has a history of taxonomic confusion. Although having been known for more than 150 years, this plant remains taxonomically little known. This paper presents a synthesis of the taxonomic and nomenclatural information available for this species and discusses its geographical distribution and possible phylogeny.

A. bowiea has been referred to as *Chamaealoe africana*, albeit illegitimately, for more than 80 years. The latter name is therefore well-known and has unfortunately become deeply entrenched in various taxonomic treatments of the Alooideae (see next section for references). However, the name *C. africana* is nowadays generally regarded as one of the synonyms of *A. bowiea*. I support this point of view and the name *Chamaealoe*, which translates as "small aloe" (De Graaf, 1983), is used as a synonym for *A. bowiea* throughout this article. This species is a small, acauline, suckering plant that grows in dense groups (Figure 1). Its linear-subulate leaves are borne in a basal rosette and have small, white spots scattered mainly on the abaxial surfaces. The margins of the pale-green leaves are armed with soft, white prickles. The inflorescence, produced irregularly throughout the year, but with a peak in the summer months, is a laxly-flowered raceme with small greenish-white flowers (Figure 2).

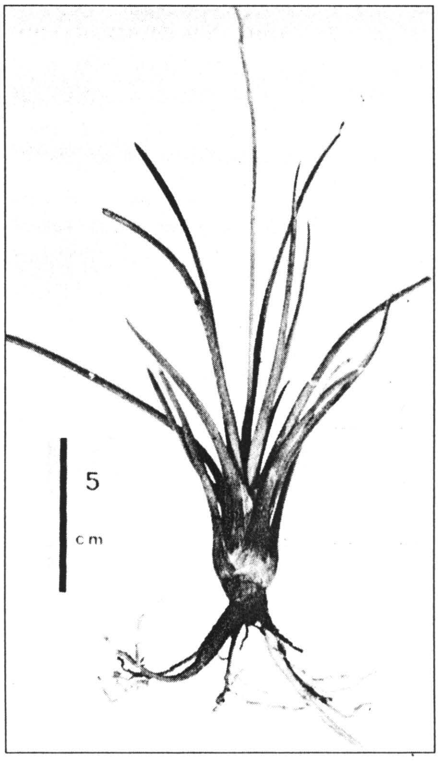

Figure 1. Growth form of *Aloe bowiea* showing rosette of linear-subulate leaves and fusiform roots. Specimen from Kariega.

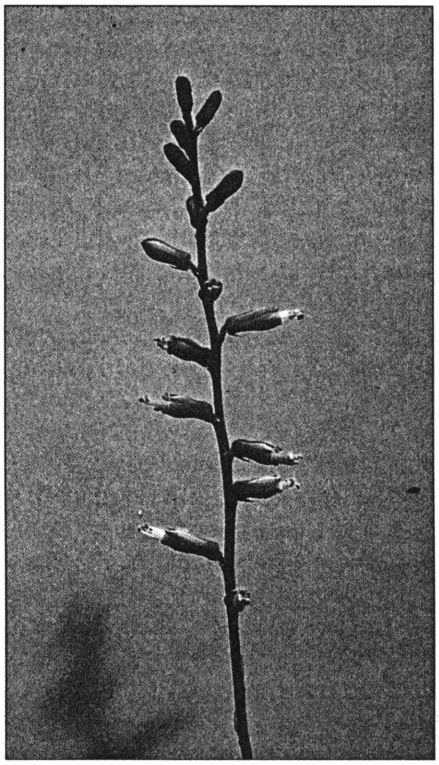

Figure 2. *Aloe bowiea* bears a laxly-flowered raceme with small, shortly pedicellate greenish-white flowers. The anthers and style are much exserted. Specimen from Coega.

The taxonomic history of *Aloe bowiea*

James Bowie (ca. 1789 - 2 July 1869), the son of a London seed merchant, took up employment with the Royal Botanic Gardens, Kew, in 1810 (MacOwan, 1887; Watson, 1897). Four years later Bowie and a colleague, Allan Cunningham, were sent to Brazil on what was to be Bowie's first collecting trip abroad. They collected in Brazil until 1816 when Cunningham was ordered to New South Wales, Australia, while Bowie was sent to collect at the then Cape of Good Hope (Smith, 1881; Lighton, 1973). In his capacity of official botanical collector for Kew Gardens at the Cape, Bowie succeeded Francis Masson (1741-1805) (Baker, 1880; Britten, 1920). Masson was an indefatigable plant collector (Bradlow, 1985; Desmond, 1987) and during two separate periods of residence at the Cape in the last quarter of the 18th century (1772-1775; 1786-1795) he contributed extensively to the discovery of southern African plants (Karsten 1958, 1959a, b, 1960, 1961).

During Bowie's initial residence at the Cape he undertook four extensive journeys into the interior. Since *Aloe bowiea* (= *Chamaealoe africana*) is known from only two populations in the south-eastern Cape (Uitenhage - Port Elizabeth and surroundings), only those journeys which took him to this area need to concern us here (Gunn & Codd, 1981). Bowie visited this region during both his third and fourth journeys, his first two expeditions only taking him as far east as Avontuur and Knysna, respectively (Hutchinson, 1946). His third journey lasted from early 1820 to 29 January 1821 and *A. bowiea* was collected a year later in 1822 (Obermeyer, 1973). Hence, Bowie's fourth journey (24 May 1821 to 4 December 1822) is implicated as the most likely expedition during which *A. bowiea* could have been collected. Table 1 presents an analysis of this journey, with special reference to visits by Bowie to the Uitenhage - Port Elizabeth (Algoa Bay) area during 1822.

Shortly after *A. bowiea* was received at Kew in 1822 an illustration, clearly identifiable with field populations, was prepared by Thomas Duncanson. For the specimens from which the plate was prepared, to attain the dimensions reflected in Duncanson's drawing, this species had to have been collected early during 1822. This is further supported by the fact that during the 1820's a sea voyage from South Africa to England took approximately two and one-half months. Also, *A. bowiea* flowers mainly during the summer (southern hemisphere) and, although it bears an insignificant inflorescence, it could have assisted in making this species easier to locate. The most likely date of collection of *A. bowiea* therefore is 30 December 1821 - 26 February 1822 (Table 1; visits 1 and 2 to Algoa Bay and Uitenhage, respectively).

On 23 May 1823, six months after having completed his fourth and final journey into the southern African interior undertaken during his initial stay at the Cape, Bowie returned to London aboard the *Earl of Egremont*. He arrived in London on 15 August 1823 and spent his days working on herbarium specimens collected during his visits abroad (White *et al.*, 1941). Four years later Bowie returned to South Africa of his own accord and until his death in 1869 made a precarious existence from private horticultural tuition and from selling plants collected on field excursions (Verduyn den Boer, 1929; Anonymous, 1970; Ffolliot, 1981). For additional biographical information on James Bowie and a detailed enumeration of his southern African travels and publications, Harvey (1838) and Smith & Van Wyk (1989) should be consulted.

Most of the undescribed material which Bowie sent to Kew between 1816 and 1823 were eventually formally described by Adrian Hardy Haworth (19 April 1768 - 24 August 1833) (Sheppard, 1901). Haworth, who trained as a lawyer, was also a competent self-taught naturalist and authority on succulents and published numerous articles and books on this topic. Stearn (1939, 1965, 1971), White and Sloane (1937), Nel (1953) and Glen (1975), Reynolds (1950) and Scott (1985) enumerates in more detail Haworth's contributions to our knowledge of succulent plants in general, the Stapelieae, *Gibbaeum* (Haworth) N.E. Brown, *Aloe* L. and *Haworthia* Duv., respectively.

In October 1824 Haworth described specimens of the taxon currently known as *Aloe bowiea* as *Bowiea africana*. In this article, which was published in the *Philosophical Magazine and Journal*, Haworth stated that the description of this species was based on specimens received from James Bowie from the Cape of Good Hope. However, the exact locality of the plant(s) which Haworth used in establishing the combination *B. africana* is not mentioned (Haworth, 1824). The name *B. africana* (Haworth, 1824) was accompanied by two Latin descriptions, a brief one for the new generic name viz. *Bowiea* Haworth and the other, more detailed, for its only constituent species, namely *B. africana*. At the generic level Haworth suggested that *Bowiea* should be classified between *Aloe* Linnaeus (1753) and *Haworthia* Duval (1809). Haworth also justifiably drew attention to the morphological similarities between *Bowiea* and *Haworthia*, especially with regard to characteristics of the leaves, scape and floral bracts. Furthermore, he likened the perigone of *B. africana* to that of *Aloe macra*. The latter combination is currently included in the synonymy of *Lomatophyllum macrum* (Haworth) Salm-Dyck *ex* Schult. & J.H. Schult. (Jackson, 1895). On vegetative and most reproductive morphological grounds *Lomatophyllum* Willd. is closely related to *Aloe*. However, it is characterized by having baccate fruit and not a dehiscent capsule as in *Aloe*. As is the case with many genera of

Table 1. Periods during which James Bowie visited the Uitenhage - Port Elizabeth (Algoa Bay) area during his fourth journey (24 May 1821 to 4 December 1822) into the southern African interior, with special reference to five visits paid to this region during 1822.

Number of visit	Duration of visit	Grid reference	Locality visited
1	30 Dec. 1821 - 18 Jan. 1822	3325 DD	Algoa Bay
2	19 Jan. - 26 Feb. 1822	3325 CD	Uitenhage
3	29 March 1822	3325 CD	Uitenhage
4	1-9 April 1822	3325 DD	Algoa Bay
5	10 April - 6 May 1822	3325 CD	Uitenhage

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Alooideae, controversy surrounds the discreetness of *Lomatophyllum* (Rowley, 1967, 1969, 1976a; Tjaden & Rowley, 1972; Bayer, 1972, 1974) and some recent authors have suggested the reduction of *Lomatophyllum* to the synonymy of *Aloe* (Rowley, 1980).

Three years after having described *A. bowiea* as *B. africana*, Haworth (1827) described, amongst others, five more South African succulents new to science. One of these he considered to be a new species of *Bowiea* and named it *Bowiea myriocantha*. The specific epithet alluding to its leaf margins which are armed with innumerable, minute, white teeth, was subsequently corrected to *B. myriacantha* (Schultes & Schultes, 1829), which accords with Article 73.1 of the *International Code for Botanical Nomenclature* (Greuter *et al.*, 1988). This Article clearly allows the correction of typographic and orthographic errors. In order to accommodate *B. myriacantha* in this genus, Haworth altered the generic character slightly and also provided an improved description of *B. africana* which he originally described in 1824. These generic modifications shifted the circumscription of *Bowiea* closer to that of *Aloe* and thereby suggested that it might be an artificial entity not worthy of recognition at generic level. This is substantiated by the fact that Haworth (1827) regarded the leaf, scape and bract features of *Bowiea* as more reminiscent of those of *Aloe* and not *Haworthia* as stated in 1824.

Two years later this point of view was brought to its full consequence when Schultes & Schultes (1829) transferred both *B. africana* and *B. myriacantha* to *Aloe*. Since the specific epithet *africana* had previously been validly published for a tall-stemmed species of *Aloe* (Miller, 1768), *B. africana* was renamed *A. bowiea*. In the case of *B. myriacantha*, the only other species of *Bowiea*, the specific epithet had not previously been used in *Aloe*, and it was correctly retained after the reclassification of this species in *Aloe*. The inclusion of *Bowiea* in the synonymy of *Aloe* was a justified step since *A. bowiea* and *A. myriacantha* are not immediately related and it is difficult to see why Haworth (1824, 1827) initially regarded them as warranting recognition in a separate genus, namely *Bowiea*.

It is noteworthy that Schultes & Schultes (1829) and Salm-Dyck (1834, 1836) also regarded *Haworthia* and *Gasteria* (Duval, 1809) as congeneric with *Aloe*, thus conforming to Linnaeus's original circumscription of this genus. Salm-Dyck (1834) proposed an elaborate system of infrageneric classification for this diverse group of rosulate, petaloid, leaf succulents and he treated the aberrant *A. bowiea* as the only member of section *Bowieae*. At the time of publication of this classification system Salm-Dyck (1834) had only *A. bowiea* at his disposal. Two years later he suggested the inclusion of *A. myriacantha* in the section (Salm-Dyck, 1836). Salm-Dyck regarded *Aloe* section *Bowieae* as transitional between *Haworthia sensu* Duval (1809) [*Parviflorae sensu* Haworth (1804)] and *Aloe sensu* Duval (1809) [*Grandiflorae sensu* Haworth (1804)]. Kunth (1843) supported this point of view while Endlicher (1836) and Bentham & Hooker (1883) in their synoptic works simply listed *Bowiea* Haw. as a synonym of *Aloe* L. In contrast to the rejection by Schultes & Schultes (1829) and Salm-Dyck (1834, 1836) of Duval's (1809) recognition of *Aloe*, *Gasteria* and *Haworthia* as separate genera, Baker (1880, 1896) upheld this subdivision. Furthermore, he also replaced the infrageneric sections of Salm-Dyck (1834, 1836) with subgenera and included both *A. bowiea* and *A. myriacantha* in Group 1 *Acaules* of *Aloe* subgenus *Eualoe*.

Berger (1905, 1908), however, maintained that *A. bowiea* represented an assemblage of characteristics that made it unique in the tribe Aloineae. Berger regarded *A. bowiea* as differing as much from *Aloe* as from *Haworthia* and *Astroloba* Uitewaal (1947) [= *Apicra* Haworth (1819) *non* Willdenow (1811)]. Characteristics of *A. bowiea* which lead Berger to this conclusion included its small, narrow leaves arranged in dense grass-like rosettes, slender inflorescence with short deltoid bracts and the subsessile flowers with exserted filaments. On the strength of the completely separate perianth segments, Berger placed *A. bowiea* closer to *Aloe* than to *Astroloba* or *Haworthia*. As the priority name, *Bowiea*, had since been allotted to a genus of Liliaceae/Hyacinthaceae (Hooker, 1867), Berger (1905) renamed the genus *Chamaealoe*. In accordance with the *International Code of Botanical Nomenclature* (Greuter *et al.*, 1988, Article 55) the specific epithet of the basionym namely *africana*, was reinstated for this monotypic entity. It should be noted that Berger validly published the combination *C. africana* in 1905 and not 1908 as claimed by Obermeyer (1973).

Berger (1908) provided a more detailed characterization and description of *Chamaealoe* and included diagnostic notes separating it from other genera of Alooideae. In this publication Berger regarded *Chamaealoe* as irreconcilable with *Haworthia* since the flowers of representatives of the latter are bilabiate while those of *C. africana* are regular. *Chamaealoe* could also not be included in *Astroloba* which has the sepals partly united. To Berger (1908) the main distinguishing features of *Chamaealoe* were its aberrant vegetative morphology and the much exserted stamens of the small, greenish-white, erect flowers which are laxly dispersed on an elongated raceme. On the basis of a combination of these characters, Berger (1908) thus confirmed his earlier removal of *Chamaealoe* from *Aloe* (Berger, 1905) where it had been classified since 1829 (Schultes & Schultes, 1829).

Chamaealoe, although published as a substitute name for *Bowiea* Haworth, was superfluous at the time of publication (*cf.* Farr *et al.*, 1979). Since *Bowiea* Haworth was included in the synonymy of *Aloe* in 1829 (Schultes & Schultes, 1829), Hooker (1867) revived this generic name for another small genus of hyacinthaceous plants. Hooker (1867) therefore created a later homonym for *Bowiea* Haworth and although this would have invalidated the use of *Bowiea* W.H. Harvey *ex* J.D. Hooker, the latter name is currently conserved in favour of *Bowiea* Haworth. This proposal to conserve was, however, only passed in 1935 (Special Committee for Phanerogamae and Pteridophyta, 1940; Dyer, 1941) at the 6th International Botanical Congress held in Amsterdam, that is, 30 years after the publication of the name *Chamaealoe* *africana*. The second sentence of Article 6.4 of *The International Code of Botanical Nomenclature* clearly states that: "A name which according to this Code was illegitimate when published cannot become legitimate later unless it is conserved or sanctioned" (Greuter *et al*., 1988). If Berger's (1905, 1908) generic concept is upheld a new name would therefore have to be given to what has been called *Bowiea* Haworth (*nom. rej*.) and *Chamaealoe* Berger (*nom. illeg*.).

In their benchmark publications on the flora of South Africa and *Aloe*, Marloth (1915) and Reynolds (1950) both upheld Berger's (1905, 1908) acceptance of *Chamaealoe*. However, this monotypic genus was not recognized in the synoptic works of Phillips (1926) and Goossens (1953) and was not given a generic number in Dalla Torre & Harms (1958). *Chamaealoe* was also excluded from both the 1901-1905 and 1906-1910 supplements of *Index Kewensis* (Prain, 1908; 1913).

On the basis of a numerical analysis of the genera of Alooideae [Aloineae *sensu* Hutchinson (1959)] and some related genera such as *Kniphofia* Moench, Rowley (1967) suggested an 88% similarity between *Aloe bowiea* (given as the monotypic *Chamaealoe*) and *Aloe albiflora* Guilluamin (1940). The latter, a miniature species from Madagascar, was originally assigned to *Aloe*, but was later transferred to the monotypic *Guillauminia* Bertrand (1956), a treatment ignored by Reynolds (1958, 1966). Rowley (1967) also suggested an 84% similarity between *C. africana* and *A. haworthioides* Baker (1887). Both *A. albiflora* and *A. haworthioides* (= *Aloinella haworthioides* (Baker) Lemeé) have histories of taxonomic confusion and parallel the generic classification of *A. bowiea*, at least in that they, too, were previously regarded as monotypes [cf. Rowley (1964, 1976b), Lemeé (1939) and Mathew (1974)]. Rowley (1967) also found *Chamaealoe* and *Aloe* (82%) and *Chamaealoe* and *Haworthia* (82%) as having high similarities, but lower than those obtained for *Chamaealoe* and *Guillauminia* and *Chamaealoe* and *Aloinella*, respectively. Rowley's (1967, 1969) investigations point out some of the inherent weaknesses in the generic concept in the Alooideae, especially where genera are recognized on the basis of combinations of reproductive characters which are not unique in the subfamily.

Although initially acknowledging the obvious affinities of *A. bowiea* with other dwarf species of *Aloe* (Lamb, 1960), Lamb & Lamb (1977) eventually regarded *Chamaealoe* as more closely related to *Haworthia*. In the latter publication they claimed that "... *Chamaealoe africana* ... is similar in plant appearance to *Haworthia bolusii*." Although Salm-Dyck (1834, 1836) considered *C. africana* to be transitional between *Aloe* and *Haworthia*, it is certainly more reminiscent of true *Aloe* species and its similarity to *H. bolusii* is due to convergence.

In an effort to establish a key to the genera of the Liliaceae *sensu lato* for inclusion in Dyer (1976), Obermeyer (1973) reduced *Chamaealoe africana* to the synonymy of *Aloe bowiea*. This point of view was supported by Jeppe (1977), Barkhuizen (1978) and Smith (1983). *A. bowiea* was eventually also taken up in Reynolds' Aloes of South Africa (cf. Hardy, 1982). Obermeyer (1973) suggested an affinity between *A. bowiea* and species of *Aloe* section *Anguialoe*. The five species classified in this section possess erect, short perianth segments and have the stamens and style much exserted. Although this is also true for *A. bowiea*, this species is a dwarf and does not exceed 130 mm. With the exception of *A. vryheidensis*, all the members of the section *Anguialoe* attain tree-like dimensions (Von Breitenbach, 1986), and they cannot be compared morphologically to *A. bowiea*.

Court (1981) still preferred to recognize *Chamaealoe*. However, she supported in large part the point of view of Obermeyer (1973) and suggested a possible affinity between *A. bowiea* and the Madagascan *A. conifera* H. Perrier, based mainly on the well-exserted stamens and short, regular perianth of both species. Despite these similarities Court (1981) upheld *Chamaealoe*, as did Jacobsen (1954, 1974, 1977, 1986) Ginns (1974), Rauh (1979) and Innes (1988).

Recently an evaluation of morphological characters was carried out with reference to *Aloe bowiea*. It is concluded that this taxon is best regarded as the only species of *Aloe* sect. *Graminialoe* Reynolds subsect. *Bowieae* (Haw.) G.F. Smith [cf. Smith (1990)].

Distribution of the genus *Aloe* and of *A. bowiea*

The distribution of *Aloe* extends from the southern tip of Africa to the Arabian Peninsula, including Madagascar and Socotra. The genus has recently been the subject of numerous scientific and popular scientific treatments (Beyleveld, 1973; Bornman and Hardy, 1971; Cutler *et al*., 1980; Groenewald, 1941; Harding, 1980; Jeppe, 1974, 1977; Judd, 1972; Lavranos, 1965, 1969; Peterson, 1969; Reynolds, 1954, 1966, 1982; Riley & Majumdar, 1979). Some members of this genus, notably *A. vera* (L.) Burm.*f.* is now widely cultivated in the Old and New Worlds for their medicinal properties (Bloomfield, 1985).

The determination of centres of diversity for large genera (10 or more species and infraspecific taxa) in the six major southern African biomes (Fynbos, Savanna, Grassland, Nama-Karoo, Succulent Karoo and Desert) showed that *Aloe* has no apparent southern African centre of diversity (Gibbs Russell, 1987). However, 44% of the southern African *Aloe* taxa occurs in Savanna (Gibbs Russell, 1987). Holland (1978) suggested the centre of origin for *Aloe* could have been in the highlands of southeast Africa whence the ancestral aloes radiated during the Tertiary. He also recognised eleven secondary centres of diversification, one of them the eastern Cape. In terms of the number of *Aloe* species in the eastern Cape (28 in the concept of the present author), it ranks fourth after the Transvaal (66), Madagascar (45) and East Africa (35). *A. bowiea* has a very restricted distribution and is known from only two localities in the eastern Cape centre of diversification (cf. Bond & Goldblatt, 1984). This species occurs in the Sundays River Scrub variation of Valley Bushveld (Veld Type 23 dii *sensu* Acocks (1988)) of the Uitenhage, Coega and Kariega regions in the south-eastern Cape (Figures 3,4 & 5). This vegetation type is a dense thicket confined mainly to the valleys of rivers which flow east and drain into the Indian Ocean.

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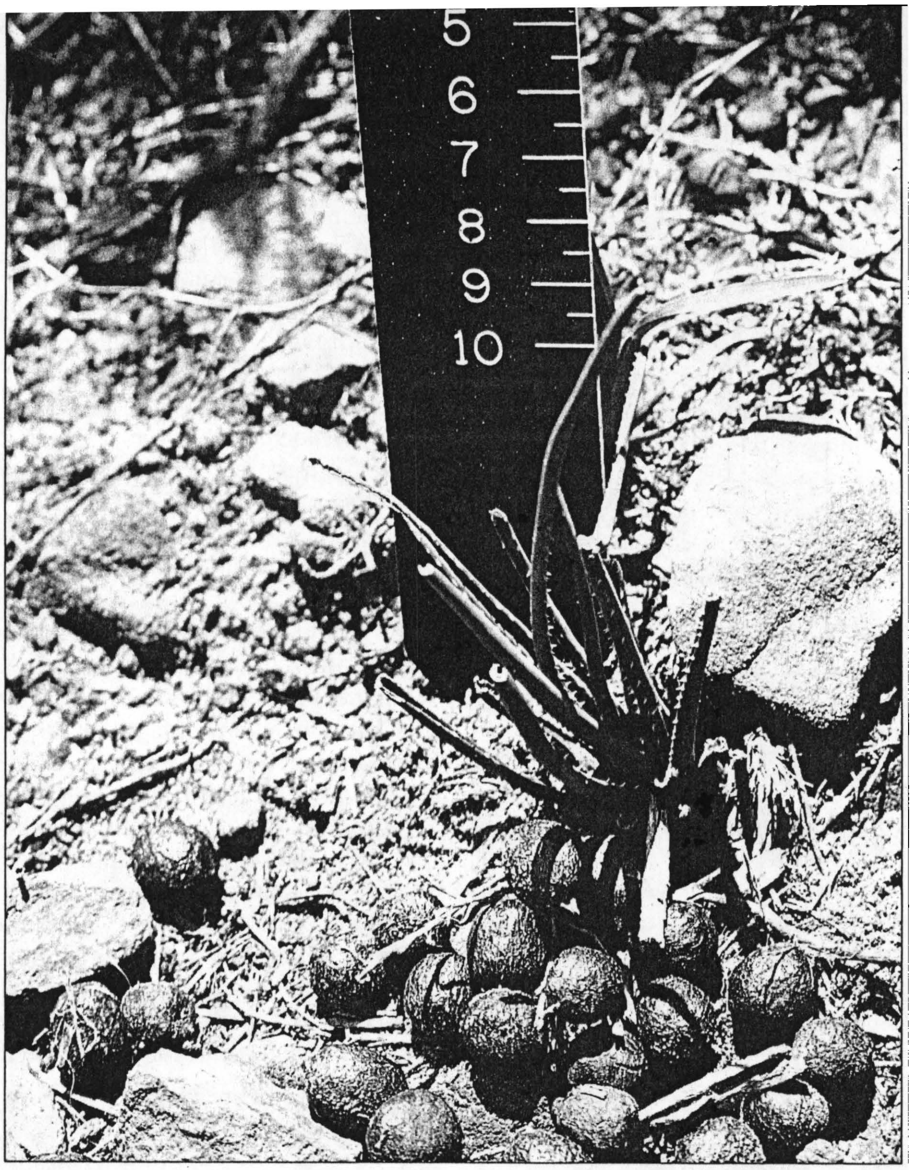

Figure 3. *Aloe bowiea* photographed near Kariega. Especially when not in flower, specimens can easily be mistaken for small tufts of grass (rule shows centimetre scale).

These valleys are relatively hot and dry in comparison to the intervening ridges.

Endemism in *Aloe* in the eastern Cape

In their discussion of endemicity in the eastern Cape, Gibbs Russell & Robinson (1981) list 6% of the *Aloe* taxa recognised by Reynolds (1950) (132 species and 23 infraspecific taxa) as being endemic to this region. (Reynolds did not consider *A. bowiea* to be a species of *Aloe*). An analysis of the distribution ranges of the 155 South African taxa of *Aloe* recognised by Reynolds (1950) revealed that nine are endemic to the eastern Cape, namely *A. africana* Mill., *A. broomii* Schonl. var. *tarkaensis* Reynolds, *A. gracilis* Haw., *A. humilis* (L.) Mill. var. *incurva* Haw., *A. humilis* var. *echinata* (Willd.) Bak., *A. striatula* Haw. var. *caesia* Reynolds, *A. tenuior* Haw. var. *densiflora* Reynolds, *A. tenuior* var. *decidua* Reynolds, *A. tidmarshii* (Schonl.) Muller ex R.A. Dyer. Everard (1985) lists only three species of *Aloe* as being endemic to the eastern Cape, namely, *A. africana*, *A. tidmarshii* and *A. bowiea*. On the other hand Cowling (1982, 1983) states that 5 of the 25 species of *Aloe* (excluding *Chamaealoe*) occurring in the eastern Cape are endemic. The discrepancies in the literature with regard to the number of *Aloe* taxa indigenous or endemic to the eastern Cape (Cowling 1982, 1983; Everard 1985; Gibbs Russell & Robinson 1981; Holland 1978) can be explained by the different delimitation of the eastern Cape by the different authors.

Since the publication of Reynolds (1950) more than 50 new species and varieties of *Aloe* have been described or newly accepted as members of the genus (Harding, 1980). Two of these are restricted to the eastern Cape: *A. bowiea*, about which Reynolds had misgivings, and which has since come to be accepted as a good species (Obermeyer, 1973; Smith, 1983) and *A. pictifolia* which was described by Hardy (1976) from the Patensie area (Laubscher & Swart, 1977). Of the taxa recognised by Reynolds (1950) as being endemic to the eastern Cape, the varieties of *A. humilis* and *A. tenuior* are no longer upheld. In addition, *A. gracilis* var. *decumbens* is currently included in the synonymy of *A. gracilis*, with the result that the ranges of distribution of the latter three species now extend beyond the limits set for the eastern Cape (Staff of the National Herbarium, 1986). These taxonomic changes bring to six the total number of *Aloe* species and infraspecific taxa endemic to the eastern Cape (Table 2).

Although few taxa or vegetation types are restricted to the eastern Cape (Gibbs Russell & Robinson, 1981), the diverse succulent flora present in the semi-arid river valleys and inland basins of this area (Court, 1981) represents an endemic centre for many karroid taxa (Cowling, 1983). For at least three genera classified in the subfamily Alooideae of the Asphodelaceae the eastern Cape is a centre of endemism, Cowling (1982, 1983) listing values of 33,3%, 55% and 29,9% for *Astroloba*, *Gasteria* and *Haworthia*, respectively. A pre-revision estimate of 14% of the succulent species of *Euphorbia* being endemic to the eastern Cape has also been reported (Court, 1988).

The origin of Aloe

Karroid taxa probably have a lengthy history in the eastern Cape (Cowling, 1983) and, at least for *Aloe*, this statement seems to be justified. Kamstra (1975) argues that the genus *Aloe* was fully developed by the early Jurassic (180 million years Before Present). In large part Holland (1978) supports this view and furthermore claims that the ancestral aloes originated in the highlands of southeast Africa some time before the complete sea invasion of the Mocambique Channel in the mid-Cretaceous (100 million years Before Present) (Flores, 1970; McElhinny *et al.*, 1976). Kamstra (1975) also provides evidence suggesting that the ancestor of the genus *Aloe*

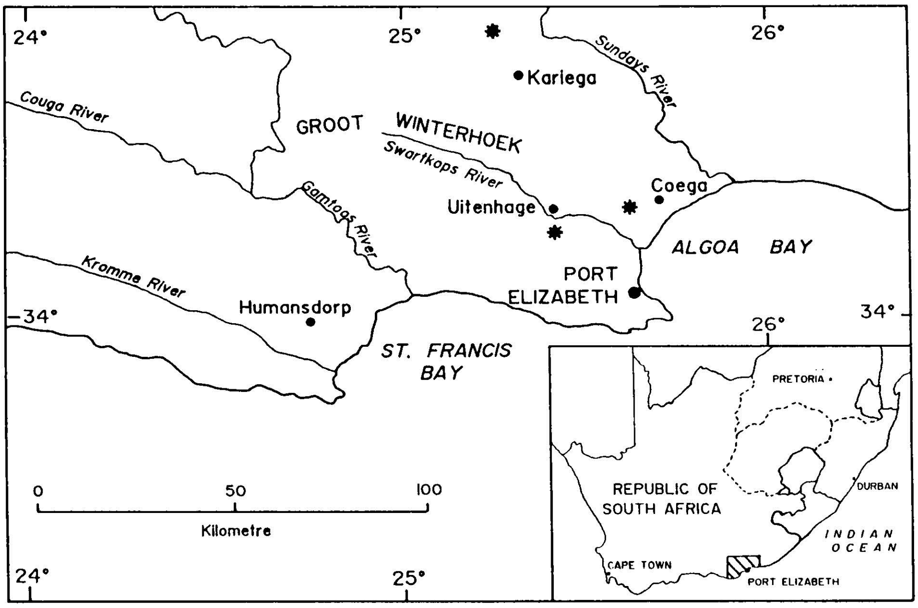

Figure 4. Map showing the restricted geographical distribution range of *Aloe bowiea* Schult. & J.H. Schult. The three localities where the species has been collected are indicated with stars.

was a small plant, probably some 150 mm high. This assumption is firstly based on the fact that other genera of the subfamily Alooideae contain species of relatively small stature, for example, *Astroloba, Chortolirion* and *Haworthia*. Secondly, this is also the case for members of the closely related subfamily Asphodeloideae of the Asphodelaceae [tribe Asphodeleae *sensu* Hutchinson (1959)] which have achieved a relatively wide Gondwana distribution, for example, *Bulbine* which also occurs in Australia and *Bulbinella* with an African-New Zealand distribution (Watson, 1986). Based on its small stature *Aloe bowiea* meets the requirements for being regarded as an old taxon within *Aloe*. However, amongst the smaller succulent-leaved species of *Aloe*, which also includes *A. aristata* Haw. *A. brevifolia* Mill. and *A. humilis* (L.)Mill., no unifying characteristics exist which might implicate them as possible progenitors for this genus. Also, the present distribution ranges of these taxa do not coincide with the southeast African centre of origin which Holland (1978) proposes for *Aloe*.

Currently there is very little phylogenetic basis for the interpretation of character states in *Aloe*, such as arborescent habit versus herbaceous habit, as either advanced or primitive. Holland (1978), for example, regarded arborescent forms as more advanced while Reynolds (1966) interpreted *Aloe suzannae*, the tallest of the Malagasy aloes as the most primitive. Furthermore, the flowers of *A. suzannae* are fragrant and nocturnally pollinated which, in *Aloe*, are considered to be advanced character states. This is supported by the fact that floral fragrance in *Aloe* is, with the exception of the African *A. modesta*, restricted to Malagasy species (Van der Riet, 1977). There is also evidence suggesting that, at least in some infrageneric *Aloe* taxa (for example series *Saponariae*), speciation still takes place in areas such as northern Natal and Zululand (Bayer, 1975; Reynolds, 1982). Of the genera of the Alooideae, both *Gasteria* and *Haworthia* contain relatively small species, many of which occur in the eastern Cape in large numbers. All the species of these genera have pronounced zygomorphic flowers, succulent leaves and show genetic variability (for example *H. cymbiformis* (Haw.) Duv. in the eastern Cape). These genera are most probably neoendemic derivatives from an aloeoid ancestor. *A. bowiea* grows sympatrically with *Gasteria* and *Haworthia* and also has zygomorphic flowers and, at least in aspect, is not unlike some species of *Haworthia*.

Although it appears that some succulents date from the Cretaceous (Holland, 1978), extensive radiation in the succulent flora presumably took place during the Oligocene (Goldblatt, 1978; Van Jaarsveld, 1987, 1989). One of the reasons advanced for the evolution of succulents during this epoch (37 - 26 million years Before Present) is that open, drier habitats became available for colonization (Deacon, 1983; Raven, 1983). Evolution usually takes place at a faster rate in these more arid climates (Axelrod, 1972; Speirs, 1980; Stebbins, 1952). The relatively dry climate and local terrain diversity in the eastern Cape thus provide the scenario for present-day speciation. Along with species of genera of the Mesembryanthemaceae (*Faucaria* Schwant., *Bergeranthus* Schwant., *Glottiphyllum*

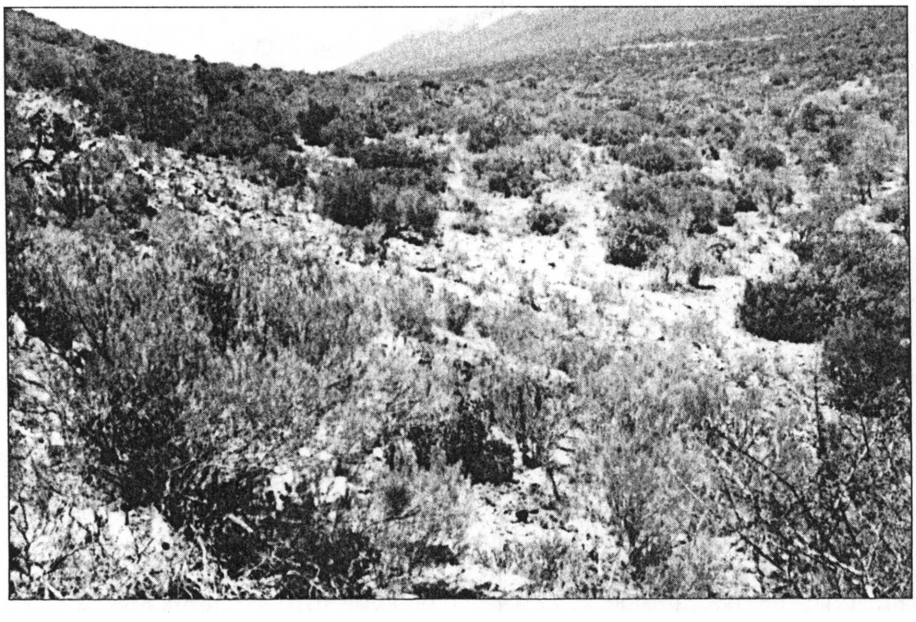

Figure 5. Sundays River scrub variation of Valley Bushveld vegetation [Veld Type 23 dii *sensu* Acocks (1988)] in habitat of *Aloe bowiea* at Kariega, eastern Cape Province. This locality is one of only two known for the species.

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Table 2. Species and infraspecific taxa of Aloe endemic to the eastern Cape.

Infrageneric classification	Taxon
Section *Graminialoe* Subsection *Bowieae*	*A. bowiea* Schult. & J.H. Schult.
Section *Aloe* Series *Longistylae*	*A. broomii* Schonl. var. *tarkaensis Reynolds*
Section *Aloe* Subsection *Humiles* Series *Echinatae*	*A. pictifolia* Hardy
Section *Aloe* Subsection *Prolongatae* Series *Macrifoliae*	*A. striatula* Haw. var. *caesia* Reynolds
	A. tidmarshii (Schonl.) Muller ex R.A. Dyer
Section *Pachydendron*	*A. africana* Mill.

N.E. Br.), Asphodelaceae (*Bulbine* Willd., *Gasteria* Duv., *Haworthia* Duv.), Crassulaceae (*Adromischus* Lem. *Crassula* L.) (Van Jaarsveld 1987) and Euphorbiaceae (*Euphorbia* L.) (White *et al.*, 1941), *Aloe bowiea* is most likely a product of recent speciation in the eastern Cape.

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Figure 6. Vally Bushveld vegetation (*sensu* Acocks 1988) in habitat of *Aloe bowiea* at Coega, eastern Cape Province. The species grows socially with *Aloe ferox* Mill. (centre foreground) and *Euphorbia ledienii.* Berger var. *lediennii* (arrowed).

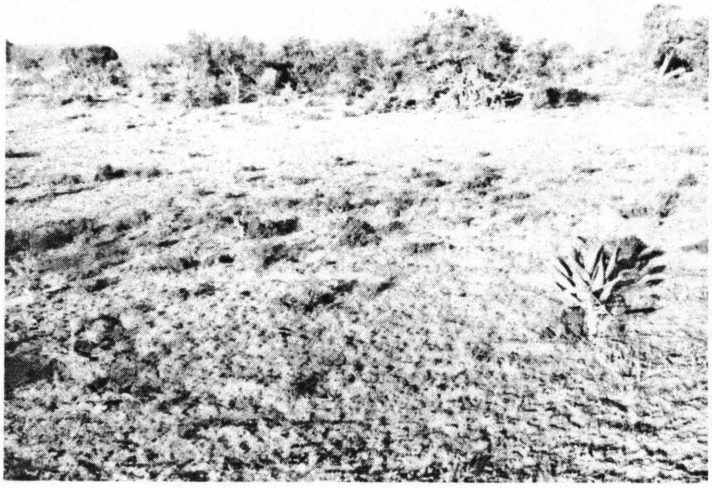

Figure 7. Degraded Valley Bushveld vegetation in habitat of *Aloe bowiea* between Uitenhage and Despatch, eastern Cape Province. *Aloe ferox* (right foreground) is common at this locality.

HISTORICAL REVIEW OF THE TAXONOMY OF *CHORTOLIRION* BERGER (ASPHODELACEAE: ALOOIDEAE).

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Abstract. The genus *Chortolirion* Berger was described 83 years ago, and has been variously combined with, and separated from *Haworthia* Duval. In the author's study of the smaller genera of the Alooideae, *Chortolirion* was found to be one of the most distinctive elements of the subfamily, and so is to be retained as a separate genus. However, its current status in the literature is, to say the least, confusing. This paper is intended as a long overdue synopsis of the taxonomic history of *Chortolirion*.

Introduction

Chortolirion Berger, a monotypic genus in the subfamily Alooideae of the Asphodelaceae *sensu* Dahlgren *et al.* (1985), has a history of taxonomic confusion and poor generic definition. Although having been known to botanists for many years, this entity is taxonomically little known. Several previous works have mentioned *Chortolirion* in passing (see next section for references), but these were largely of an incidental nature. To date there has been no synthetic treatment of all the taxonomic and nomenclatural information available for the genus. This article presents such a synthesis and discusses the taxonomic and nomenclatural history of *Chortolirion*. Whether or not *Chortolirion* is recognized as congeneric with *Haworthia* Duval, or as warranting acceptance as a segregate genus largely concerns generic delimitation. The aim of this article is not to discuss generic concepts in the Alooideae as a whole. The following is rather an annotated history of the relationship of *Chortolirion* with other Alooideae genera, with special attention to characters used to combine or separate them.

A study of the historic aspects of the naming, delimitation and circumscription of plant taxa provide insight into taxonomic groupings and genus and species concepts prevalent when these taxa were described. Unfortunately this aspect which forms a critical and integral part of any taxonomic revision is nowadays often neglected even though similar studies on certain taxa have often proved extremely useful, for example, Glen (1975) on *Gibbaeum* (Haworth) N.E. Brown (Mesembryanthemaceae), Schmid (1980) on *Heteropyxis* Harvey and *Psiloxylon* Thou. ex Tul. (both Myrtaceae), Cannon & Minter (1983) on *Hypoderma* De Candolle and *Lophodermium* Chevalier (two fungal genera in the Rhytismatales), Millar (1986) on *Pinus* Linnaeus subsection *Oocarpae* Little & Critchfield (Pinaceae), Källersjö (1988) on *Pentzia* Thunberg *sensu lato* (Asteraceae) and Alverson (1989) on *Quararibea* Aublet and *Matisia* Humboldt & Bonpland (both Bombacaceae). An analysis of these articles clearly shows that to use a classification properly, it helps to know what the categories within the classification system represent and how it was constructed. In a synopsis of all the information available on the baobab tree (*Adansonia digitata* L., Bombacaceae), Wickens (1982) mentions that there are surprisingly large gaps in our knowledge of this well-known species. If we know so little about this widespread and remarkable tree, it should be clear that even less information would be available for the lesser known constituents of the African flora. *Chortolirion* is no exception to this generalization.

Chortolirion, a perennial, deciduous herb with a subterranean bulb (Figure 1) is widely distributed mainly in the summer rainfall region of southern Africa. With short, annual, succulent shoots arising from a perennial underground bulb, *Chortolirion* presents a combination of a geophytic and succulent habit. The Afrikaans vernacular name of this spring flowering taxon is "kleinaalwyn" (Smith 1966), a direct translation of which would be "small aloe". The generic name *Chortolirion* means "from grasslands" or "heath lily" (De Graaf 1983) and alludes to the fact that it usually grows in grasslands (cf. Van Wyk & Malan 1988). When not in flower they can be mistaken for tufts of grass.

[INSERT FIGURE 1 NEAR HERE]

Taxonomic history of *Chortolirion* Berger

Baker (1878) published the first reference to a taxon which is currently classified in the genus *Chortolirion*. However, he described this species as *Haworthia angolensis* (Figure 2). The article in which this description appeared was published as a result of a systematic survey of specimens of the Liliaceae, Iridaceae, Hypoxidaceae and Haemodoraceae which were found in the Angolan section of the herbarium of Dr. Friedrich M.J. Welwitsch who had died six years earlier in 1872 (Bornman 1978). Contrary to the current point of view, Baker referred to the Liliaceae as an order and not a family. According to Baker's (1878) interpretation of the classification of this taxon which was discovered at Huilla, Angola, the genus *Haworthia* was no longer endemic to South Africa. The specific epithet meaning "of Angola" recognizes the intertropical distribution which the latter genus then enjoyed.

[INSERT FIGURE 2 NEAR HERE]

In 1880 Baker published a revision of the tribe Aloineae as part of his proposed monograph of the Liliaceae. In accordance with his original point of view, he again referred to the presence of a species of *Haworthia* in Angola. Baker (1880) included *Haworthia angolensis*, together with *H. angustifolia* Haw. and *H. chloracantha* Haw. at infrageneric level in the *Chloracanthae*. He gave the distinguishing characteristics of this subseries as: leaves coriaceous, denticulate and devoid of striations. Whilst this definition was very vague, these characteristics were in the broader sense reconcilable with the original description of *H. angolensis*.

Eight years later a further species was described which should have been included in the *Chloracanthae sensu* Baker (1880). This species and several other undescribed taxa were discovered by Dr. Rudolph Marloth, (1855--1931), chemist and amateur botanist, during an expedition to Griqualand West and Botswana (Engler 1888). After this expedition, which took place between December 1885 and February 1886, part of the material collected was sent to Adolph Engler in Germany. Engler studied the material which belonged to the Liliaceae and in 1888 he described, amongst others, *Haworthia tenuifolia* (Figure 3). In addition to drawing up the description, a sketch of this taxon was prepared by Engler and Pohl and published as Tab. 1 along with the article. Although this portrayal was highly stylised, it is undoubtedly identical to the species now known as *Chortolirion angolense* (Bak.) Berger, at least in respect of leaf and floral characteristics. However, no details of the root system were shown. The applicability of the specific epithet which means "with thin slender leaves" (De Graaf 1983) was clear from this illustration. In spite of the striking similarities between *Haworthia angolensis* and *H. tenuifolia*, Engler suggested that it should be classified in the subseries *Pallidae sensu* Baker (1880). This interpretation was inexplicable as *H. tenuifolia* did not, except for a pale green leaf colour, possess any characteristics which corresponded with those of the five species which Baker included in this subseries. The latter species were *H. translucens* Haw., *H. pallida* Haw., *H. pilifera* Baker and *H. minima* Baker.

[INSERT FIGURE 3 NEAR HERE]

Engler (1888) listed the type locality of *H. tenuifolia* as "Bechuanaland" (presently Botswana), "Manjering near Kuruman". Riley & Majumdar (1979) were of the opinion that Manjering was a wrong spelling for Maneering, which apparently does occur near Kuruman in the Cape Province. This means that this species might have been collected in the Cape Province and not in Botswana. It is noteworthy that Marloth, who discovered the specimens on which the name *C. tenuifolia* was based, claimed that a species of *Chortolirion* does occur in Botswana (Marloth 1915). Marloth travelled and collected widely in southern Africa and it is unlikely that he would have confused a locality in Botswana with one in the Cape Province. Furthermore, Prof. D.T. Cole (personal communication) and Dr. L.E. Codd (personal communication) have also collected specimens of *Chortolirion* in Botswana. There is, however, little doubt that Maneering is situated in the Cape Province and not Botswana (Leistner & Morris 1976). The confirmed existence of Manyeding not far from Kuruman further complicates the matter and it is unlikely that the correct type locality of *H. tenuifolia* will ever be established. Berger (1908) and Jacobsen (1954) gave the locality of *H. tenuifolia* Engler as "Southern Botswana: Kumuran: Manjering near Kubuman". Both Kumuran and Kubuman are orthographic errors as Engler (1888) used the correct spelling of Kuruman in the original description.

In 1891 Baker described the third taxon now included in the synonymy of *Chortolirion angolense*, viz. *Haworthia stenophylla* (Figure 4). However, this species must not be confused with *Aloe stenophylla sensu* Schultes & Schultes (1829). These two authors did not recognize *Gasteria* Duval and *Haworthia* Duval as warranting generic status and interpreted *Aloe* in the broad Linnaean sense. Their *Aloe stenophylla* was based on *Haworthia angustifolia* Haworth and is presently regarded as a synonym for the latter species (Bayer 1982a; Scott 1985). As Bayer (1982b) pointed out, Salm-Dyck (1836) endorsed the nomenclatural interpretation of *Aloe stenophylla* Schult. & J.H. Schult. (1829). However, Salm-Dyck published a colour plate and description of *A. stenophylla* in 1836 and not in 1849 as stated by Bayer (1982b) (cf. Stearn 1938).

[INSERT FIGURE 4 NEAR HERE]

Baker (1891) regarded *Haworthia stenophylla* as closely related to two taxa, namely *H. tenuifolia* and *H. saundersiae* Baker *nom. nud.* Apart from two further references to *Haworthia saundersiae* (Baker 1896; Berger 1908) no further information regarding this taxon is available. According to Berger (1908) the flowers of this "species" are pale pink. The impression is therefore created that Baker here unwittingly compared *Haworthia stenophylla* to a specimen with similar bulb and leaf characteristics only. *Aloe saundersiae* (Reynl.) Reynolds, a unique grass àloe from Zululand, was described in 1936. Although the pale pink flower colour which Berger indicated for *Haworthia saundersiae nom. nud.* corresponded with the pale pink flower colour of *Aloe saundersiae*, it is unlikely that these two species could have been confused with oneanother as early as 1891. However, the mystery of *H. saundersiae nom. nud.* was clarified whilst the present author recently worked through specimens of *Haworthia* kept at the Herbarium of the Royal Botanic Gardens, Kew. A sheet was found which has attached to it a water colour painting and three dried inflorescences of a species clearly belonging to *Chortolirion* (Figure 5). The following was written on the painting in an indistinct and unknown hand: "Haworthia Saundersia (sic) Baker Johannisberg (sic) Neh(?) 1880 Ms(?) K. Saunders copied from a drawing by Ms(?) Saunders 8/89 by Ms(?) Baker" [my question marks]. Two labels had also been attached to the sheet. The first, also in an unknown handwriting, reads: " 9 Haworthia 'Found near Steyn near Johannisberg (sic)' Collected on a trip to Johannisberg (sic) by Mrs K. Saunders of Tongaat Natal Recd. July 31. 1889." The second label is an undated Determinavit slip initialled by C.E. Moss, Professor of Botany (1917--1930) in the South African School of Mines and Technology, later University of the Witwatersrand, and reads: "The scaly bulb + the pronounced ciliation of the leaves on this drawing point to H. tenuifolia; but the inflorescence + flowers are much nearer H. stenophylla." The remarks made by Moss probably explain why Baker never validated his proposed combination *H. saundersiae*. *Chortolirion* displays a bewildering range of variation in most vegetative and some reproductive characters and a pinkish flower colour certainly does not constitute ground for the recognition of species in this genus. For additional biographical information on Katherine Saunders, who initially figured this plant, Gunn & Codd (1981) should be consulted.

[INSERT FIGURE 5 NEAR HERE]

Baker (1891) gave the locality of *H. stenophylla* as the grass covered slopes of the Saddleback Mountains near Barberton. Berger (1908) extended this distribution to include specimens collected at Steyn in the vicinity of Johannesburg (wrongly spelt Johannisberg). The latter were clearly the collections of Saunders referred to as *H. saundersiae nom. nud.* by Baker (1891).

It is significant that, once again, Baker (1891) did not regard *Haworthia stenophylla* as closely related to *H. angolensis* which he described in 1878. The similarities between these two taxa in regard to both leaf and floral morphology are striking when the original Latin descriptions are compared. Baker, who never visited South Africa, probably regarded the disjunct distribution of these species as adequate motivation for ignoring their morphological similarities.

The description of *H. stenophylla* Baker was accompanied by a sketch which was again, although stylised, strikingly reconcilable with specimens which are now known as *Chortolirion angolense*. Whilst discussing the synonyms of *Haworthia angolensis* Obermeyer (1973) initially mentioned *H. stenophylla* Bak. without reference to an author. This gives rise to the wrong impression that the name *H. stenophylla*, which Baker published in Hooker's Icones Plantarum in 1891, is attributable to Hooker.

In the Flora Capensis a monographic treatment of the genus *Haworthia* was provided (Baker 1896). In this work Baker divided the latter genus into three series and fourteen subseries. The two bulbous *Haworthia* species which were known from South Africa at that time, namely *H. stenophylla* and *H. tenuifolia*, were both placed in a new subseries *Linearifoliae*. In this work Baker suggested that his earlier *nom. nud., Haworthia saundersiae*, was a synonym of *H. stenophylla* Bak. Two years later Baker briefly discussed *Haworthia angolensis*, the remaining bulbous species of *Haworthia*, in the Flora of Tropical Africa (Baker 1898).

Thirteen years after the appearance of the description of *Haworthia stenophylla*, Baker (1904) published the description of another taxon which he regarded as closely related to *H. tenuifolia* (Figure 6). This species was published under the name *H. subspicata* and its locality was given as "Transvaal: Modderfontein". The plant on which the original description was based, was discovered by Paul Conrath (1861--1931), a chemist and assistant manager of the explosives factory at Modderfontein from 1895 to 1902 (Gunn & Codd 1981). Berger (1908) extended the distribution of this taxon to include a collection of Drège (probably I.L. Drège) from Nummejaarsprint, probably an orthographic mistake of Nuwejaarspruit, near the Orange River. Although the derivation of the specific epithet, which means "vestigially veined" is unclear (De Graaf 1983), it probably referred to the incomplete striated appearance on the abaxial leaf surfaces, a phenomenon observed in certain clones of *Chortolirion angolense*. No sketch or figure was included with the description of *Haworthia subspicata*. Baker clearly did not regard this species as closely related to *H. angolensis* which he described in 1878. The description of *H. subspicata* was Baker's final contribution to the circumscription of taxa currently included in the synonymy of *Chortolirion angolense*.

[INSERT FIGURE 6 NEAR HERE]

The period which followed was dominated by Alwin Berger (1871-1931), a German horticulturist and botanist, who, inter alia, revised the tribe Aloineae for Adolph Engler's Das Pflanzenreich (Berger 1908). Although Berger never had the opportunity to examine the South African succulents which he studied for many years (Uitewaal 1949) growing in their natural habitats, his taxonomic work was generally very accurate and some of his taxon circumscriptions are still accepted at present (Herre 1971).

Berger (1908) regarded the characteristics of *H. angolensis*, *H. tenuifolia.*, *H. stenophylla* and *H. subspicata* as irreconcilable with Duval's circumscription of the genus *Haworthia* and proposed that these four species be placed in a separate genus, *Chortolirion*. The main reason advanced by Berger (1908) for this proposal was the presence of an underground bulb in these species. He further stated that their growth pattern differed markedly from that of *Haworthia* species in general, and especially in regard to the deciduous nature of their leaves as well as in certain floral and fruit characteristics. In the latter two instances he particularly stressed the fact that both the distal part of the seed capsules (Figure 7) as well as the styles and developing seed capsules were always attenuated.

[INSERT FIGURE 7 NEAR HERE]

In January 1913 Moritz Kurt Dinter (1868--1945), a well-known German botanist who undertook several study expeditions to South West Africa, discovered a fifth species which belongs to *Chortolirion* Berger. In 1914 he described it as *C. bergerianum* thereby honoring Alwin Berger who distinguished this genus from *Haworthia*. The type locality of the species was given as the farm "Voigtland", 29 km to the east of Windhoek (Dinter 1914). To distinguish *C. bergerianum* from *C. tenuifolium* (Engl.) Berger and *C. subspicatum* (Bak.) Berger, Dinter pointed out that the leaf edges of the firstnamed taxon were finely serrated, a phenomenon which, according to him, was not found in the two lastnamed taxa. He differentiated between *C. angolense* (Bak.) Berger and *C. bergerianum* on the ground that the latter taxon bore brownish-white flowers in contrast to the reddish-brown flowers of *C. angolense*. *C. stenophyllum* (Bak.) Berger differed from *C. bergerianum* in that the pilose abaxial leaf surface which apparently was present in *C. stenophyllum*, did not occur in Dinter's species. He also stated that the leaves of *C. bergerianum* were in no way articulated --- a phenomenon found in all four other species of *Chortolirion* (Dinter 1914).

With the exception of Jacobsen (1954, 1974, 1977), Riley & Majumdar (1979) and Court (1981) who were aware of the description of *C. bergerianum*, this taxon was ignored by most of the taxonomists who paid attention to the tribe Aloineae. Even Obermeyer (1973) neglected to mention *Chortolirion bergerianum* M.K. Dinter and limited her discussion to the four *Chortolirion* species mentioned by Berger

(1908). In this revision Obermeyer (1973) regarded *Chortolirion* as synonymous with *Haworthia*. In contrast to the latter point of view, Marloth (1915) and Farden (1934) accepted Berger's proposed new genus, *Chortolirion*, and listed in it the same four species that Berger had proposed.

In February 1943 Mr. B. Meintjes collected specimens of *Chortolirion stenophyllum* against the south-eastern slopes of North Cliff Ridge in Johannesburg. An excellent illustration of this plant, executed by Edith K. Burgess, appeared the next year (Dyer 1944). A whole plant was shown together with detailed sketches portraying both the leaf and floral morphology. Dyer (1944) used this portrayal of C. *stenophyllum* as basis for the discussion of the natural variation found amongst the four species which Berger classified in *Chortolirion*. He was therefore the first to propose a reduction in the number of species in *Chortolirion*. To substantiate his statement he drew attention to the great morphological variation which was found amongst individuals of the same species in the genus. According to Dyer the interspecific differences between *C. stenophyllum* and *C. subspicatum* on which first Baker and later Berger recognized two separate species, should be reconsidered with the possible acceptance of the latter taxon as a synonym of the former.

Uitewaal (1899--1963), well-known Dutch botanist and expert on succulents, also published several articles on the tribe Aloineae. He supported the generic classification of the four species which Berger (1908) placed in *Chortolirion* (Uitewaal 1947). The thin leaves with their enlarged bases and articulated appearance were mentioned by Uitewaal (1947) as characteristics irreconcilable with the generic delimitation of *Haworthia*. He also drew attention to the superficial floral similarities which exist between these two genera.

In an effort to establish a key for the family Liliaceae which could be included in Dyer (1976), Obermeyer (1973) decided that *Chortolirion* Berger could not be afforded separate generic status. This decision was based on the apparent floral resemblances which exist between *Chortolirion* and *Haworthia* (Figure 8). She also drew attention to the fact that the thin, narrow leaves and bulbous bases of the species which had been included in *Chortolirion* by Berger (1908) resembled the vegetative morphology of *Haworthia graminifolia* G.G. Smith. She regarded the presence of a bulb in *Chortolirion* as insufficient motivation for the creation of a separate genus. She also claimed that the short terete style was clearly distinguishable from the ovary during the early flowering stage and that these two structures thus did not coalesce. She attributed the presence of acuminate ovaries and capsules in *Chortolirion* to the fact that the distal ovules were infertile and stated that this phenomenon was also noted in other species of *Haworthia*. These were, however, not mentioned. Rowley (1972) expressed the opinion that *Chortolirion* was closely related to the section *Fusiformes* W.F. Barker of the genus *Haworthia*. *H. graminifolia* G.G. Smith, the taxon which Obermeyer (1973) compared with *Chortolirion* Berger, was also included in this section (Jacobsen 1977, 1986). Rowley (1972), however, offered no further evidence in support of this apparent resemblance between the abovementioned species. Obermeyer (1973) further claimed correctly that the differences on which Baker (1896, 1898) and later Berger (1908) based the four species in the genus *Chortolirion*, provided insufficient evidence for the recognition of more than one species. Bayer (1972) had also stated that it would be a logical step to reduce *Chortolirion* Berger from a genus consisting of five species to a monotype. On the ground of this formal taxonomic proposal by Obermeyer (1973) *H. tenuifolia*, *H. stenophylla* and *H. subspicata* were placed in synonymy under *H. angolensis*. It is significant that in her discussion of the synonyms of the latter species, Obermeyer did not mention *Chortolirion bergerianum*.

[INSERT FIGURE 8 NEAR HERE]

Bayer (1974, 1975) argued that the genus *Haworthia* could not be accepted as being uniform. He recognizes the latter genus as consisting of three clearly distinguishable subgenera. This interpretation allows the inclusion of *Chortolirion* in *Haworthia* only if due note is taken of the differences within *Haworthia*. Although Scott (1985) rejected Bayer's (1974, 1975) subgeneric approach to the genus *Haworthia*, he supported the recognition of *Chortolirion* as a genus in its own right. Court (1981) supported the generic approach which Bayer (1974a, 1975) proposed and recognized the genus *Chortolirion* as monotypic with *C. angolense* the only species. Fabian and Germishuizen (1982), however, supported Obermeyer (1973) and classified this taxon as *H. angolensis*. Rowley (1980) accepted the approach which Obermeyer (1973) followed only in part since he regarded *Chortolirion* as synonymous with *Haworthia*, but recognized the generic status of *Astroloba*. Obermeyer (1973) preferred to accept *Astroloba* as a synonym of *Haworthia*. In their synoptic works Dyer (1976) and Gibbs Russell *et al.* (1984, 1985) supported the approach that Obermeyer (1973) followed. Phillips (1951), however, still recognized the generic status of *Chortolirion*. Jacobsen (1977) and Riley & Majumdar (1979) did not accept the morphological resemblances which exist amongst the *Chortolirion* species as pointed out by Obermeyer (1973). In strict accordance with the traditional generic approach (Berger 1908), they interpreted *Chortolirion* as a genus with five species.

Summary

This analysis of the taxonomic history of *Chortolirion* revealed that the criteria previously used to distinguish five species in the genus, represents nothing more than natural variation in the vegetative morphology of a widespread species more or less restricted to the summer rainfall region of southern Africa. A multidisciplinary revision of taxa of *Chortolirion*, with as many populations represented as possible was recently carried out. The revision has shown that *Chortolirion* warrants recognition as a monotypic genus, with *C. angolense* the only species.

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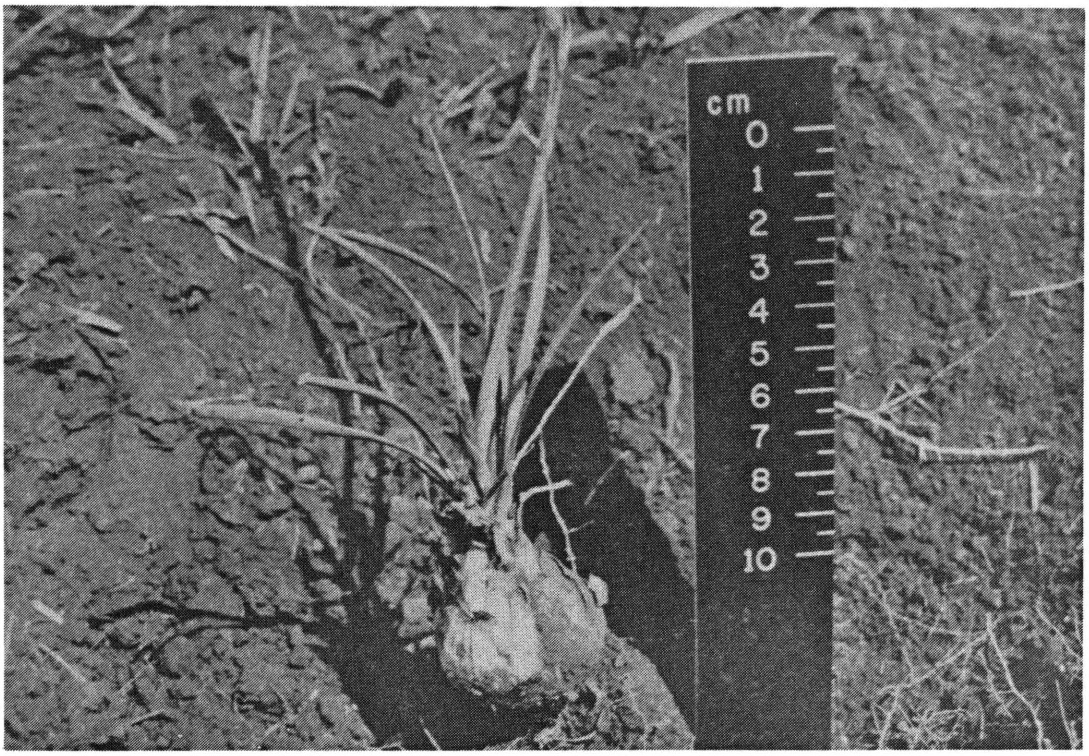

Figure 1. Growth form of *Chortolirion angolense* in habitat in grassland at Potchefstroom, south-western Transvaal. The soil has been removed to show the bulb morphology.

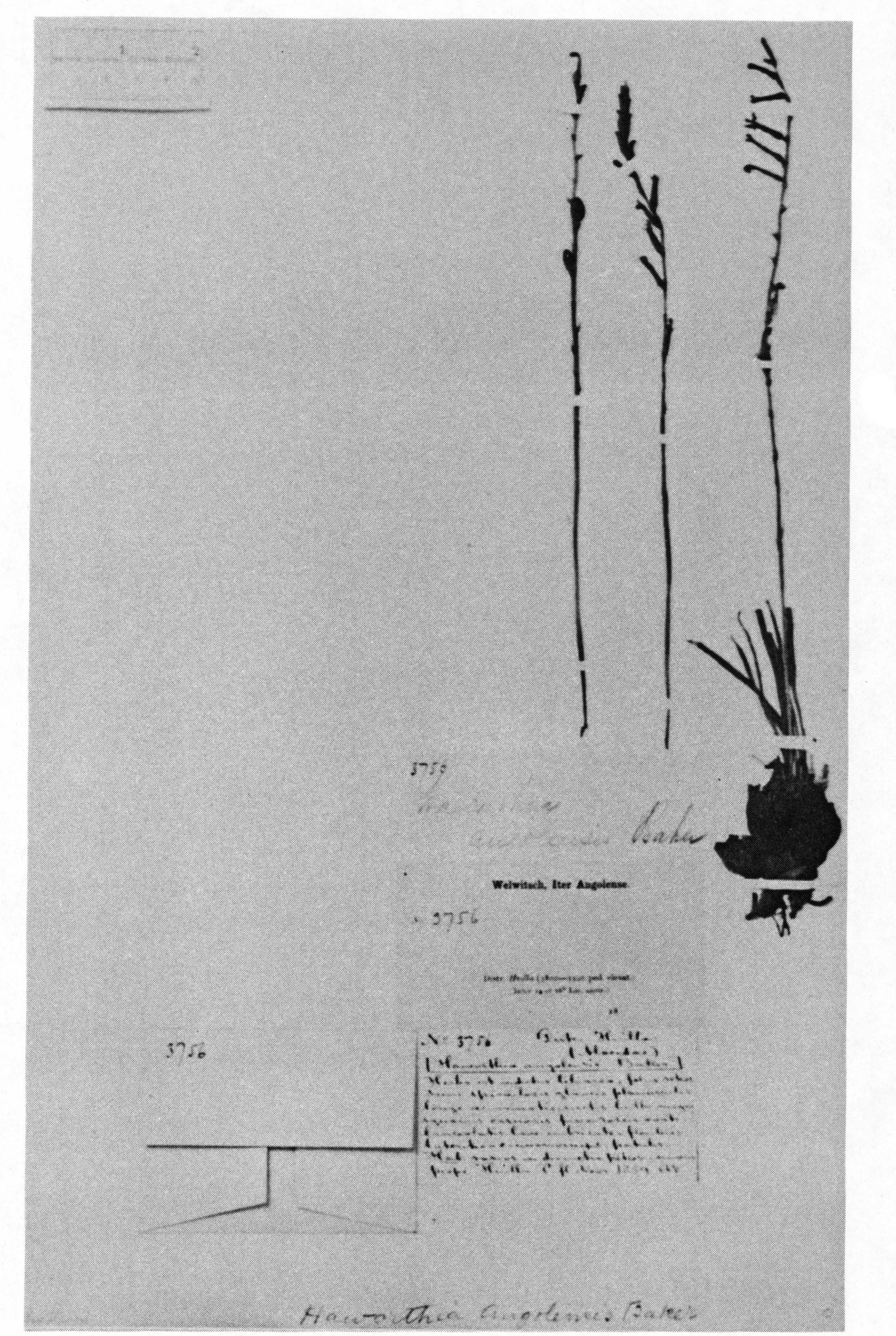

Figure 2. Type specimen of *Haworthia angolensis* Baker. [*Welwitsch 3756*, Herbarium of the British Museum (Natural History) (BM)]. Reproduced with permission.

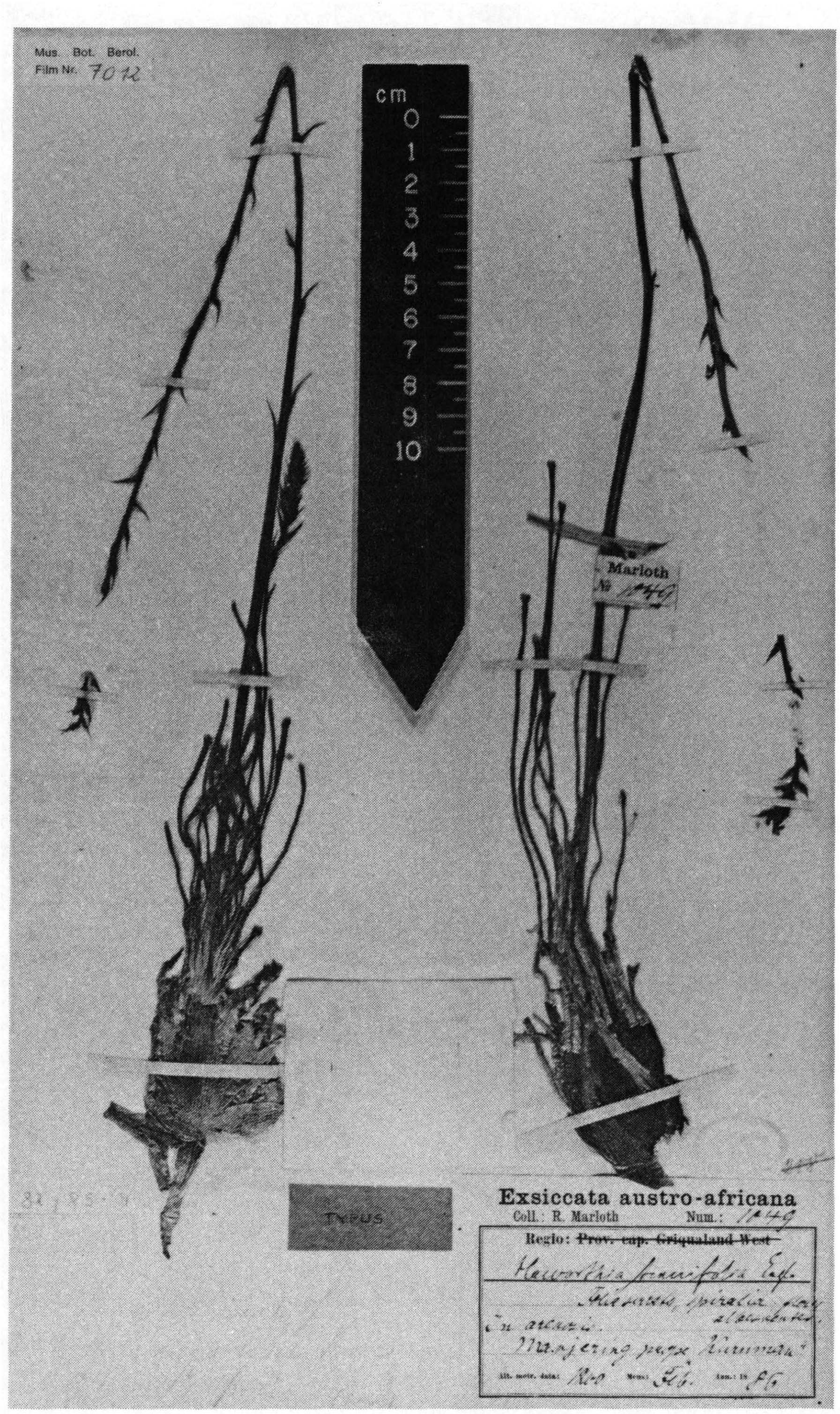

Figure 3. Type specimen of *Haworthia tenuifolia* A. Engler. *[Marloth 1049,* Herbarium of the Botanischer Garten und Botanisches Museum Berlin-Dahlem (B)]. Reproduced with permission.

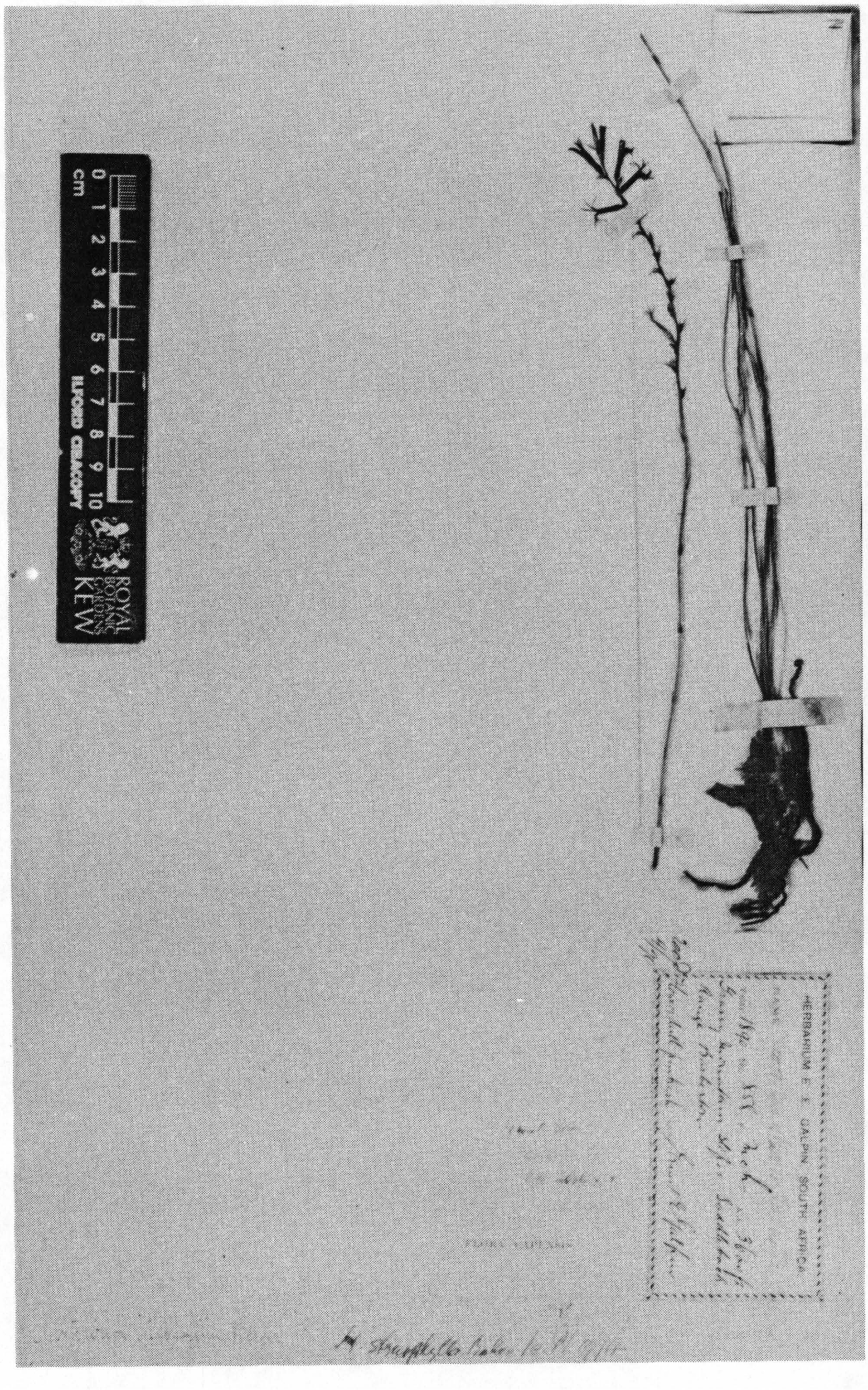

Figure 4. Type specimen of *Haworthia stenophylla* Baker. [*Galpin 858,* Herbarium of the Royal Botanic Gardens, Kew (K)]. (c) RBG, Kew.

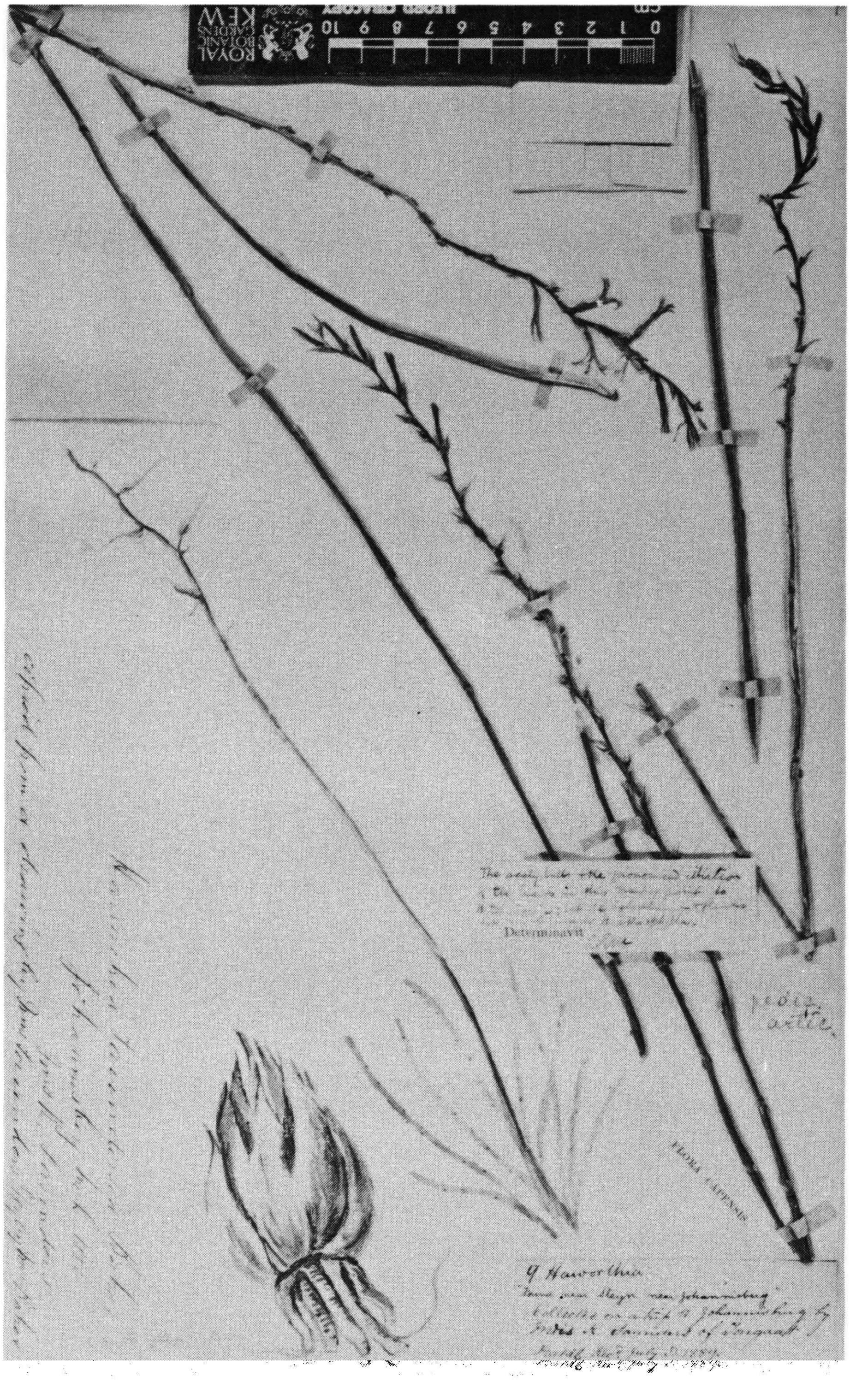

Figure 5. Specimen of *Haworthia saundersiae nom. nud.* kept at K. (c) RBG, Kew. (See text for explanation).

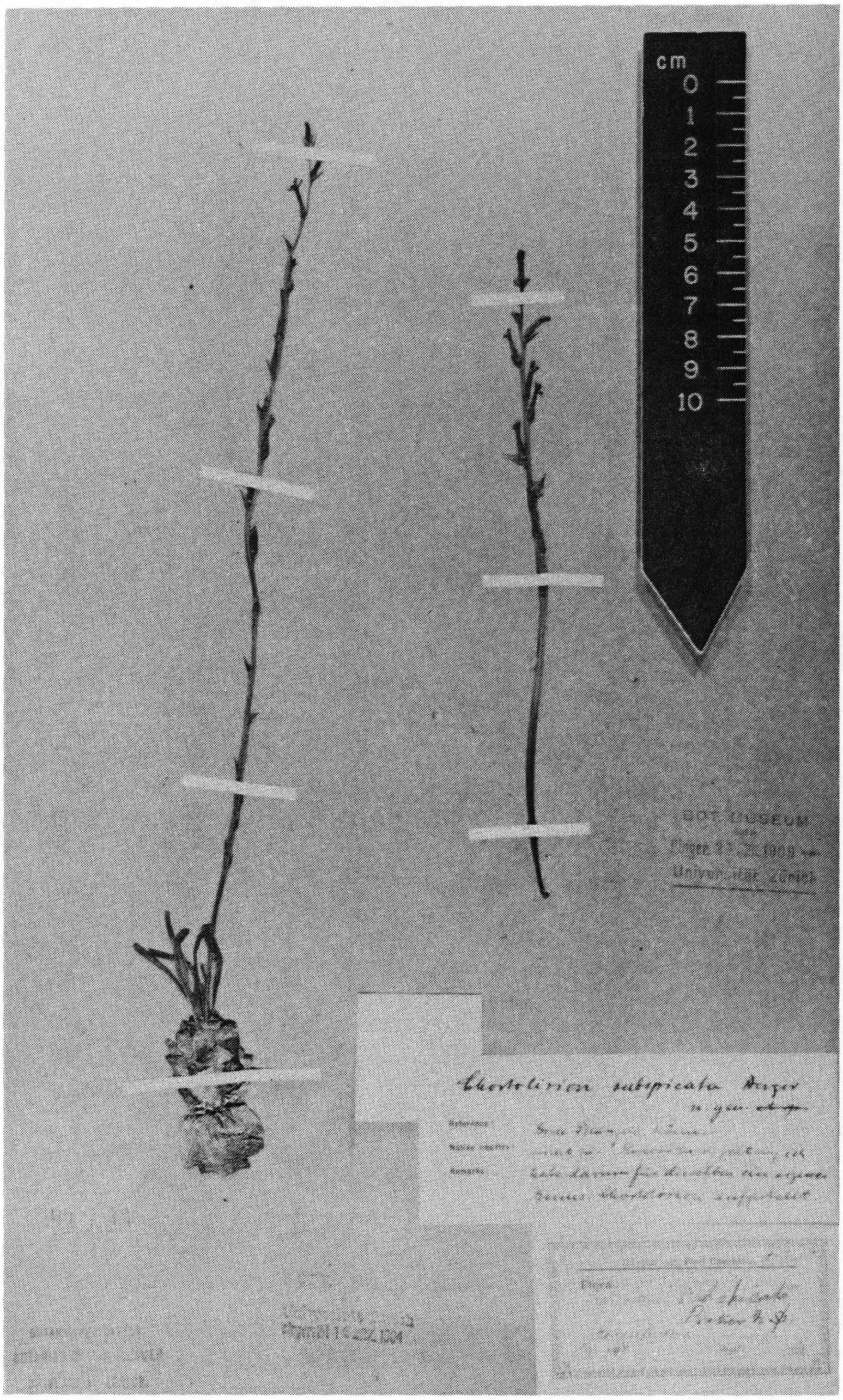

Figure 6. Type secimen of *Haworthia subspicata* Baker. [*Conrath 645,* Herbarium of the Institut für Systematische Botanik der Universität Zürich (Z)]. Reproduced with permission.

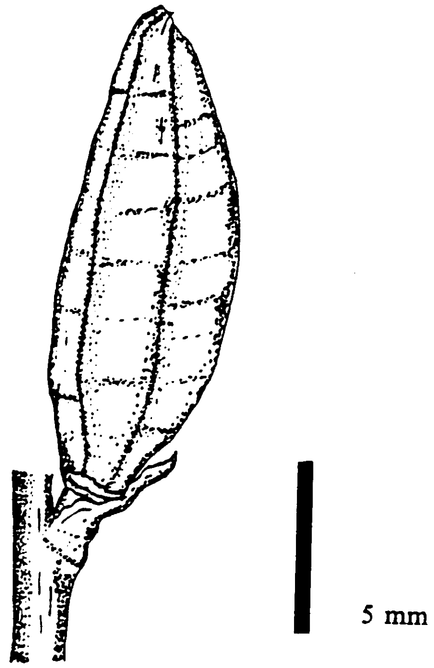

Figure 7. Acuminate capsules of *Chortolirion angolense*. (Specimen from Pretoria).

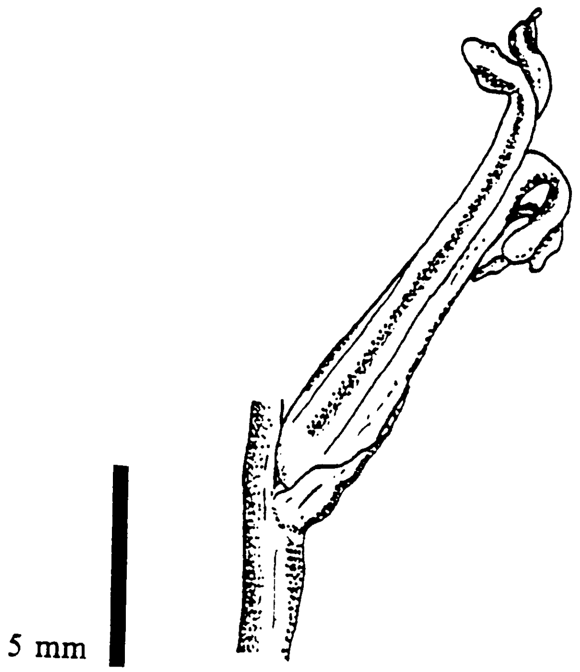

Figure 8. Single flower of *Chortolirion angolense*. (Specimen from Pretoria).

Taxonomic history of *Poellnitzia* Uitewaal, a monotypic genus of Alooideae (Asphodelaceae)

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Abstract

The genus *Poellnitzia* Uitewaal was described 51 years ago and have been variously combined with, and separated from *Aloe* L., *Apicra* Haworth *non* Willdenow, *Haworthia* Duval and *Astroloba* Uitewaal. In the author's study of the smaller genera of the Alooideae, *Poellnitzia* was found to be one of the most distinctive elements of the subfamily, and so is to be retained as a separate genus. However, its current status in the literature is, to say the least, confusing. This paper reviews briefly the taxonomic history of this monotype.

Introduction

Poellnitzia rubriflora (L. Bol.) Uitewaal is a low-growing, caulescent, succulent herb. Stems can reach a length of some 250 mm and are densely leaved. The ovate leaves are pungent-acuminate and up to 40 mm long (Figure 1). The inflorescence, produced during the summer months, is an unbranched raceme and bears red to brightly orange flowers in secund fashion. *P. rubriflora* has a restricted distribution in the Robertson and Bonnievale districts of the south-western Cape Province of South Africa. This region receives its precipitation mainly during the winter months whilst the summer months are hot and dry. *P. rubriflora* grows in a fairly arid region and shares its range of distribution with a number of other succulent plant species (Figure 2).

In terms of conservation status Hall *et al.* (1980) and Hall & Veldhuis (1985) list *P. rubriflora* in the category **indeterminate.** This conservation status category is defined as one for plants that are known to be either endangered, vulnerable or rare, but due to lack of study, cannot yet be placed convincingly in one category in preference to another.

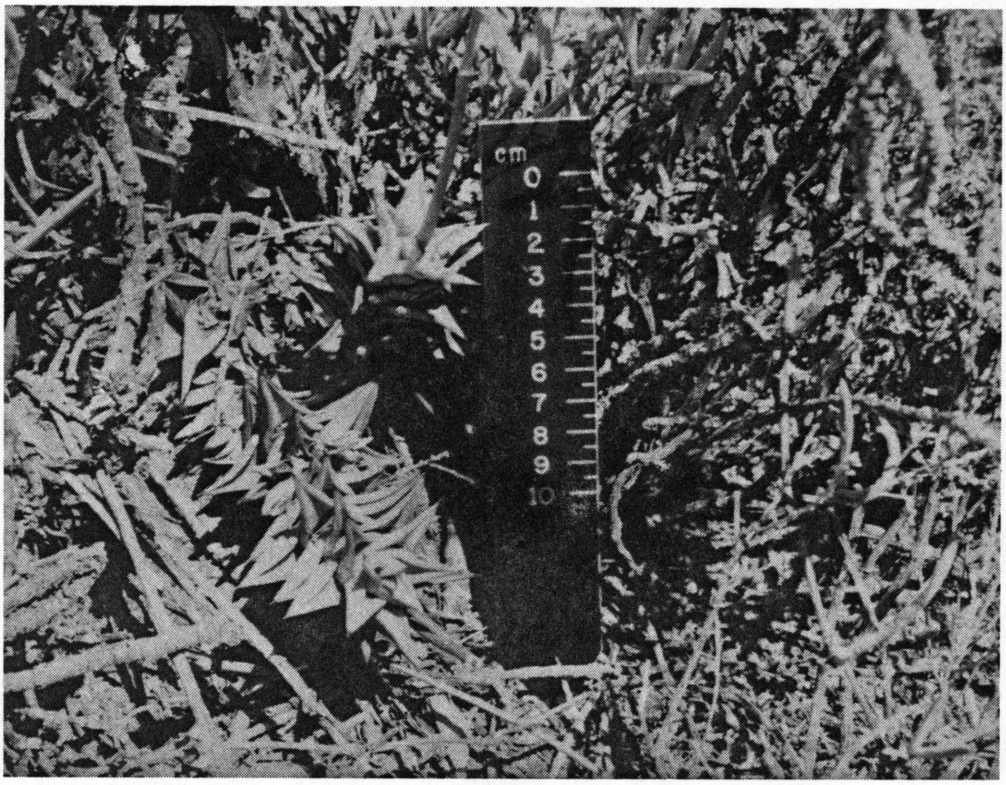

Figure 1. *Poellnitzia rubriflora* in habitat at Langverwacht near Bonnievale, south-western Cape Province. The leaves are usually glaucous-green but turn brown in the sun.

The genus name *Poellnitzia* honours Dr. Joseph Karl Leopoldt Arndt von Poellnitz (4 May 1896 – 15 February 1945). He was a German agriculturist and botanist and had a general interest in succulent plants, particularly the tribe Aloineae [*sensu* Hutchinson (1959)]. As a child Von Poellnitz suffered from scarlet fever and subsequently from poliomyelitis. Although regaining sufficient use of his legs to walk again with difficulty, he also suffered disturbance of eye sight, hearing and speech which he could not get rid of (Bayer 1982). Both Von Poellnitz and his only daughter died tragically in bombing raids during World War II. Von Poellnitz cultivated specimens on which his descriptions of new taxa were based at the family estate at Oberlödla near Altenburg, Thürigen. Unfortunately he prepared few herbarium specimens and the application of names published by Von Poellnitz present many difficulties to taxonomists. For additional biographical information on Von Poellnitz, Stafleu and Cowan (1983) should be consulted. The typification of some species names published by Von Poellnitz have been discussed by Bayer (1982). Selections of his publications are enumerated by Bullock (1978) and Newton (1987).

The taxonomic history of *Poellnitzia* Uitewaal

The first reference to a taxon which is currently included in *Poellnitzia*, was published by Dr. H.M.L. Bolus (1877–1970), then curatrix of the Bolus Herbarium at the University of Cape Town as well as editress of the Annals of the Bolus Herbarium. However, she classified this taxon, which was collected in 1917 by a certain Smith, in the genus *Apicra* Haworth *non* Willdenow. With reference to the bright red flowers, a phenomenon which up to that time was unknown in the genus, she named the species *Apicra rubriflora* (Bolus 1920). The type specimen consists of four inflorescences and a vegetative shoot (*Smith s.n.* sub NBG 2/17, Herbarium Bolusianum 45213). An illustration by Mary M. Page, showing a vegetative shoot, part of an inflorescence and some floral characteristics accompanied the description. The type locality of *A. rubriflora* was given as the Swellendam division, Bonnievale. Bayer (1982) rightly expressed his surprise over the fact that this distinctive species only became known to botanical science at such a late stage. He pointed out that Oldenland's "28 Aloe africana rotunda, folio parvo et in acumen rigidissimum exeuente" which was mentioned in Valentijn (1726), probably referred to this taxon. However, no proof of this exists.

Figure 2. In habitat specimens of *Poellnitzia rubriflora* usually grow under the protection of other xerophytic, sclerophyllous species.

Von Poellnitz (1939) described a second species closely related to *Apicra rubriflora,* viz. *Apicra jacobseniana*. This species apparently differed from *A. rubriflora* in that it possessed somewhat smaller leaves, whilst there were also slight differences of phyllotaxy (the arrangement of leaves along a shoot axis) between these two species (Uitewaal 1939). *A. jacobseniana* was allegedly gathered near Worcester (Hunt 1981). Uitewaal later reduced this species, of which the type specimen was sterile, to varietal rank under *A. rubriflora* (Jacobsen 1977). The leaf characteristics originally used to distinguish this taxon initially known as *A. jacobseniana* and later as *Poellnitzia rubriflora* (H.M.L. Bol.) Uitew. var. *jacobseniana* (V. Poelln.) Uitew. were, however, insufficient ground for its segregation from *Apicra rubriflora* (Jacobsen & Rowley 1955).

Especially the flowers of *Apicra rubriflora* differed from that of the other known species of *Apicra.* Uitewaal (1940) regarded these differences as sufficient motivation for the creation of monotypic generic status for this taxon as *Poellnitzia rubriflora.* The fact that the edges of the outer perianth segments of the flowers were fused with the main veins of the inner perianth segments, the connivence of the perianth lobes (Figure 3) as well as the elongated bright red to orange-red perianth tube, convinced Uitewaal (1940) that this species did not belong in *Apicra* Haw. *non* Willd.

Although *Apicra* Haw. was a later homonym of *Apicra* Willd., and therefore illegal, Stearn (1939a, b) suggested that it should be conserved in favour of *Apicra* Willd. However, eight years later, Uitewaal (1947) published a new name, *Astroloba,* for *Apicra* Haw. *non* Willd. This proposal of Uitewaal was accepted since a large number of changes in author citation would otherwise have been required in both *Haworthia* Duval and *Astroloba* Uitewaal. *Poellnitzia rubriflora,* originally described as *Apicra rubriflora,* was therefore at no stage known as *Astroloba rubriflora* as the monotypic genus *Poellnitzia* Uitew. was established some seven years before publication of the name *Astroloba* Uitewaal. Lamb (1978) therefore designated this species incorrectly as *Astroloba rubriflora* L. Bolus.

Parr (1971, 1972) suggested that *P. rubriflora* and *P. rubriflora* var. *jacobseniana,* together with the species of *Astroloba,* be placed in a new section, the *Quinquefariae,* in the genus *Haworthia.* However, with regard to *Poellnitzia* he offered no reasons for this decision. Bayer (1972) objected to this taxonomic revision by Parr and suggested that *Poellnitzia* and *Astroloba* be reinstated at generic level. Both Obermeyer (1973) and Dyer (1976) accepted the inclusion of *Poellnitzia* in the synonymy of *Haworthia.* In contrast to this approach, Rowley (1980) suggested that *Poellnitzia* shares more characteristics with the genus *Aloe* L. The following year Rowley validated his proposed combination, viz. *Aloe rubriflora* (L. Bol.) G.D. Rowley (1981). Rowley (1985) motivated the generic shift of *Poellnitzia* to *Aloe* by stating that the bright orange red flowers of *Poellnitzia* are probably bird-pollinated and likens its habit to that of *Aloe aristata* Haw., *A. humilis* (L.) Mill., *A. descoingsii* Reynolds "... and others". However, *Poellnitzia* shares few characteristics with the *Aloe* species mentioned above. Furthermore, it is unlikely that the connivent flowers of *Poellnitzia* could be exclusively bird-pollinated. A pencil drawing of a vegetative stem of *Poellnitzia rubriflora* (then known as *Apicra rubriflora*) executed by J.T. Bates in 1933 is reproduced in Rowley (1985). He also provided a comprehensive biography of Bates (1884–1966), a well-known English collector of succulent plants. Both Rowley and Bates incorrectly list Marloth as the author of *Apicra rubriflora.*

Riley & Majumdar (1979) and Court (1981) upheld *Poellnitzia* as a monotypic genus, whilst Gibbs Russell *et al.* (1984, 1985) followed Parr's view and accordingly referred to this taxon as *Haworthia rubriflora* (L. Bol.) Parr. Hunt (1981) wrote a short historical review of the nomenclature of *Poellnitzia rubriflora* which was published together with an illustration which in particular showed the floral characteristics according to which this taxon could be clearly distinguished from the genera *Haworthia, Astroloba* and *Aloe.*

Summary

Since the description of *P. rubriflora* as *Apicra rubriflora,* this taxon has already been referred to four genera in the Alooideae. In summary, morphological differences between *Poellnitzia, Astroloba, Haworthia* and *Aloe* that were elucidated more than fifty years ago still serve to readily distinguish them, especially in floral characteristics. Based on the correlated characters of flower colour, connivence of the tips of the perianth segments and secund floral disposition, *Poellnitzia* forms a distinct entity that should be maintained as a separate monotypic genus.

Acknowledgements

I am indepted to Prof. Gordon D. Rowley and Dr. Colin C. Walker for supplying copies of scarce publications and illustrations. Mr. M. Bruce Bayer is thanked for many useful discussions on the classification of Alooideae

Figure 3. Inflorescence of *Poellnitzia rubriflora* bearing bright red to orange flowers in secund fashion. The tips of the perianth segments are connivent.

genera. Mr. Ben Engelbrecht, curator of the Karoo Botanic Garden is thanked for hospitality extended while I did field work in the Robertson Karoo.

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CHAPTER 4

PALYNOLOGY AND REPRODUCTIVE BIOLOGY

"Pollen is the vital link between each generation of flowering plants."

S.C. Ducker & R.B. Knox: 1985

"The paucity of data on monocot pollen represents a considerable handicap to paleobotanists and evolutionary botanists interested in studying the evolution of monocots and, in general, the early evolution of the angiosperms."

M.S. Zavada: 1983.

CONTENTS

CHAPTER 4

PALYNOLOGY AND REPRODUCTIVE BIOLOGY

4.1 INTRODUCTION

4.1.1 Background

The second quoted passage that heads this chapter provided the impetus and rationale for the palynological investigation of selected genera of the Alooideae. Palynology is the study of pollen [fossil (Arnold 1947; Zavada & Crepet 1985, 1986; Traverse 1988) and extant (see Faegri & Iverson 1975 for and overview)] and spores, generally focusing on the structure of the wall rather than on living, internal features. Palynological evidence has proven useful at all taxonomic levels. One objective particularly of paleopalynologists is to provide additional data that can either support, refine or refute the proposed phylogenetic schemes based on, amongst others, studies of extant pollen (Zavada 1984). Data obtained from palynological investigations have also been of value in studies such as stratigraphy (Daghlian *et al.* 1984), paleoecology (Zavada & Taylor 1986; Zavada 1987), reproductive biology (Smith 1991) and, along with wood (Taylor 1981), in archaeology.

In its widest sense reproductive biology is the study of structures, processes, mechanisms, and significant biotic and abiotic factors involved in the reproduction of an individual, population or species. These data contribute information for use in interpreting relationships amongst taxa and their possible phylogeny (Jones & Luchsinger 1986; Radford 1986). The reproductive biological aspects of *Chortolirion* and *Poellnitzia* which are discussed in this chapter include comparative physiology of pollen grain germination (*in vivo* and *in vitro*), reproductive potential, pollination type, floral biology and flowering periodicity.

To avoid possible misunderstanding in this chapter the descriptive terminology pertaining to pollen development will be clarified in the next few paragraphs [see for example the attempts of Green (1980) at a revised terminology for the spore-containing parts of anthers]. The following terminological explanation is based largely on Stanley & Linskens (1974). In angiosperms the microspores (male spores) are formed by the anthers. The anther normally consists of two lobes (thecae) each with two locules [see also Keijzer (1987a, b) and Keijzer *et al.* (1987) on the anthers of *Gasteria verrucosa* (Mill.) Duv.]. Each locule contains a single elongated microsporangium (pollen sac). Pollen development takes place in the microsporangia. Upon maturation two bordering locules dehisce by means of one longitudinal slit. The two anther lobes (thecae) are fused together by connective tissue which consists of vegetative cells. The connector which supports the anthers and attaches it to the receptacle of the flower is called the filament. A stamen consists of the filament and the anther. After formation of the microspores in the anther, they undergo one, two or three mitotic divisions, followed by a resting period varying from a few hours to many months. After mitosis the mature microspore is referred to as a pollen grain.

The term microspore refers only to the uninucleate structure released from tetrads after meiosis. The term pollen grain describes the above structure after mitosis of the microspore nucleus and therefore containing the developed vegetative (tube) and generative (male) cells. The pollen grain, ready to germinate and grow is considered the multicellular male gametophyte. Male gametes (sperm cells) are formed in the pollen grain (or the pollen tube) which forms on germination of the pollen grain.

Young anthers contain archesporial cells which differentiate to form the parietal cell layer and sporogenous tissue. The parietal cells produce the outer wall of the anther and an inner layer, the tapetum. In *Aloe* the outer wall consists of three layers: an epidermis, an endothecium and one middle layer. The fourth, innermost locule wall layer is the tapetum (Keijzer 1987a, b; Keijzer & Cresti 1987). Cells of the sporogenous tissue give rise to many pollen mother cells (microsporocytes or meiocytes) which divide to yield the microspores which mature and are shed as pollen grains. The multicellular pollen grain transfers the male genome to the female organ by pollination on the stigma (Ducker & Knox 1985).

This chapter is primarily concerned with the morphology and physiology of mature pollen grains and their transferral to receptive stigmatic surfaces. It is noteworthy that the standardization of terminology in pollen and spore morphology has also been a concern of palynologists for many years. In spite of attempts by, amongst others, Reitzma (1970), Praglowski (1971), Praglowski & Punt (1973), and Nilsson & Muller (1978), general agreement on terminology is yet to be achieved. For the purposes of the present investigation the pollen morphological terminology of Erdtman (1966, 1969) was found to be suitable and is used throughout.

The lilialean complex (*sensu lato* but exclusive of the Orchidaceae) includes some 550 genera and 10 000 species distributed amongst more than 50 families [see for example Goldberg (1989)]. In the complex four main groups can be recognized: a) a primitive, basal melantheaceous group, b) an anthericaceous group, c) a liliaceous group, and d) an asparagaceous group. Roth *et al.* (1986) investigated the pollen morphology of 140 genera and 640 species from the complex, concentrating on the groups mentioned under a) and b) above. They came to the following general conclusions:

i) the overwhelming majority has monosulcate pollen;
ii) reticulate exine sculpturing occurs frequenthy; and
iii) parallel evolution of pollen with distinct areas of coarse and fine reticulum was observed in many taxa.

These three conclusions are also applicable to *Aloe bowiea*, *Chortolirion*, *Poellnitzia* (see 4.3, 4.4.1, 4.4.2 and 4.5.1 for discussions) and *Haworthia* (Greyling *et al.* 1990). However, the five taxonomically important pollen features which Roth *et al.* (1986) established for the lilialean complex are absent from the aloeoid taxa and need not concern us here.

Zavada (1983, 1984) has suggested that monosulcate pollen grains with a tectate-columellate wall (perforate or imperforate) is most probably primitive in extant monocotyledons. However, it is noteworthy that this primitive pollen wall structure differs significantly from the atectate or granular walls found in the Nymphaeaceae. Based on morphology it has been suggested that the monocotyledons separated from an early nymphaeacean-like ancestor (Cronquist 1981). The tectate-columellate wall structure also occurs among ranalean taxa and appears to be an early palynological development in the dicotyledons. This places the primitive monocots on the same evolutionary level as the derived tectate-columellate ranalean dicots, lending support to the dicotyledonous origin of monocots (Zavada 1983).

The tectate-columellate pollen type (perforate condition) is also present in the Alooideae. However, the pollen morphology of the subfamily has not been extensively investigated [see Smith (1991) for references]. Although various authors have described the pollen of species of one or more genera of the Alooideae as part of pollen floras or of wider surveys of pollen grain ultrastructure, there has been no real attempt at deriving taxonomic useful characters from palynological investigations. With the possible exception of the Cactaceae [see for example Anderson & Stone (1971) on *Lophophora* Coult.] and the Mesembryanthemaceae [see Dupont & Hartmann (1982) on *Leipoldtia* L. Bol.] succulent plants in general have not received the palynological attention that they deserve.

This chapter includes contributions on improved methodology for studying pollen by means of scanning electron microscopy (Smith & Tiedt 1991), the pollen morphology of *Aloe bowiea* (4.3) the pollen morphology and reproductive biology of *Chortolirion* (Smith 1988, 1991) and the pollen morphology (Smith & Van Wyk submitted) and biology and ecology of pollination (4.5.2) of *Poellnitzia*.

The palynological investigation of the Alooideae should not be regarded as having been completed with the contributions included in this chapter. Future surveys of pollen in the subfamily should have three primary goals in mind: a) to provide comparative morphological date for assessing the relationships between the Alooideae and Asphodeloideae within the family Asphodelaceae, b) to assess at which level of the subfamilial hierarchy pollen characters are useful in determining taxonomic position (if at all) and, c) to assess the phylogenetic relationships of taxa within the Alooideae as elucidated by pollen morphology. Studies of pollination ecology and pollination biology would also benefit greatly from less speculation and more detailed studies and careful observations in habitat.

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A rapid, non-destructive osmium tetroxide technique for preparing pollen for scanning electron microscopy

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Summary

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A new, rapid, non-destructive technique for the preparation of pollen is described, in which dissected anthers are fixed with osmium tetroxide vapour. This method permits the examination without modifying the pollen grain morphology and ultrastructure and the natural state of hydration. Apertural structures are perfectly preserved and neither debris nor artifacts are deposited on the grains. The pollen cementing substances, such as pollenkitt, remain intact and can assist in the functional interpretation of pollen types. This new method may help to obtain optimal structural and functional information from pollen study.

Introduction

Scanning electron microscopy (SEM) has become the most common means to examine pollen morphology (Skvarla & al., 1989; Rowley & al., 1987-1988). Since Erdtman (1966, 1969) introduced the well-known acetolysis method a number of different methods have been developed to prepare pollen for SEM, e.g., methods to observe single grains (Daghlian, 1982), ultrasonication (Lynch & Webster, 1975), and a filtering technique (Bredenkamp & Hamilton-Attwell, 1988). However, in most light and electron microscopic investigations of pollen morphology and ultrastructure acetolysed material is used exclusively (Hesse & Waha, 1989). Therefore acetolysis is widely considered as the common basis for the comparison of pollen grains (Coetzee & Van der Schijff, 1979). Although acetolysed pollen grains are clear and give excellent topographic information of the pollen wall, this method has numerous disadvantages, as discussed in detail by Hesse & Waha (1989).

We came across these problems when studying the pollen of *Chortolirion* Berger and *Poellnitzia* Uitewaal as part of our taxonomic revision of the monotypic genera in the *Alooideae* (*Asphodelaceae* sensu Dahlgren & al., 1985). During this study acetolysis was initially employed. However, use of this method resulted in the loss of large numbers of pollen grains, and in changes in shape and volume of the acetolysed grains (Fig. 1). Changes in pollen grain volume are usually associated with harmomegathic mechanisms, that is, mechanisms enabling the complete pollen wall to react (contract or stretch) to the turgor pressure of the cytoplasm during de- or rehydration (Wodehouse, 1935; Blackmore & Barnes, 1986). Although the acetolysis procedure is known to cause dehydrated, collapsed pollen grains to resume their normal shape (Coetzee & Van der Schijff, 1979), it often makes bilaterally symmetrical

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grains appear radially symmetrical and may result in incorrect measurements being taken for the polar and equatorial axes. Pollen grains might therefore be classified in the wrong symmetry and size classes.

To alleviate these disadvantages, we prepared pollen samples for SEM using the ultrasonication method of Lynch & Webster (1975). Use of this method, however, resulted in the deposition of visually interesting artifacts and debris on and around the grains, thereby obscuring the microstructure of the pollen exine (Fig. 2), and also in a considerable loss of material. In view of these problems, we then resorted to the less damaging and cleaner filter technique of Bredenkamp & Hamilton-Attwell (1988). This method, however, improved the results only for *Chortolirion* (cf. Smith, 1988, 1991), whereas the grains of *Poellnitzia* were still swelling excessively (Fig. 3). A further disadvantage common to all methods discussed above is the loss of pollen surface coatings, for example of pollenkitt. The removal of such non-sporopollenin substances hampers the functional classification of pollen grains and distorts the interpretation of adaptations to specific modes of pollen dispersal and pollination (Hesse, 1981; Hesse & Waha, 1989).

We therefore settled on a rapid, non-destructive osmium tetroxide technique for the preparation of our pollen samples of live material for SEM (Tiedt & al., 1987). Whereas none of the previously used techniques (acetolysis, ultrasonication and filtering), had proved completely satisfactory, the osmium tetroxide method entirely circumvented damage to and distortion of pollen grains. To evaluate the osmium tetroxide vapour fixation method, its results were photographically compared with pollen preparations obtained by conventional preparation schedules.

Materials and methods

Pollen samples taken from herbarium specimens, having dried naturally over years of storage, can be prepared for SEM (for example by acetolysis) without preliminary treatment (Arens & Traverse, 1989). However, fresh pollen must be dehydrated prior to the preparation for SEM. This process involves a sequence of steps, the first usually being fixation (Clark & al., 1986). Palynologists usually fix their material in a standard formalin-acetic-acid-alcohol (FAA) solution (Lynch & Webster, 1975). However, fixatives containing alcohol are coagulative and may cause specimen distortion and loss of details (Hesse, 1981; Clark & al., 1986). In the method used by us fixation is accomplished by means of osmium tetroxide (OsO_4), an extremely toxic substance that must always be handled with great care under a fume hood.

Our material was prepared as follows: Freshly collected polliniferous parts (usually carefully dissected post-anthesis anthers) were taken from living specimens and placed in a petri dish next to, but not in direct contact with, small drops of 2 % OsO_4. The petri dish was again covered with its lid and left in the fume hood for 24 h, after which the OsO_4 drops were removed and the samples left to air-dry for 24 h. The fixed plant material was then removed and mounted onto SEM-stubs with conductive carbon cement ("Leit-C nach Göcke", Neubauer Chemikalien). Critical- point drying was not considered necessary as sturdy structures such as pollen grains with intact intines retain their shapes when treated as above. The stubs were subsequently carbon-flash-evaporated and sputter-coated with a gold/palladium alloy (60 : 40) to a thickness of 3 nm. The samples were studied with a Cambridge Stereoscan 250 S operating at 10 kV.

Results

The ultrastructure and morphology of pollen grains of *Chortolirion* have been reported in detail elsewhere (Smith, 1988) and will not be repeated here. Pollen grains of *Poellnitzia* are monosulcate and reticulate (Fig. 3, 5; tectum perforatum sensu Praglowski & Punt, 1973).

Figures 1-6 demonstrate the results obtained when the respective methods were compared. The swelling of acetolysed pollen grains of *Poellnitzia* is clearly visible in Fig. 1. It is therefore evident that such typical monocotyledonoid cymbiform pollen grains will be incorrectly interpreted as radially symmetrical unless results based on acetolysed samples are compared to those obtained from samples of untreated grains. Ultrasonication alleviated the problem of rehydration of post-anthesis pollen grains but resulted in the deposition of extraneous material on the grains, both in *Chortolirion* (Fig. 2) and *Poellnitzia*. When the filtering technique was applied, pollen of *Poellnitzia* again showed an excessive increase in diameter, and artifacts were also deposited on the grains (Fig. 3, 4).

In contrast, pollen samples of *Poellnitzia* prepared by means of the osmium tetroxide technique show no aberrations of morphology or symmetry (Fig. 5, 6). The grains are free of debris and their clean surface adequately reveals the tectum and perforations. Furthermore, this method enables the observation of the sticky, viscous pollenkitt (Hesse 1981, 1986) which, in *Poellnitzia*, partly covers the reticulum and some of the exine cavities (Fig. 6).

Discussion

Although it has become customary to use acetolysis in most pollen morphological studies, some authors argue that this is unnecessary for most studies based on SEM alone (Blackmore, 1984; Hall, 1988; Vincent & Getliffe Norris, 1989). In many investigations such as those considering pollen ontogeny and function, there are good reasons for examining unacetolysed pollen grains. For these purposes the new technique has obvious advantages. Very small samples of pollen grains can be studied as there is no loss of grains. The technique is less time-consuming than most other methods and can be used to rapidly assess, on a comparative basis, the potential taxonomic value of palynological studies in a particular group. Since the detrimental effects of corrosive chemicals and of centrifugal force are circumvented, this method may also prove invaluable for the preparation for SEM of samples of pollen of taxa which have a low resistance against acetolysis, e.g., *Lauraceae* and *Hernandiaceae* (Kubitzki, 1981; Hesse & Kubitzki, 1983). The intine of grains is not removed, and they are therefore not liable to collapse in the vacuum under the SEM. The method also permits examination without modifying the natural state of hydration of pollen grains. Thus distortion due to shrinkage or stretching is circumvented. Furthermore, colpar structures which are non-resistant to acetolysis are not destroyed and pollen tubes germinating in the anther remain intact.

Poellnitzia is an entomophilous genus and, since pollen grains are shed as monads, successful pollination depends on the adherence of sticky pollen grains to the flower visitor (Smith & al., 1989; Theron & al., 1990). The presence of pollenkitt suggests how this process takes place (Fig. 6).

Considering the fact that the new method involves no distortion of pollen morphology or loss of eminent functional pollen characters, it is obvious that it is in various ways superior to more destructive techniques commonly used for preparing

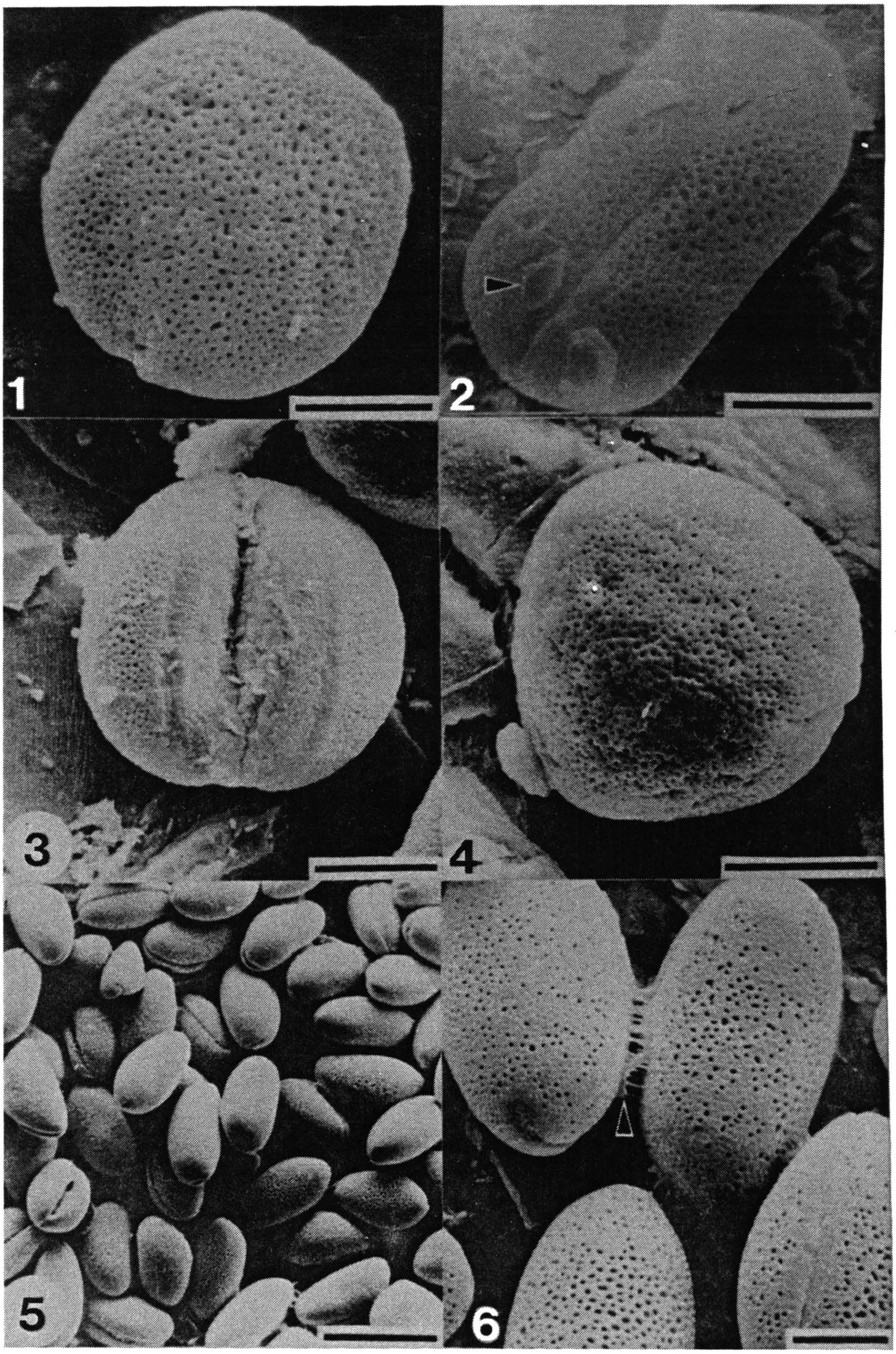

Fig. 1-6. Scanning electron micrographs of examples demonstrating the effect of various treatments on pollen grains of *Chortolirion* (Fig. 2) and *Poellnitzia* (Fig. 1, 3-6). *1.* Acetolysis: swollen post-anthesis grain. 2. Ultrasonication: extraneous deposits (arrowed) on the surface of a pollen grain. *3.* Filter technique: sulcus of a swollen grain with deposited material on the surface. *4.* Proximal view of a pollen grain prepared as in Fig. 3. *5.* Osmium tetroxide technique: undamaged grains showing elongated aperture (sulcus) and inaperturate proximal surface. *6.* Detail of pollen grains prepared as in Fig. 5 showing pollen cementing adhesive substance (arrowed). Scale bar = 10 µm in Fig. 1-4 and 6; 40 µm in Fig. 5.

pollen for SEM. To obtain as much palynological information as possible, this method should be used to supplement other standard preparation schedules such as acetolysis.

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4.3 POLLEN MORPHOLOGY OF *ALOE BOWIEA*

4.3.1 Introduction

The pollen morphology of *Aloe bowiea* has been illustrated and discussed in detail by Smith & Van Wyk (submitted). However, the latter contribution also includes the *Flora of southern Africa (FSA)* treatment (Anonymous 1991) of the species and has, for obvious reasons, been included in Chapter 9. For comparative purposes the pollen morphology of the species is briefly enumerated and discussed below.

4.3.2 Pollen morphology of *Aloe bowiea*

The morphology of pollen grains of *Aloe bowiea* is the same throughout the specimens examined. Furthermore, morphologically typical *Aloe bowiea* pollen cannot be distinguished from pollen of a number of related genera, such as *Chortolirion*, *Haworthia* and *Poellnitzia*. The following description of *A. bowiea* pollen includes the entire range of variation for the investigated samples.

Pollen shed as monads. Grains bilaterally symmetrical. Amb elliptical (occasionally pyriform). Grains heteropolar with an inaperturate proximal wall and a distal, monosulcate aperture. Sulcus well-defined and equal to the dominant equatorial axis. Grain size (dominant axis) varying within fairly narrow limits (34 (41,4) 46 μm) within and between samples. Pollen grain surface perforated by numerous minute micropores. Sexine discontinuous and subtectate. Lumina in general circular and less than 0,1 μm in diameter. Muri *ca.* 0,3 μm wide, smooth. The proximal surface of some grains prepared for SEM by means of the filtering technique displayed a degree of sculpturing superimposed on the perforated sexine.

4.3.3 Discussion

The pollen of *Aloe bowiea* specimens examined agrees in general with that described for other genera of the Alooideae [see Smith & Van Wyk (submitted) for references]. Pollen grains of the species are free, medium in size (dominant equatorial axis), bilaterally symmetrical and heteropolar (monosulcate) with a perforated tectum. No narrow, unsculptured zone bordering the sulcus was observed. The existence of such a zone had previously been reported for pollen of *Haworthia*. The proximal surface of most pollen grains prepared for SEM using the filtering technique displayed some degree of sculpturing. Due to its inconsistent occurrence this feature does not have any taxonomic significance. The micropores which occur in the pollen grain surface of *Aloe bowiea* are in general smaller than those of pollen grains of related genera. This feature, too, is taxonomically insignificant since pollen of especially *Chortolirion* often displays very small perforations in the pollen grain surface. The mean pollen grain size of *A. bowiea* is slightly greater than that of related genera. However, the range of grain size of *A. bowiea* overlaps with that of pollen of *Haworthia* and *Poellnitzia*. It is therefore clear that no single pollen morphological character or combination of characters are diagnostic at the specific or generic levels.

4.3.4 References

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A scanning electron microscopic investigation of the pollen morphology of *Chortolirion* Berger (Aloineae; Liliaceae)

Chortolirion Berger (tribe Aloineae, family Liliaceae) has a history of taxonomic confusion and doubtful generic delimitation. In this study, the taxonomic significance of its pollen morphology was assessed by means of scanning electron microscopy. It is suggested that *Chortolirion* is best regarded as being a variable monotypic genus within the tribe Aloineae with *C. angolense* (Bak.) Berger the only species.

Background

The Aloineae is one of 28 tribes recognized by Hutchinson[1] in the family Liliaceae. From its modest beginning in 1753 as a single genus, namely *Aloe*,[2] this taxon has rapidly gained more genera and species. According to Rowley,[3] 27 generic names have, at various times, been proposed for taxa currently classified in this tribe.

Berger[4] regarded the specific characteristics of *Haworthia angolensis* Bak., *H. tenuifolia* Engl., *H. stenophylla* Bak. and *H. subspicata* Bak. as irreconcilable with Duval's circumscription of the genus *Haworthia* and proposed that these four species be placed in a separate genus, namely *Chortolirion*. The possession of an underground bulb by these species was the main reason advanced by Berger for this decision. He claimed further that their growth pattern differs from that of *Haworthia* in general and especially in the deciduous nature of the leaves. In addition the distal part of the seed capsules as well as the styles and developing capsules were always attenuated, the last two character states being absent in *Haworthia*.

Thirty-six years after the erection of the genus *Chortolirion*, Dyer[5] suggested the reduction of at least *C. subspicata* (Bak.) Berger to the synonymy of *C. stenophyllum* (Bak.) Berger. Obermeyer[6] justifiably concluded that the interspecific differences on which previous authors[4,7] based the four species in *Chortolirion* were nothing more than localized variations of a variable taxon. Obermeyer, however, did not mention *C. bergerianum* M.K. Dinter[8] in her revision. She claimed that the evidence provided by Berger for distinguishing the now monotypic taxon, *Chortolirion*, as a separate entity was insufficient for segregation at genus level. Dyer[9] supported this interpretation.

According to Bayer,[10,11] the taxonomically complex succulent genus, *Haworthia*, consists of three clearly distinguishable subgenera, namely *Haworthia, Hexangulares* Uitewaal ex Bayer and *Robustipedunculares* Uitewaal ex Bayer. This subdivision is based on floral morphology and does not allow the inclusion of *Chortolirion* in *Haworthia*. Bayer[10] especially denied the similarity which apparently exists between *Chortolirion angolense* and *Haworthia graminifolia* G.G. Smith regarding the presence of an underground bulb. Obermeyer,[6] on the other hand, overemphasized this superficial similarity. Furthermore, *H. graminifolia* is classified in the type subgenus whereas *Chortolirion angolense* is florally more closely related to the subgenus *Hexangulares* Uitewaal ex Bayer.[11]

Chortolirion is accepted here as a monotypic genus *sensu* Bayer.[10,11] It is a perennial, deciduous herb with a subterranean bulb and is widely distributed in the summer rainfall region of Southern Africa. With short annual succulent shoots arising from a perennial underground bulb-like structure, *C. angolense* presents a combination of a geophytic and succulent habit. The Afrikaans vernacular name of this spring flowering taxon is *'kleinaalwyn'*,[12] a direct translation of which would be 'small aloe'.

Detailed taxonomic and biosystematic research aimed at establishing the true intra- and intergeneric affinities of the smaller genera in the tribe Aloineae has been lacking. Recent revisions have mostly been unsatisfactory. In order to provide an objective sub-tribal classification of the Aloineae, a research programme in which all aspects of their biology will be considered was initiated. A study of a large number of taxonomic criteria is required to provide data on the affinities of this natural group recently included in the segregate family Asphodelaceae.[13]

Palynological research on the Aloineae is fragmentary and incomplete. Majumdar[14] and Yuhl and Majumdar[15] reported on the application of transmission electron microscopy and scanning electron microscopy (SEM) for interpretation of pollen ultrastructure of some taxa included in this tribe. To the best of my knowledge the topography of pollen grains of *Chortolirion* have not been reported before. In this investigation the scanning electron microscope was used to obtain quantitative and qualitative data on the pollen of diploid *C. angolense* ($2n = 14$). The purpose is to employ palynological evidence as an aid towards deciding whether to retain *Chortolirion* as a monotypic genus, or to classify it as a species within *Haworthia*.

Materials and methods

Specimens of *Chortolirion angolense* were collected at three disjunct populations, namely from Potchefstroom, Pretoria and Middelburg (Transvaal). The localities of these collections are listed according to the grid reference system of Leistner and Morris.[16] The abbreviations of herbarium names are according to Holmgren *et al.*[17] The following voucher specimens were deposited:

TRANSVAAL.—2528 (Pretoria): Botanic Garden of the Botanical Research Institute (–CB). *Smith 8*(PRU).

2529 (Witbank): 'Rietvlei' 41 km N of Middelburg (–AD), *Bronkhorst s.n.* sub *Smith 12*(PUC).

2627 (Potchefstroom): 1 km W of Botanic Garden of the PU for CHE (–CA), *Smith 14*(PUC).

Five flowering plants from each locality were studied. Polleniferous parts (usually anthers) were taken from freshly collected specimens and fixed in FAA[18] for at least 24 hours. In the case of *Smith 14*, anthers were removed from herbarium sheets. Measurements of the respective diameters were made from the SEM micrographs and were usually based on at least 20 grains per sample. The descriptive terminology used was mainly that of Erdtman.[19]

Two methods commonly used for preparing pollen for SEM were employed, namely ultrasonification[20] as modified by Bredenkamp *et al.*[21] and acetolysis[19] as modified by Coetzee and Van der Schijff.[22] The latter method yielded less satisfactory results. Trace amounts of the reagents left in the suspension medium resulted in the deposition of an unevaporable film on the pollen surface prior to vacuum coating. This deposit obscured the surface detail of the pollen. The modified ultrasonification has obvious advantages when compared to acetolysis. Small numbers of pollen grains can be used and debris is effectively removed from the pollen surface. This method is less time consuming and the effect of centrifugal force is eliminated.[21]

To prepare the material for SEM, the filters were air dried in a desiccator from 90% ethyl alcohol and fixed on electron microscope stubs. The samples were subsequently sputter-coated in an argon atmosphere with Au/Pd (60:40) to a thickness of 3 nm.

Results

Pollen grains of *Chortolirion* are regularly differentiated on size, shape and aperture features. The results obtained for all the collections were identical. Grains are heteropolar with an inaperturate proximal wall (Fig. 1) and a distal monosulcate aperture (Fig. 2). Polar regions cannot be clearly distinguished in individual grains of *Chortolirion* after separation from the tetrad stage. Feagri and Iverson,[23] however, justifiably remark that the axis of symmetry can be detected easily in individual grains of flower-

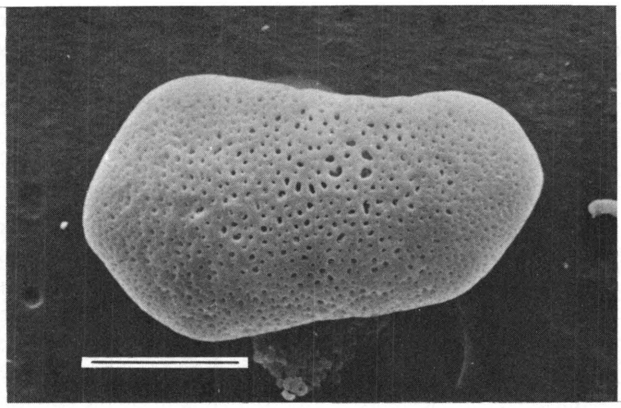

Fig. 1. SEM micrograph of pollen grain of *Chortolirion angolense* (*Smith 14*) showing smooth, inaperturate proximal wall with numerous pori. Bar = 10 μm.

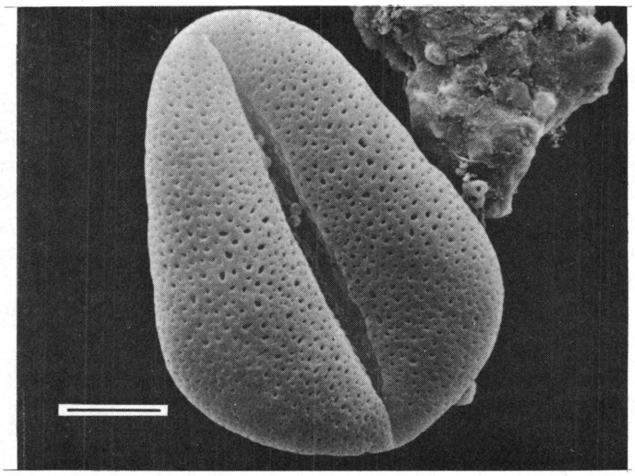

Fig. 2. SEM micrograph of distal side of pollen grain of *Chortolirion angolense* (*Smith 14*) showing smooth surface and elongated aperture (sulcus). Bar = 5 μm.

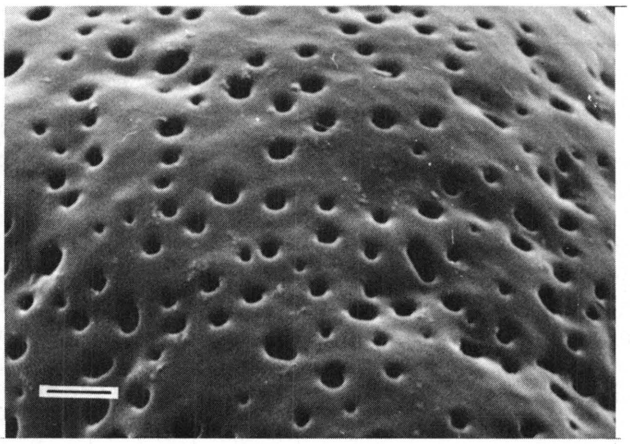

Fig. 3. Detail of tectum surface showing perforations and smooth muri interconnected to form a tectum perforatum (*Smith 8*). Bar = 1 μm.

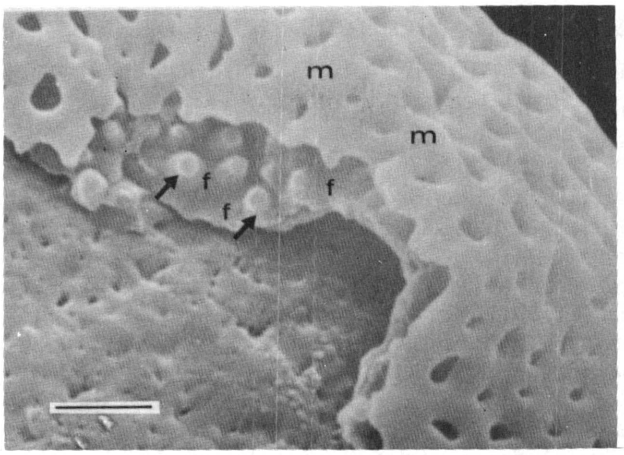

Fig. 4. A damaged sexine layer exposing the foot layer (*f*), bacula (arrowed) and muri (*m*), giving rise to the tectum perforatum of *Chortolirion angolense* pollen (*Smith 12*). Bar = 1 μm.

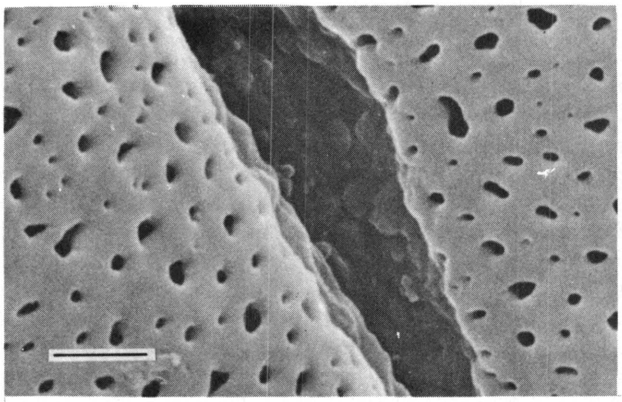

Fig. 5. Detail of sulcus showing absence of smooth area bordering the aperture (*Smith 8*). Bar = 2 μm.

ing plants in general. Pollen grains can thus be regarded as regular ellipsoids with the polar axis being the rotation axis. Grains are shed as monads. The heteropolarity of *Chortolirion* pollen thus refers to morphological differences between the polar walls and not to ontogenetic differences.

Two distinct pollen types could be identified with regard to symmetry. The majority of the grains are bilaterally symmetrical according to the definition of Cook.[24] They have a pronounced inflation at one end of the dominant axis and therefore only one plane of symmetry down the length of the aperture (Fig. 2). A minority of the grains have two planes of symmetry and are bilaterally symmetrical *sensu* Erdtman.[25] These planes, which are both vertical, are of unequal length, the equatorial one being the longer of the two.

The amb/outline of the pollen grains is best described as pyriform to elliptical. Apiculate grains are rarely encountered, but this may be due to volume changes within the grain. Along the equatorial axis the pollen grains vary between 20 and 29 μm with an average of 28,5 μm, and along their polar axis they range between 15 and 20 μm with an average of 16,5 μm. The grains are monotreme and anatreme[19] with the aperture situated on the distal wall. The aperture, a sulcus, is more than twice as long as it is wide and usually about equal to the dominant equatorial diameter. The sulcus (ectoaperture) is well defined, about 1,3 μm wide and crosses the polar plane at a right angle (Fig. 2).

The pollen grain surface is perforated by numerous pori (Fig. 3). The sexine is discontinuous, subtectate and can be classified as a tectum perforatum *sensu* Praglowski and Punt.[26] The relief of the grain is thus only partly formed by the tectum. Figure 4 shows a torn distal wall of a pollen grain exposing the infratectal bacula. As reported previously for *Haworthia*,[15] it is apparent from this micrograph that the pori is formed by numerous lumina which occur between the muri. The diameter of the pori which forms in the central zone on both sides of the pollen wall is considerably larger than the diameter of those found towards the ends of the longest equatorial axis (Figs 1 and 2). No secondary sculpturing superimposed on the perforated sexine is present. The existence of a narrow, smoother zone bordering the sulcus was previously reported for pollen of *Haworthia*.[15] This zone was not observed in *Chortolirion*. The pori in the latter area, however, have a much smaller diameter than those found elsewhere on the pollen wall (Fig. 5).

Table 1. Summary of main morphological distinctions between pollen of *Haworthia* and *Chortolirion*.

Character	*Haworthia* (from ref. 15)	*Chortolirion*
Proximal surface sculpturing	Faint or distinct	Absent
Size (dominant equatorial diameter)	29 – 33 μm	20 (25,8) 29 μm
Amb/outline	Elliptical	Pyriform; occasionally elliptical
Perforation of surface bordering sulcus	Absent	Tectum perforatum
Symmetry	Bilaterally symmetrical *sensu* Erdtman[19,25]	Bilaterally symmetrical *sensu* Cook[24]

Discussion

The taxonomy of the Aloineae remains in flux as the existence of some taxa is questioned and the boundaries of others debated. Of the genera which are particular sources of confusion, the genus *Chortolirion* presents several taxonomic uncertainties which need clarification. Previous studies on the taxonomic affinities of this monotypic genus were often based on poorly defined criteria. *Chortolirion* has already been considered as a monotypic genus;[11,27] a separate genus with five species;[4,8,28] a single species of *Haworthia*[6,9] or as four separate species in *Haworthia*.[7,29] It should be noted that *C. bergerianum* M.K. Dinter has never been treated as a species of *Haworthia*.

The pollen grains of diploid specimens of both *Chortolirion* and *Haworthia*[30] are free, anatreme and monosulcate with a tectum perforatum. Outstanding differences between the pollen of these taxa are summarized in Table 1.

Studies on the relation between pollen size and chromosome number of *Haworthia*[15,31,32] have shown that size increases with each additional set of chromosomes. This increment was found to be significant up to the tetraploid level. In the present study only diploid plants were included, polyploids thus far being unknown in *Chortolirion*. The mean pollen size of *Chortolirion* was found to be smaller than that of diploid taxa of *Haworthia* (Table 1).

In *Chortolirion* the transition from a perforated sexine to a smoother area around the aperture is not distinct. The diameter of the pori in this area is, however, much smaller than that of the pori encountered elsewhere on the walls. In the case of *Haworthia*, an abrupt transition to a smooth surface lacking pori was noted in this region.[15]

By far the majority of the pollen grains of *Chortolirion* are bilaterally symmetrical,[24] displaying a pronounced thickening at one end of the dominant axis. The only plane of symmetry which these grains exhibit coincides with the latter axis. Pollen grains of *Haworthia* were found also to be bilaterally symmetrical.[15] It should however be noted that the definition of bilateral symmetry in the traditional palynological context is applied to grains having two vertical planes of symmetry.[19,25] Since pollen of *Chortolirion* exhibits only a single plane of symmetry, it cannot be classified as bilaterally symmetrical *sensu* Erdtman[19,25] (Table 1).

Certain fine structural differences exist between the pollen of *Chortolirion* and *Haworthia*, especially with regard to symmetry, size of pollen from diploid specimens and the perforation of the surface bordering the sulcus. It is not suggested that *Chortolirion* should be recognized as a monotypic genus on these palynological grounds alone. This taxon represents a unique assemblage of both floral and vegetative characters that makes it unique in the tribe Aloineae.[10,27] The differences in pollen morphology between *Chortolirion* and *Haworthia* do, however, offer additional evidence for recognizing *Chortolirion* as a separate entity. It is thus recommended that this taxon be best regarded as a monotypic genus with *Chortolirion angolense* (Bak.)Berger as the only species.

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Studies on the reproductive biology and palynology of *Chortolirion* Berger *(Asphodelaceae: Alooideae)* in southern Africa

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Summary

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While conducting biosystematic investigations towards a revision of the smaller genera of the subfamily *Alooideae* of the *Asphodelaceae* in southern Africa to be published in the *Flora of southern Africa*, I became aware that *Chortolirion bergerianum* Dinter had not been dealt with in recent treatments of this genus. A comparative palynological and morphological study indicates that *C. bergerianum* and *C. angolense* (Baker) A. Berger sensu lato are conspecific. Pollen grains of these taxa are free, monosulcate, bilaterally symmetrical, medium in size and have a perforated tectum.

The morphological investigation and in-vitro and in-vivo pollen germination studies also confirmed that *Chortolirion* Berger represents an assemblage of both reproductive and vegetative characters that makes it unique in the *Alooideae*. However, the differences on which five species were previously based in *Chortolirion* are nothing more than local variations of a variable and widespread taxon. *C. bergerianum* should be included in *C. angolense*, the only species of *Chortolirion*. The taxonomic history of *C. bergerianum* is also briefly discussed.

Introduction

Berger (1908) regarded the characteristics of the four bulbous species of *Haworthia* Duval then described, *H. angolensis* Baker (1878), *H. tenuifolia* Engler (1888), *H. stenophylla* Baker (1891) and *H. subspicata* Baker (1904) as irreconcilable with the circumscription of *Haworthia* as proposed by Duval (1809). He thus assigned these four species to a separate genus, *Chortolirion*. Not only were these the only species of *Haworthia* which have an underground bulb, but Berger (1908) also claimed that their growth pattern differed markedly from that of other species of *Haworthia*, especially in regard to the deciduous nature of their leaves as well as in certain floral and fruit characteristics (cf. Smith, 1988). The name *Chortolirion* means "heath lily" (De Graaf, 1983) and refers to the fact that the abovementioned taxa usually occur in grassland and, especially when not in flower, can easily be mistaken for small tufts of grass.

In January 1913 the German botanist Moritz Kurt Dinter (1868-1945) discovered specimens of a bulbous, liliaceous plant which clearly belonged to *Chortolirion* Berger. In 1914, six years after the erection of the genus, Dinter described these plants as *C. bergerianum*, the fifth and final species recognized in *Chortolirion*, thereby honouring Alwin Berger, the author of the genus (Fig. 1). The type locality of this species was given as the farm "Voigtland" which is situated 20 km to the east of Windhoek (Dinter, 1914). Dinter was an indefatigable plant collector and it is estimated that

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he covered more than 40 000 km in the course of his expeditions into the south-western African interior (Herre, 1971; Gunn & Codd, 1981). During four separate periods of residence in Namibia, then South-West Africa, Dinter collected more than 8 400 specimens. *C. bergerianum* was gathered on the seventeenth journey (January 1913) which he undertook during his initial residence (June 1897 - March 1914) in the territory (Gunn & Codd, 1981).

Ever since the publication of the name *Chortolirion*, recently included in the *Asphodelaceae*, subfamily *Alooideae* (Dahlgren & al., 1985), the genus has been the subject of taxonomic confusion. It has been considered as a monotypic genus (Bayer, 1972; Smith, 1985), as a genus with five species (Dinter, 1914; Jacobsen, 1977, 1986), reduced to a single species of *Haworthia* (Obermeyer 1973; Dyer, 1976) or transferred as four separate species to *Haworthia* (Baker, 1896, 1898). *C. bergerianum*, has been ignored by most taxonomists dealing with *Alooideae*, with the exception of Jacobsen (1977, 1986), Riley & Majumdar (1979), Court (1981) and Smith (1985). It is significant that even Obermeyer (1973) who revised the monotypic *Alooideae* genera for Dyer's (1976) generic flora, neglected to mention *C. bergerianum*. In her treatment she regarded the four *Chortolirion* species mentioned by Berger (1908) as synonyms of *Haworthia angolensis* Baker (1878). The purpose of this article is to ascertain whether *C. bergerianum* represents a species in its own right, inadvertently omitted from Obermeyer's (1973) revision of *Chortolirion* and the synoptic work of Gibbs Russell & al. (1985) that includes the monocotyledonous taxa of southern Africa.

The pollen morphology of the *Alooideae* has not been extensively investigated. Various authors have described the pollen of species of one or more genera as part of pollen floras or of wider surveys of pollen grain ultrastructure (e.g. Erdtman (1966) for *Aloe*, *Gasteria* and *Kniphofia*; Majumdar & Lowry (1971a, b) for *Gasteria*; Majumdar (1972) for *Astroloba* and *Haworthia*; Majumdar & Riley (1970, 1973) and Yuhl & Majumdar (1981) for *Haworthia*; Zavada (1983) writing on the palynology of monocotyledons in general, and Riley & Majumdar (1979) in an overview of palynological research carried out on *Alooideae* taxa up to the late 1970's). Smith (1988), in a biosystematic investigation of the smaller genera of the *Alooideae*, studied and illustrated *Chortolirion* pollen by scanning electron micrographs. Since the latter study has shown that the appearance of the pollen grain surface and other pollen grain characters such as size and shape can be of taxonomic value in the delimitation of *Chortolirion*, the pollen morphology of the aberrant *C. bergerianum* was investigated. Apart from a comparative pollen morphological investigation of *C. angolense* and *C. bergerianum*, some physiological pollen characters (in-vitro and in-vivo germination) were also investigated. In this respect *C. angolense* was compared to *Haworthia attenuata* (Haw.) Haw. because *Chortolirion* has been included in *Haworthia* by some authors (Obermeyer, 1973; Dyer, 1976; Rowley, 1972, 1980).

A comparative floral and vegetative morphological study of *Chortolirion* taxa was conducted in parallel to complement the palynological investigation.

Fig. 1. Representative specimen of *Chortolirion bergerianum* Dinter collected in January 1923 near Windhoek, South West Africa/Namibia, on the farm Lichtenstein which belonged to Ernst Julius Rusch, amateur botanist and succulent plant enthusiast (*Dinter 4672*, B).

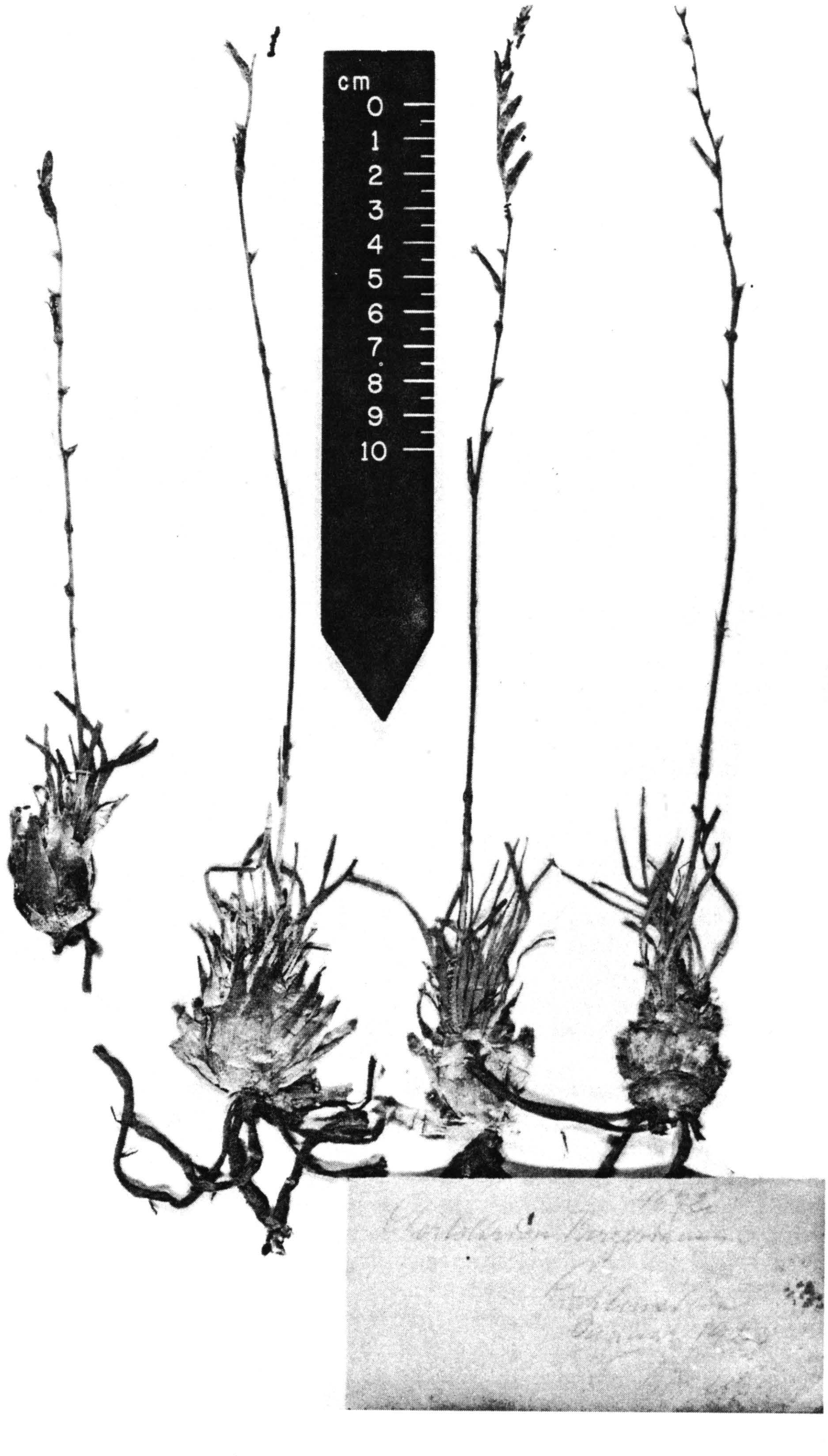
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Table 1. Species and voucher specimens of *Chortolirion* from which pollen was studied.

Name	Collector, date	Locality	Herbarium
C. angolense (Baker) A. Berger	G. F. Smith 12, 30 Sept. 1985	Middelburg (2529 CD)	PUC
	J. D. Sutton 381, 27 Jan. 1930	Lichtenburg (2626 AA)	PUC
	W. J. Louw 334, 30 Aug. 1939	Potchefstroom (2627 CA)	PUC
	B. Ubbink 318, 10 Sept. 1975	Potchefstroom (2627 CA)	PUC
	G. F. Smith 14, 12 Sept. 1986	Potchefstroom (2627 CA)	PUC
C. bergerianum Dinter	M. K. Dinter 4295, 14 Jan. 1923	Lichtenstein (2217 CC)	B
	M. K. Dinter 4320, 20 Jan. 1923	Lichtenstein (2217 CC)	B
	M. K. Dinter 4672, Jan. 1923	Lichtenstein (2217 CC)	B

In my revision of *Chortolirion* (in preparation) for the 'Flora of southern Africa' the genus *Chortolirion* will be reinstated and Berger's (1908) four species, *C. angolense* (Baker) A. Berger, *C. tenuifolium* (Engler) A. Berger, *C. stenophyllum* (Baker) A. Berger and *C. subspicatum* (Baker) A. Berger, will be united under the oldest name, *C. angolense*. For the purposes of this article, this conspecificity is assumed.

Materials and methods

Herbarium specimens of *Chortolirion* housed at B, BM, BOL, GRA, HBG, J, K, KMG, M, NBG, PUC, PRE, PRU, SAM, STE and Z were studied in order to gain a clearer understanding of the relationship between *C. bergerianum* and the other species previously described in *Chortolirion*. Holmgren & al. (1981), Stafleu & Cowan (1976) and Gunn & Codd (1981) state that some of Dinter's material is also kept at GRO and WIND. However, no Dinter collections of *C. bergerianum* have been found in the two latter herbaria. A full list of *Chortolirion* specimens examined is given in Smith (1985).

The morphology of the pollen of *Chortolirion angolense* and *C. bergerianum* was investigated using scanning electron microscopy (SEM). In the case of *C. angolense* anthers were taken from material collected in natural habitats and from herbarium specimens, while polleniferous parts of *C. bergerianum* were removed only from herbarium sheets. The localities of these collections are listed according to the grid reference system of Leistner & Morris (1976) and Raper (1987). Pollen sources and voucher specimens are indicated in Table 1.

Pollen was prepared for SEM using the filter technique of Bredenkamp & Hamilton-Attwell (1988), except that grains were fixed in FAA not 4% paraformaldehyde (Smith, 1988). Filter membranes containing pollen samples were air dried in a desiccator from 90% ethanol and attached to electron microscope stubs using conductive carbon cement. Samples were subsequently sputter-coated in an argon atmosphere with Au/Pd (60:40) to a thickness of 3 nm and studied with a Cambridge Stereoscan 250 S scanning electron microscope operated at 10 kV (for pollen dimensions) and 20 kV (for details of tectum).

Pollen dimensions were measured from scanning electron micrographs of at least 20 grains per sample. The descriptive terminology used mainly follows Erdtman (1969).

For the general assessment of pollen viability, specimens of *Chortolirion angolense* collected in situ in the Botanical Garden of the Botanical Research Institute, Pretoria, and of *Haworthia attenuata* cultivated in the Manie van der Schijff Botanical Garden of the University of Pretoria were used. The hanging drop technique (Stanley & Linskins, 1974) was adopted for the in-vitro pollen germination testing. Distilled water containing 0.0084% boron (added as boric acid) and 2% sucrose was used as the basic germination medium. Pollen of *C. angolense* and *H. attenuata* was collected at midday from newly opened flowers. Samples were taken directly from a dehiscing anther and dusted onto the drop of medium, then incubated at 37°C. Observations of germination percentage and tube length were made at regular intervals during a 12 hour period.

To confirm the viability of pollen of the specimens of *Chortolirion angolense* and *Haworthia attenuata* used in the in-vitro germination testing, intraspecific pollination was effected according to Brandham (1973) using the same specimens as pollen donors. Pistils of flowers of the seed parents were investigated in vivo. For the examination of pollen tubes in the style, the uppermost, withered, pollinated flowers of inflorescences of *C. angolense* and *H. attenuata* were fixed in Carnoy's fixative (absolute ethanol : chloroform : acetic acid in the ratio 6:3:1). The pistils were cleared and softened in 0.8 mol dm^{-3} NaOH at 50°C for 50 minutes and stained with 0.1% water soluble aniline blue in 0.3 mol dm^{-3} $K_3PO_4 \times 7H_2O$ for at least 2 hours. Specimens were gently squashed in a drop of staining medium to spread stylar tissue and enable the viewing of the pollen tubes. Aniline blue positive staining material (probably callose) occurs as plugs along the length of pollen tubes and enables their being followed in the style under ultraviolet light (Martin, 1959).

Results

Palynology of Chortolirion. – The morphology (size, shape, aperture features) of the pollen of *C. bergerianum* and *C. angolense* is basically the same throughout the specimens examined (Fig. 2-7). Although pollen samples of specimens of *Chortolirion* collected from localities to the west of Potchefstroom, western Transvaal, do not contain such large percentages of clavate grains as those from localities to the east of Potchefstroom, the results obtained during this study agree in large part with those previously reported for *Chortolirion* (Smith, 1988). The morphology of *Chortolirion* pollen is described below so as to include the entire range of variability for all investigated samples.

Pollen shed as monads. Grains bilaterally symmetrical (sensu Erdtman, 1966, 1969; cf. Nilson & Muller, 1978) (Fig. 2-3), occasionally with a pronounced inflation at one end of the dominant axis (clavate) and therefore only one plane of symmetry down the length of the dominant equatorial axis (bilaterally symmetrical sensu Blackmore & Tootill, 1988; cf. Smith, 1988) (Fig. 6). Amb pyriform (occasionally elliptical). Grains heteropolar with an inaperturate proximal wall and a distal, monosulcate aperture (Fig. 2-3; 5-6). Sulcus well-defined, usually about equal to the dominant equatorial axis and c. 1.3 μm wide towards the centre of the latter axis. Grain size (dominant axis) varying within fairly narrow limits (27 (30.7) 35 μm) within and between samples. Pollen grain surface perforated by numerous micropores (Fig. 4, 7). Sexine discontinuous and subtectate. Tectal ornamentation variable, from sparsely perforate in some pollen grains to densely perforate in others. Lumina in general, subcircular, somewhat rectangular or triangular and 0.3-0.8 μm in diameter. Muri c. 0.5 μm wide, smooth and rounded. Very few grains of *C. bergerianum* have irregular bands of thickenings which are seen as raised ridges in the SEM (Fig. 2).

The in-vitro germination results showed that more then 80% of the pollen grains of *Haworthia attenuata* germinated consistently in the basic medium (Fig. 8). The first germinations usually occur within 30 minutes of commencement of the test and the germination rate increases rapidly, the highest rate being normally reached within 3

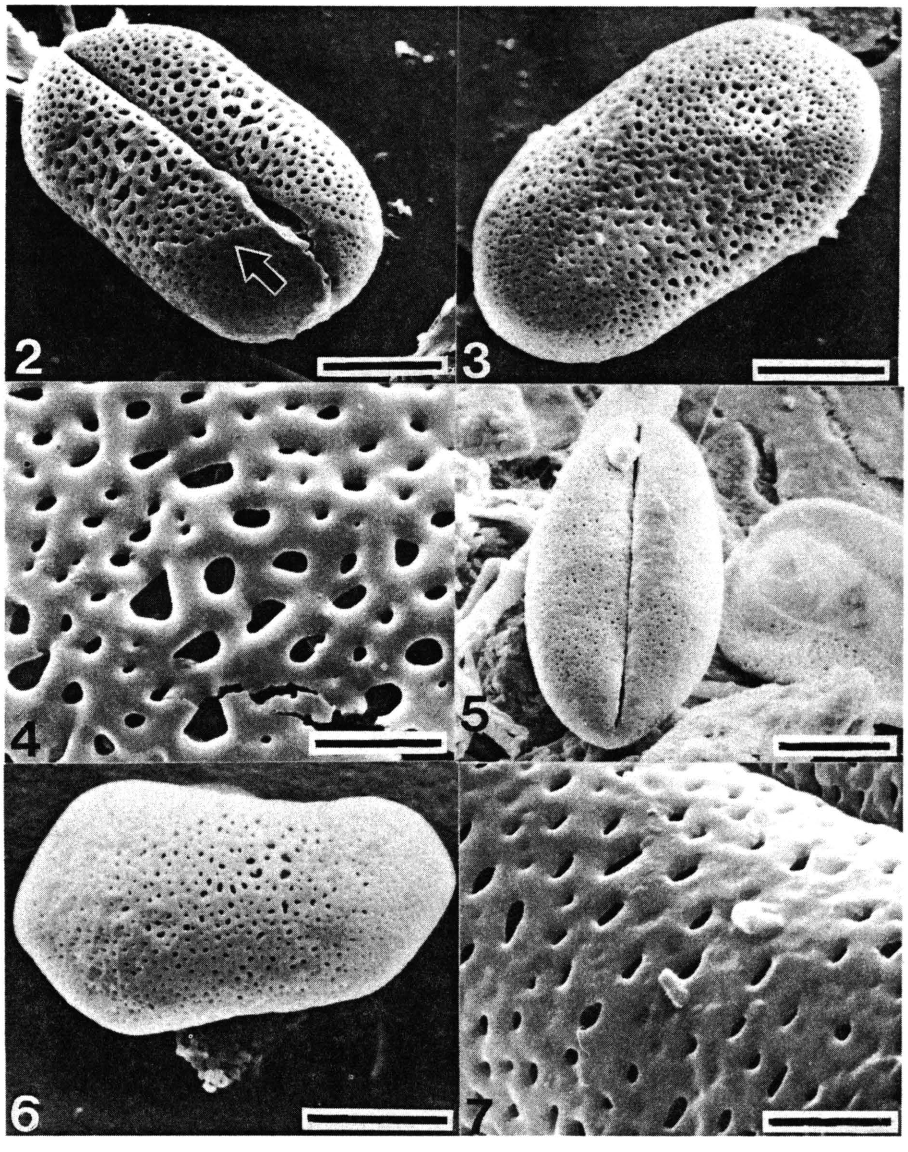

Fig. 2-7. SEM micrographs of pollen of *Chortolirion*; *C. bergerianum* (Fig. 2-4) and *C. angolense* (Fig. 5-7). *2.* Distal face showing irregular thickening seen as raised ridge (arrowed) and elongated aperture (sulcus). *3, 6.* Proximal surface. *4, 7.* Detail of proximal tectum surface in the apertural region showing perforations and smooth muri. *5.* Distal face showing elongated aperture (sulcus). (2, from *Dinter 4295*; 3, from *Dinter 4320*; 4, from *Dinter 4672*; 5, from *Ubbink 318*; 6, from *Smith 14*; 7, from *Louw 334*.) Scale bar = 10 μm in Fig. 2, 3, 5, 6; 2 μm in Fig. 4, 7.

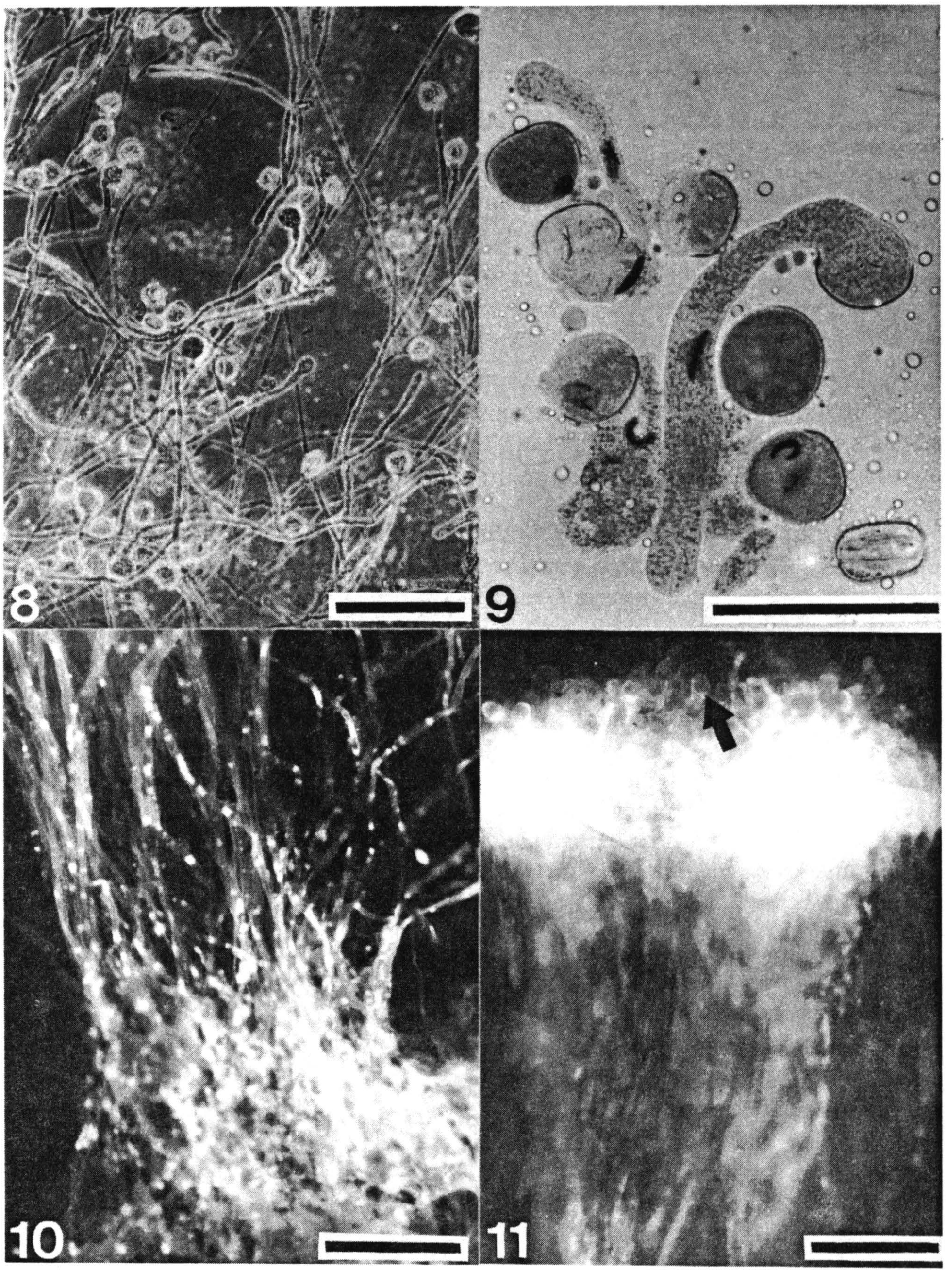

Fig. 8-11. Germination of pollen grains in *Haworthia* and *Chortolirion*. *8*. *H. attenuata*, in-vitro germinating pollen grains. *9*. *C. angolense*, in-vitro germinating pollen grains. *10, 11*. In-vivo pollen germination. *10*. Part of a squashed style of a pollinated flower of *H. attenuata* showing numerous fluorescent pollen tubes with plugs of callose under ultraviolet light. *11*. Squashed stigma of a pollinated flower of *C. angolense* showing numerous germinating pollen grains (arrowed) and UV-fluorescent pollen tubes. Scale bar = 100 μm in Fig. 8, 10, 11; 50 μm in Fig. 9.

Table 2. Summary of main morphological distinctions between *Chortolirion bergerianum* and other species of *Chortolirion* as given by Dinter (1914).

Species	Leaf margins	Floral buds	Leaf surface	Leaf articulation
C. angolense (Baker) A. Berger	—	reddish brown	—	present
C. tenuifolium (Engler) A. Berger	teeth absent	—	—	present
C. stenophyllum (Baker) A. Berger	—	—	abaxial pilose	present
C. subspicatum (Baker) A. Berger	teeth absent	—	—	present
C. bergerianum Dinter	finely toothed	brownish white	ab- and adaxial glabrous	absent

hours. No bursting of pollen tubes was observed. In contrast, less than 10% of *Chortolirion angolense* pollen germinated in vitro in the same basic medium (Fig. 9). The rate of in-vitro pollen tube growth of *C. angolense* were also much slower than in the case of *H. attenuata*.

Intraspecific cross-pollinations and subsequent staining of pollen tubes within the pistil of both *Chortolirion angolense* and *Haworthia attenuata* showed that a profusion of pollen grains germinate in vivo (Fig. 10, 11). The appearance of pollen tubes was similar in both species, with brightly UV-fluorescing plugs laid down at unequal intervals along their entire length. The pollen tubes were identifiable in the stigmatic region and could be traced along the entire length of the style. For both *C. angolense* and *H. attenuata* quantification of pollen germination on the stigmas and estimates of the total number of pollen tubes in styles were impossible because of the large numbers of pollen grains and pollen tubes. Since pollen grains of *C. angolense* germinated in vivo in large numbers (Fig. 11), there can be little doubt that the pollen samples of the same provenance used in the in-vitro investigation were viable. Furthermore, pollen of *C. angolense* has been observed to germinate spontaneously in the anther (Fig. 12).

Morphological variation in Chortolirion. – Since *Chortolirion bergerianum* was first described (Dinter, 1914), doubt has existed as to whether it is a distinct species. In his original description Dinter distinguished *C. bergerianum* from the four other species of *Chortolirion* recognized at that time by its denticulate leaf margins, brownish white floral buds, smooth ab- and adaxial leaf surfaces and by the absence of a leaf articulation zone (Table 2).

Examination of herbarium material and of live material from a wide range of localities grown under similar conditions indicated little difference in bulb morphology and a marked similarity in flowers and fruits throughout the complex. In contrast *Chortolirion* shows considerable variation in the denticulation of leaf margins, leaf shape and size, and flower colour over the whole of its distribution range. The present study has shown that *Chortolirion* is polymorphic with respect to the morphological features used by Dinter (1914) to distinguish the five species he recognized in this genus, which represent nothing more than local variants of a single, widespread and variable summer rainfall species. Unifying morphological features such as the presence of a bulb and the deciduous nature of the leaves are far more useful at the generic level and can be used to discriminate between *Chortolirion* and *Haworthia*.

Discussion

General. – The pollen of *Chortolirion* specimens studied agrees in general with that described for other genera of the *Alooideae* (see *Introduction* for references). Within *Chortolirion* there are no constant features by which individual grains could be allocated with confidence to different species. In particular, I could not find any consistent palynological differences between *C. angolense* sensu lato and *C. bergerianum.* In general the pollen grains of both *C. angolense* and *C. bergerianum* are free, medium in size (dominant equatorial axis), heteropolar and monosulcate with a pyriform amb and a perforated tectum. The majority of *Chortolirion* pollen grains studied have two vertical planes of symmetry and are bilaterally symmetrical sensu Erdtman (1966, 1969). Contrary to a previous report (Smith, 1968), only a small number of pollen grains were found to be clavate, that is, to have a single vertical plane of symmetry (bilaterally symmetrical sensu Blackmore & Tootill, 1988). The observed clinal variation in pollen grain symmetry (bilaterally symmetrical in western southern Africa, becoming clavate in eastern southern Africa) is not paralleled by any other reproductive or vegetative morphological feature. No significant secondary sculpturing superimposed on the perforated sexine is present. The irregular bands of thickenings seen as raised ridges on a number of *C. bergerianum* pollen grains are probably associated with thickenings of the nexine (Fig. 2). Due to its inconsistent occurrence this feature does not have any taxonomic significance. No narrow, unsculptured zone

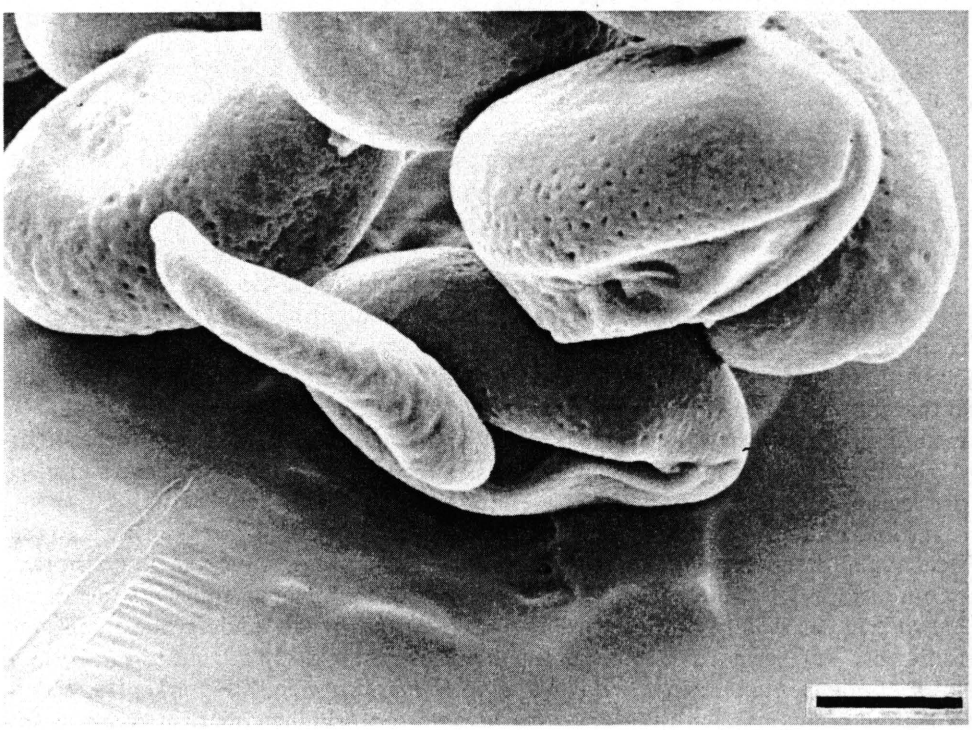

Fig. 12. Scanning electron micrograph of pollen tube of *Chortolirion angolense* which germinated in the anther. Untreated pollen sample taken from *Ubbink 318*, PUC. Scale bar = 10 μm.

bordering the aperture (sulcus) was observed. The existence of such a zone had previously been reported for pollen of *Haworthia* (Yuhl & Majumdar, 1981).

Significant physiological differences were found in the germination requirements of pollen grains of *Chortolirion angolense* and *Haworthia attenuata.* Pollen of *H. attenuata* germinated profusely in the basic medium whereas very few grains of *C. angolense* germinated under similar conditions. Since the quantity of pollen in a drop can affect the capacity of pollen to grow (Stanley & Linskens, 1974), care was taken to transfer pollen samples of more or less equal magnitude to the respective hanging drop apparatuses. The possibility that *Chortolirion* pollen has a desiccation requirement cannot be ruled out. This, however, would also be a significant physiological difference between *Chortolirion* and *Haworthia* pollen. Cleared styles and stigmas of *C. angolense* and *H. attenuata* showed that pollen of both species germinated readily following intraspecific cross-pollination.

Although on gross morphological grounds *Chortolirion angolense* is quite distinct from *Haworthia attenuata*, *Chortolirion* shares most reproductive morphological features with *H.* subg. *Hexangulares* Uitewaal ex Bayer (Bayer, 1971) to which *H. attenuata* belongs. The subgeneric classification of *Haworthia* of Bayer (1971) is supported by the fact that *H.* subg. *Haworthia* does not hybridize readily with plants of *H.* subg. *Hexangulares* (Cumming, 1987).

Neither vegetative nor reproductive morphology support the division of *Chortolirion* into more than one species. No single morphological character or combination of characters could be found to be diagnostic at the species level. The observed constancy in morphological features also agree with earlier observations on *Chortolirion* (Obermeyer, 1973; Smith, 1985).

Distribution and generic delimitation of Chortolirion. – *Chortolirion* is a perennial, deciduous herb with a subterranean bulb and is widespread mainly in the summer rainfall region of southern Africa. It has been recorded from all four provinces of the Republic of South Africa and from Angola, Zimbabwe, Botswana and Lesotho. It is summer-growing and is ecologically adapted to grassland which is subject to seasonal burning and to extreme temperature fluctuations (up to -10°C in winter and +39°C in summer). The genus *Haworthia* consists of about 68 species subendemic to South Africa (Bayer, 1982). Most species occur in the south-western Cape Province and respond to a winter growth cycle. A centre of endemism for *Haworthia* has also been reported from the eastern Cape Province (Smith & Marx, 1990). Two outliers occur further north, *H. limifolia* Marloth (Bayer, 1962) in Natal, Swaziland and the Transvaal, and *H. koelmaniorum* Obermeyer & Hardy (Obermeyer, 1968), probably including *H. mcmurtryi* Scott (1984), in the Transvaal. Limited to the southern tip of Africa, *Haworthia* is a floristic component of the coastal arid, semi-arid and summer-dry regions below the climatically severe inland escarpment.

In the subfamily *Alooideae* of the *Asphodelaceae* some work has been done in the field of generic concepts and it does not seem premature to pass judgement on the taxonomic status of *Chortolirion.* This genus is morphologically quite distinct from *Haworthia*, especially with regard to the presence of an underground bulbous rootstock. Furthermore, *Chortolirion* is florally more closely related to *Haworthia* subg. *Hexangulares* Uitewaal ex Bayer than to *H. blackburniae* W. F. Barker (1937) and *H. graminifolia* G. G. Smith (1942) which also possess thin, narrow, denticulate leaves but are classified in *H.* subg. *Haworthia. Chortolirion* is unique amongst haworthioid species in that it is the only grassland taxon of which the leaves are deciduous and die back to ground level after fires or frost. The combination of these features support the proposed recognition of *Chortolirion* as a separate entity. For the sake of nomenclatural stability (cf. Greuter & al., 1988) I have avoided transfer of *Chortolirion* to infrageneric rank under *Haworthia*. Such a transfer had previously been proposed for the related genera *Astroloba* Uitewaal and *Poellnitzia* Uitewaal (Parr, 1971-1972) but was not accepted by Bayer (1982), Groen (1986, 1987), Scott (1985) and Smith (1985), amongst others. Such a treatment would thus not be in accordance with traditional usage within the *Alooideae*.

Conclusion

The present study has shown that the pollen morphology of *Chortolirion bergerianum* and *C. angolense* sensu lato is identical. Furthermore, efforts to distinguish between *C. bergerianum* and the other species previously published in *Chortolirion* on the basis of gross morphology were unsuccessful. In view of the lack of characters which support the discreteness of *C. bergerianum* from Namibia I am convinced that this entity is conspecific with *C. angolense*. It is thus proposed that, along with *C. tenuifolium* (Engler) A. Berger, *C. stenophyllum* (Baker) A. Berger and *C. subspicatum* (Baker) A. Berger, *C. bergerianum* Dinter should be included in the synonymy of *C. angolense* (Baker) A. Berger, the only species in this natural, monotypic genus. Additional support for the recognition of *Chortolirion* as an entity discrete from *Haworthia* is provided by the different pollen germination requirements of these genera.

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Pollen morphology of the monotypic genus *Poellnitzia* (Alooideae: Asphodelaceae)

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Abstract

Poellnitzia Uitewaal (subfamily Alooideae, family Asphodelaceae) has a history of taxonomic confusion and doubtful generic delimitation. It has previously been variously combined with, and separated from, four other genera of the Alooideae. In this study, the taxonomic significance of its pollen morphology was assessed by means of scanning electron microscopy. Plants collected from two populations in the Robertson area, where *Poellnitzia* is endemic, were included in the survey. *Poellnitzia* is remarkably homogeneous in its pollen morphology; grains are free, monosulcate, bilaterally symmetrical, medium in size and have a perforated tectum. The mean pollen size of *Poellnitzia* (36,4 µm) is greater than that of *Chortolirion* and *Haworthia*. However, no significant differences in pollen symmetry, shape, aperture features and fine structure between *Poellnitzia* and other genera of the Alooideae could be detected. This is in striking contrast to the strong macromorphological evidence for separating *Poellnitzia* from the other Alooideae genera. The similarity in pollen morphology merely supports the inclusion of *Poellnitzia* within the subfamily.

Uittreksel

Poellnitzia Uitewaal (subfamilie Alooideae, familie Asphodelaceae) het ´n geskiedenis van taksonomiese verwarring en onduidelike genusafbakening. Dié monotipiese genus is voorheen as ´n spesie van vier ander Alooideae-genusse geklassifiseer. In hierdie ondersoek is die taksonomiese waarde van

stuifmeelmorfologie met behulp van die skandeerelektronmikroskoop ondersoek. Plante wat in twee populasies in die Robertson-omgewing versamel is, is in die ondersoek ingesluit. *Poellnitzia* is endemies tot die Robertson Karoo. Stuifmeelkorrels van *Poellnitzia* is vry, monosulkaat, bilateraal-simmetries, medium-groot en het ´n geperforeerde tektum. Die gemiddelde stuifmeelkorrelgrootte van *Poellnitzia* (36,4 µm) is groter as dié van *Chortolirion* en *Haworthia*. Op grond van stuifmeel-korrelsimmetrie, -vorm, -apertuur en -skulptuur, bestaan daar egter geen beduidende verskille tussen *Poellnitzia* en die ander Alooideae-genusse nie. Stuifmeel van die spesies stem bykans volkome ooreen en dit is onmoontlik om op grond van palinologiese kenmerke tussen die genusse te onderskei. Stuifmeel weerspieël dus nie die makromorfologiese kenmerke aan die hand waarvan *Poellnitzia* van die ander Alooideae-genusse onderskei kan word nie.

Keywords: Alooideae, Asphodelaceae, palynology, *Poellnitzia*, pollen, scanning electron microscopy

Introduction

In a reclassification of the inclusive family Liliaceae, Dahlgren *et al*. (1985) reinstated the family Asphodelaceae, as well as several other segregate families. Within the Asphodelaceae two subfamilies, namely Asphodeloideae and Alooideae are recognised. The Alooideae constitutes a natural assemblage of more or less succulent-leaved taxa which were previously placed in the Aloineae, one of 28 tribes recognized by Hutchinson (1959) in the family Liliaceae (*sensu lato*). According to Rowley (1976) 27 generic names are available for taxa included in the subfamily Alooideae. However, only seven genera are currently upheld. This reflects to some extent the considerable difficulties with generic delimitation in the subfamily. Widely recognised genera include: *Aloe* L., *Astroloba* Uitewaal, *Chortolirion* Berger, *Gasteria* Duval, *Haworthia* Duval, *Lomatophyllum* Willdenow and *Poellnitzia* Uitewaal. Of these *Chortolirion* and *Poellnitzia* warrant monotypic generic status (Bayer 1972; Smith 1988), but are included under *Haworthia* by Obermeyer (1973) and Dyer (1976).

Specimens on which the name *Poellnitzia rubriflora* (L. Bol.) Uitewaal is based were originally described in the genus *Apicra* Haworth *non* Willdenow as *A. rubriflora* (Bolus 1920). However, in terms of its red flowers and aberrant floral morphology, this species differs considerably from other members of *Apicra*. This prompted Uitewaal (1940) to afford the taxon monotypic generic status as *Poellnitzia rubriflora*. Parr (1971-1972) transferred *Poellnitzia* to the genus *Haworthia* whilst Rowley (1981) claimed that it has more characters in common with Aloe. In a revision of the smaller genera of the Alooideae currently undertaken by one of us (G.F. Smith) the genus Poellnitzia will be reinstated with P. rubriflora [including P. rubriflora var. jacobseniana (Von Poellnitz) Uitewaal] the only species. It is a low-growing, caulescent, succulent herb with densely leaved stems up to 250 mm long. The ovate leaves are pungent-acuminate and up to 40 mm long. Poellnitzia has a restricted geographical distribution in the south-western Cape Province of South Africa. It is a floristic component of the Robertson Karoo which is one of the drier winter rainfall areas bordering the Fynbos Biome.

Palynologicial evidence for the Alooideae is fragmentary and incomplete (Majumdar 1972; Yuhl & Majumdar 1981; Smith 1988, 1991). Since the pollen of Poellnitzia has not previously been examined by scanning electron microscopy (SEM), nor illustrated, the present study aims to explore whether this source of evidence might provide clues to its intergeneric relationships, including possible additional support for its segregation from Aloe, Astroloba (a new name for Aprica Haw. non Willd.) and Haworthia.

Materials and Methods

For SEM study pollen of Poellnitzia rubriflora was obtained from mature flowers on dried herbarium specimens kept in the herbarium of the Potchefstroom University for Christian Higher Education (PUC), from post-anthesis flowers of specimens grown in the greenhouse of the Department of Plant Sciences and from FAA fixed material. All the specimens examined originated from two populations about two kilometres apart on the farm "Langverwacht" (34°06′S 20°02′E), 180 m altitude, approximately 24 km from Robertson to Bonnievale, south-western Cape Province, South Africa (G.F. Smith 174, G.F. Smith 177).

Pollen of Poellnitzia was found to be sensitive to standard SEM preparation schedules and therefore two non-destructive techniques were employed. For examining exine sculpture pollen grains were prepared using the filter technique of Bredenkamp & Hamilton-Attwell (1988) (herbarium material and fixed material). Filter membranes containing pollen samples were air dried in a desiccator from 90% ethanol and attached to electron microscope stubs using conductive carbon cement. For determining pollen grain dimensions, symmetry and shape the osmium tetroxide method of Smith & Tiedt (1991) was used. Freshly collected post-anthesis anthers were placed in a petri dish containing small drops of 2% OsO_4. The lid of the petri dish was replaced and it was left in a fume hood for 24h. The OsO_4 drops were then removed and the samples left to air-dry. The fixed plant material was subsequently mounted onto electron microscope stubs and, along with the material prepared by means of the filter technique, sputter coated with a thin layer of Au/Pd (60:40) and examined with a Cambridge Stereoscan 250 S SEM. Pollen dimensions were measured from scanning electron micrographs. The descriptive terminology used mainly follows Erdtman (1966, 1969).

Results

Pollen grains of *Poellnitzia* are regularly differentiated on size, shape and aperture features. The results obtained are therefore basically the same throughout the specimens examined. The morphology of *Poellnitzia* pollen is described below so as to include the range of variability for all the investigated samples.

Pollen shed as monads. Grains bilaterally symmetrical (Figure 1A, B) and heteropolar with an inaperturate proximal wall (Figure 1A, C) and a distal, monosulcate aperture (Figure 1B, C). Sulcus well-defined and usually about equal to the dominant equatorial axis. Aperture margins are usually very narrow, but conspicuous (Figure 1B, F). Grain size (dominant axis) varying within fairly narrow limits (33-) 36,4 (-42) µm within and between samples. Amb pyriform (occasionally elliptical).

Exine surface perforated by numerous pori (Figure 1D-F). Sexine discontinuous, semitectate; classified as a tectum perforatum *sensu* Praglowski & Punt (1973).

Figure 1E shows a torn distal wall of a pollen grain exposing the infratectal bacula (columellae) and a thin footlayer. It is apparent from this micrograph that the perforations are formed by numerous lumina which occur between the muri, thus agreeing with the state in *Haworthia* (Yuhl & Majumdar 1981) and *Chortolirion* (Smith 1988). As in the case of *Chortolirion* (Smith 1988) distinct areas of coarse (central zone on both sides of pollen grain) and a fine (ends of longest equatorial axis; areas bordering sulcus) reticulum are present in *Poellnitzia* pollen (Figure 1A, B, F) (see also Roth *et al*. 1986).

Discussion

Morphologically the pollen of *Poellnitzia* agrees with that described for other genera of the Alooideae (Smith 1988, 1991). As in other Alooideae, pollen grains of *Poellnitzia* are free, bilaterally symmetrical, medium in size (dominant equatorial axis), heteropolar and monosulcate with a pyriform amb and a perforated tectum. It also agrees with other members in that the ektexine is composed of a foot layer, infratectal bacula (columellae) and tectum. The mean pollen size of *Poellnitzia* is, however, greater than that of *Haworthia* and *Chortolirion* (Smith 1988), although not significantly so. In both *Poellnitzia* (this study) and *Haworthia* (Yuhl & Majumdar 1981) there is an abrupt transition from a perforated sexine to a smooth surface lacking pori in the apertural region. Such apertural margins have not been observed in *Chortolirion* (Smith 1988).

Although geographical isolation may have played a role in the diversification of the Alooideae, (*e.g.* *Poellnitzia* which is endemic to the Robertson Karoo), specialization through isolation has not resulted in the concomitant evolution of distinctive pollen morphological features useful as generic indicators [see also Takahashi (1987) on *Erythronium* L. (Liliaceae) and Rogers (1985) on *Cliococca* Babington (Linaceae)].

Owing to the lack of palynological variation amongst genera of the Alooideae, pollen morphological features are difficult to apply taxonomically at the generic level. Hence, the lack of differentiating characters between the pollen of Poellnitzia and other aloeoid genera does not necessarily invalidate or justify the proposed treatment of Poellnitzia as a separate genus. However, a recent cladistic analysis of the subfamily (G.F. Smith & B-E. van Wyk unpublished), based on a wide range of vegetative and reproductive characters, has shown that Poellnitzia cannot be realistically included in any other genus of the Alooideae. Pollen morphological similarities rather support the claimed monophyly of the subfamily. Despite the lack of palynological support, it is recommended that Poellnitzia be regarded as a monotypic genus with P. rubriflora as the only species.

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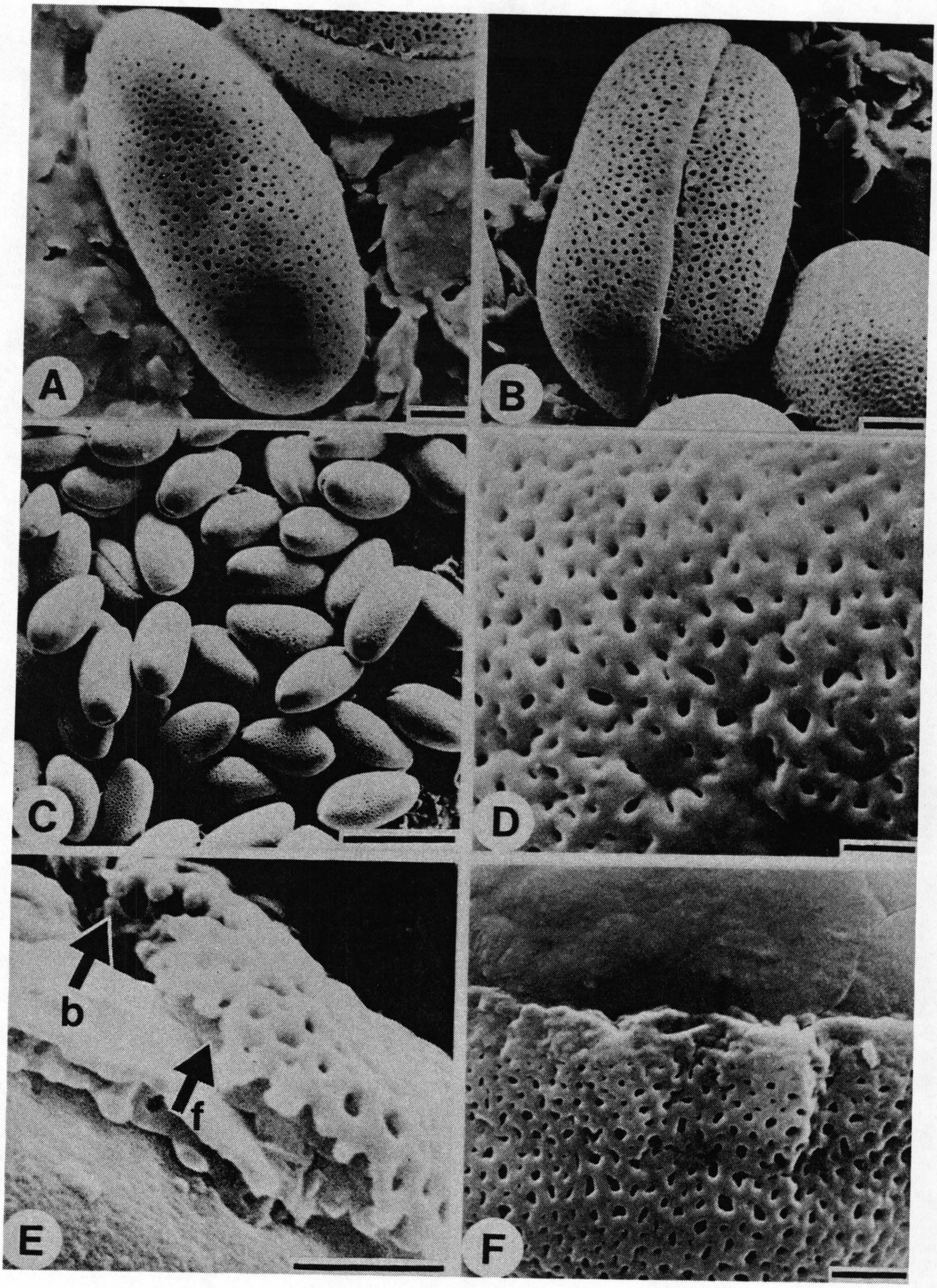
Caption to Figure

Figure 1 Scanning electron micrographs of pollen of *Poellnitzia rubriflora*. (A) Proximal surface. (B) Distal face showing elongated aperture (sulcus). (C) Group of pollen grains showing uniform symmetry, tectal ornamentation and aperture shape/length within a sample. (D) Detail of tectum surface in a non-apertural region showing perforations and smooth muri interconnected to form a tectum perforatum *sensu* Praglowski & Punt (1973). (E) Damaged sexine layer exposing the bacula (b) and foot layer (f). (F) Detail of distal tectum surface in the apertural region showing the transition from a coarse to a fine reticulum and the presence of a smooth area bordering the sulcus. Figure 1A, B, C from *Smith 174*, prepared for SEM using the osmium tetroxide technique of Smith & Tiedt (1991); Figure 1D, E, F from *Smith 177*, prepared for SEM using the filtering technique of Bredenkamp & Hamilton-Attwell (1988). Scale bar = 5 µm in Figure 1A, B; 40 µm in Figure 1C; 2 µm in Fig. 1D-F.

a:monognus.spr


A
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NOTES ON THE MICROFAUNAL COMPLEMENT AND POLLINATION MECHANISM OF *POELLNITZIA RUBRIFLORA* (ASPHODELACEAE: ALOOIDEAE)

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Summary

The monotypic *Poellnitzia* Uitewaal is one of seven genera currently recognized in the subfamily Alooideae, family Asphodelaceae. It is endemic to a small area in the Robertson Karoo, south-western Cape Province, South Africa. A synthesis of natural history observations, breeding experiments and all available information on, amongst others, inflorescence architecture, flower morphology, floral attractants and rewards and several floral inhabitants and visitors, suggest that an undescribed species of mite, *Adhaerenseius floralis* Loots & Theron *ined.*, and its phoretor probably fulfil the role of pollination agents. It is also proposed that the connivent flowers of *Poellnitzia* serve as acarodomatia and that this association is comparable in scope to the widely recognized mite-leaf domatia associations.

Introduction

Although the Alooideae is the largest and best-known of the two subfamilies of the Asphodelaceae (*ca.* 450 species) there is a dearth of basic information regarding the ecology and biology of its pollination. This situation is symptomatic for the Asphodelaceae as a whole and for monocotyledonous taxa in general, where floral biology usually has been over hypothesized and understudied (see for example Goldblatt *et al.* 1989 on *Moraea* Mill. and Iridaceae). In the course of this investigation, too, it has become apparent that anthecological (= pollination biological) studies in the Alooideae will benefit greatly from less speculation and more, detailed field observations and controlled pollination experiments.

Descriptions of pollination syndromes in the Alooideae are limited to *Aloe*. Prior to the detailed study of the pollination ecology of *A. ferox* Mill. (Hoffman 1988), only very brief descriptions of ornithophyly in the genus have been published by Vogel (1954) and Skead (1967). As noted by Marloth (1915), Rowley (1976) and Baker (1983) bees also visit the flowers of most species of *Aloe* and probably play some part in its pollination.

This contribution is primarily concerned with the pollination mechanisms of the monotypic and little-known aloeoid genus, *Poellnitzia* Uitewaal. *P. rubriflora* (L. Bol.) Uitewaal is a low-growing, caulescent, succulent herb. Stems are up to 250 mm long and densely leaved. The ovate leaves are pungent-acuminate and up to 40 mm long. The inflorescence, produced during the summer months, is an unbranched raceme, up to 500 mm long and bears red to brightly orange flowers in secund fashion. The genus has a restricted distribution in the Robertson and Bonnievale districts of the south-western Cape Province of South Africa (Wood 1991). This region receives its precipitation mainly during the winter months whilst the summer months are hot and dry.

In contrast to the open, broadly tubular flowers, often with exserted stamens and styles, of most other members of the Alooideae, the limb of flowers of *Poellnitzia* is formed by six segments closely adhering apically. The fact that *Poellnitzia* flowers do not open in the true sense of the word, suggests that it deviates from the typically ornithophilous and/or mellittophilous pollination syndromes that have been suggested for the subfamily (Hoffman 1988; Stokes & Yeaton 1991).

Materials and Methods

Study sites

Two populations of *Poellnitzia rubriflora* which occur east of "Langverwacht" (34°06'S 20° 02'E), 180 m altitude, approximately 24 km from Robertson to Bonnievale, south-western Cape, were observed during day-time for three approximately six hour periods between December 3 and 6, 1988. A third population of the species which occur in the Vrolijkheid Nature Reserve, McGregor (33°56'S 19°54'E), 15 km south of Robertson, was observed for a two hour period on December 5, 1988. These populations were used for determining:

a. Inflorescence and floral development and morphology;
b. Fruit production;
c. Number of microfaunal visitors.

All observations were made by G.F. Smith and P.D. Theron.

Individuals collected at the respective sites were grown in the greenhouse of the Department of Plant Sciences, Potchefstroom University for Christian Higher Education, and were used for determining:

a. Self-compatibility;
b. Nectar volume and sugar composition.

Herbarium specimens, *Smith 174, 177, 182* were deposited at PUC. *Poellnitzia rubriflora* occupied open, north and west facing slopes with rocky outcrops and isolated shrubs of, amongst others, *Pteronia incana* (Burm.) DC. and *Tylecodon paniculatus* (L.*f.*) Toelken which cast shade locally.

Collection of insects

Arthropods were collected by hand when they were observed visiting the flowers of *P. rubriflora*. Insects were placed in a killing jar containing carbon tetrachloride. Acarine and insect specimens were subsequently preserved in 75% ethanol and were submitted for identifcation to specialists on the respective taxa (Table 1).

[INSERT TABLE 1 NEAR HERE]

Results

Presentation of inflorescence and floral morphology

The flowering stem consists of an arched, unbranched peduncle of which the lower half is more or less sterile bracteate. The comparatively widely spaced bright orange to red flowers are borne in secund fashion (upward-pointing) in a raceme which takes up the upper half of the flowering stem. The entire inflorescence can be up to 500 mm long. The erectly-spreading racemes protrude above the low xerophytic shrubs with which *Poellnitzia* is usually associated. Especially during the dry summer months these lax racemes are·conspicuous against the otherwise drab vegetation.

The flowers can reach maturity at any time of day or night. Up to three inflorescences can be produced consecutively by a single specimen, and each consists of many flowers. The flower buds mature acropetally and sequentially with usually only between three and eight post-anthesis flowers being borne between immature and shrivelled floral tubes. This encourages a pollinator to visit other plants as well and therefore favours cross-pollination. Plants have mature flowers every day during the flowering time.

Similar to most species of Alooideae the *Poellnitzia* flower consists of two whorls of three tightly packed tepals each, the outer series being slightly larger than the inner. The flowers are narrowly tubular and slightly constricted above the ovary and below the segment lobes. Flowers of *Poellnitzia* are elongate (18 (20,7) 24 mm), especially in comparison to those of *Astroloba* and *Haworthia* to which *Poellnitzia* has been likened on vegetative morphological grounds. However, the flower morphology of *Poellnitzia* is unique in the Alooideae in that the dark green, free portion of the segment lobes (upper one-tenth of perigone members) are connivent and reduplicate-valvate with the very tips of the segments scarcely separated. The apex margins are minutely crenulate-erose and yellowish. The upper one-third of the flowers is usually slightly decurved and, along with the perianth connivence, afford the flowers a lantern-like appearrance (Figure 1). Six small but distinct cuspidate ostioles are present at the point where the perianth segments can be basally distinguished as separate entities (approximately 3 mm from the point of attachment of the flower to the pedicel). Similar ostioles have also been observed in the flowers of representatives of the related genus *Haworthia*.

[INSERT FIGURE 1 NEAR HERE]

Floral attractants and rewards

The buds, anthesis flowers and shrivelled flowers of *Poellnitzia* are predominantly bright orange to red and odourless. The existence of a yellow-flowered form (Keen 1982), has not yet been substantiated by field observations. For the purposes of this study anthesis is defined as beginning when the reduplicate-valvate perigone apices are fully expanded, *i.e.* when potential pollinators can gain comparatively unhindered access to the anthers and pollen. The anthers and pollen are pale to bright yellow. The anthers, however, remain enclosed within the floral tube and are never visible to floral visitors. Clearly they cannot play any part in attracting potential pollinating agents. In contrast, pollen accumulates on the external margins of the flower apex and enhances their yellowish colour. This phenomenon has never been observed in specimens grown *ex situ* and can probably be attributed to microarthropod activity in the flower tube.

Although colour is clearly the main pollinator attractant (especially avian species), flower size is also remarkably constant and probably is functionally important. It appears that strong selective pressures acting on flower size and colour have served to restrict variability. Any flower visitor therefore responds to a very constant search image (see for example Balfour & Linder 1990 on *Disa uniflora* Berger, Orchidaceae).

Individual flowers of most taxa of the Alooideae are nectariferous, *Poellnitzia* being no exception. (Nectar secretion has never been observed in the Madagascan miniature, *Aloe albiflora* Guill.). In the subfamily nectar secretion occurs by means of septal nectaries (Schnepf & Pross 1976), the nectar accumulating at the base of the flower tube. Flower size is correlated with nectar volume, the large-flowered species of *Aloe*, *Gasteria* and *Poellnitzia* producing nectar in much larger quantities (ca. 25--50 μl) than representatives of, for example, *Chortolirion* and *Haworthia* [cf. Beyleveld (1973) on selected species of series *Saponariae* of *Aloe* and Mottram (1977) and Hoffman (1988) on *A. ferox*]. The sugar composition (glucose, fructose, sucrose) of the nectar of representative samples of *Kniphofia* and all the genera of Alooideae was recently determined. This investigation revealed that sugar composition is remarkably constant within a genus and that three distinct nectar types can be recognised (B-E. van Wyk personal communication). The nectar of *Poellnitzia* is of the aloeoid type (sucrose virtually absent; fructose and glucose present in more or less equal quantities). This nectar type is also present in *Aloe* (including *Chamaealoe* Berger), *Kniphofia* Moench and *Lomatophyllum* Willd. In contrast to other ornithophilous taxa, such as *Strelitzia reginae* Ait. which shows considerable change in sugar composition over the nectar producing period (Kronestedt-Robards *et al.* 1989), all the investigated aloeoid taxa were shown to be very constant in their nectar sugar composition throughout the flowering period (Van Wyk 1991).

There is little correlation between flowering time and the rainy season. As is the case for most southern African species of *Aloe*, *Poellnitzia* flowers in the non-rainy season. This appears to be an adaptation to seed dispersal prior to and subsequent successful seedling establishment during the following rainy season. Since moisture in the form of rainfall is therefore not readily available when *Poellnitzia* flowers, copious nectar secretion might be limited. However, at higher altitudes (for example the Elandsberg south of Robertson which appears to be the epicentre of *Poellnitzia* distribution) mist precipitaiton probably provides sufficient water to sustain nectar production (Rebelo 1987).

Breeding system and fruit production

Self-compatibility is a common phenomenon in the Alooideae [see for example Hoffman (1988) on *Aloe ferox*]. However, some clones of *Gasteria disticha* (L.) Haw., *G. carinata* (Mill.) Haw. and *G. bicolor* Haw. (Marshak 1934), *G. vlokii* Van Jaarsveld (1987) and *Haworthia longiana* Von Poellnitz (personal observation) have been found to be self-compatible. Sears (1937) established that self-incompatibility in *Gasteria* was due to the inhibition of gametic fusion and not to stylar inhibition of pollen tube growth. This was confirmed by Brewbaker & Gorrez (1967) who suggested that self-incompatibility in *Gasteria* probably results from the inhibition of syngamy or ovule integument enlargement. Although the microperforate exine sculpturing of pollen of *Poellnitzia* [Smith & Tiedt (1991); tectum perforatum *sensu* Praglowksi & Punt (1973)] correlates with the proposed exine morphological requirements for a gametophytic self-incompatibility system, (Zavada 1984), predictions of the type of self-incompatibility mechanism from pollen morphology should be treated with considerable caution (Gibbs & Ferguson 1987). However, the perforations in the tectum would greatly increase the surface area for pollenkitt adhesion in animal pollination (Bolick 1986).

In the case of the protandric flowers of *Poellnitzia*, the stigma reaches the level of the anthers shortly after anthesis and self-pollination is therefore inevitable. However, all attempts at self-fertilization (autogamy, geitonogamy) have been unsuccessful during seven consecutive flowering seasons (1984--1990). In fact, not a single capsule has ever been produced from selfing of clones of *Poellnitzia rubriflora*. The species is clearly an obligate outbreeder. In general the stigma is not exserted beyond the connivent flower apex. In very few cases the stigma has been observed to protrude beyond the flower apex. Stigmatic exposure would also promote cross-pollination.

Percentage fruit success (the number of fruits produced as a percentage of the number of flowers available) is very erratic and varies from 0 to more than 90. An average of approximately 40% of the flowers in an inflorescence (26--32 flowers/inflorescence) develop into capsules. However, there is a marked periodicity in capsule set. A number of developing and mature capsules, equal to about 25--50% of the number of flowers on an inflorescence, would usually be bordered by regions similar in size lacking any fruit. Unfertilized flowers usually abscise within four days after anthesis, whereas successful fertilization results in the almost immediate enlargement of the ovary. The periodicity in fruit production can probably be attributed to drosophilid infestations.

Floral visitors and inhabitants

Two species of ant belonging to a single family, two acarine species belonging to one of two families, a species of thrips and a dipteran (fly) species were collected from the flowers of *Poellnitzia rubriflora* (Table 1). Since many of the animal species that frequent the flowers of *Poellnitzia* are inhabitants and not visitors, the frequency categories (rare, occasional, common, very common) used in Table 1 refer to numbers of a species present (relative to the very common *Adhaerenseius*), rather than to number of visits.

By far the most common inhabitant of *Poellnitzia* flowers was an acarine (mite) species which, upon investigation, proved to be undescribed. Loots & Theron (1991) have since established that a new genus should be created for the species and have proposed the name *Adhaerenseius floralis* Loots & Theron *ined.* for the taxon. Large numbers of this species, which belongs to the family Ascidae, occur inside each flower throughout the flowering period. The second acarine species belongs to the genus *Brevipalpus* (family Tenuipalpidae) and was present in the flowers in much smaller numbers.

Camponotus fulvipilosus, a large species of formicine ant, frequents the inflorescences of *Poellnitzia rubriflora* and rapidly moves between different, usually adjacent, clones of the plant. The second species of ant, *C.* cf. *werthi*, observed on *Poellnitzia* is considerably smaller than *C. fulvipilosus* and occurs inside the flowers. They gain access to the flowers by chewing away part of the connivent flower apex.

The small, black, drosophilid species parasitizes the ovaries and/or capsules of *P. rubriflora*. They lay their eggs in these structures which are subsequently destroyed by feeding larvae. Any aberration of the otherwise very smooth and regularly tubular flower is a clear indication of drosophilid infestation.

The full-grown species of thrips is only about 1 mm in length, yellowish-green in colour and inhabits *Poellnitzia* flowers. They occur in fairly small numbers and are not nearly as plentiful as *Adhaerenseius floralis*. In general thrips are common on flowers of especially Asteraceae, and most feed on juices of plants (Ledger 1979).

Discussion

Of the microfaunal visitors to and inhabitants of *Poellnitzia* flowers the *Brevipalpus* species and the unidentified species of thrips are present in such low numbers that they probably play no part in pollination. The larvae of the drosophilid species extensively parasitize the flowers of *Poellnitzia*, particularly the ovaries and capsules, thereby depressing seed yield significantly. Furthermore, they were not observed to forage on different clones of *Poellnitzia* and probably leave the habitat once they have laid their eggs. It is therefore unlikely that they can affect cross-pollination.

Probably the most significant observation that was made during the study period was that not a single avian species was seen to visit or even approach specimens of *Poellnitzia*. In fact, birds were not observed at the study sites at all, even though large numbers of the distinctly ornithophilous *Tylecodon paniculatus* (L.f.) Toelken (family Crassulaceae) were also in full bloom. The latter species has broadly tubular, yellowish flowers which secrete nectar copiously and bright crimson peduncles which probably serve as the most important secondary attractant of pollinators. The only explanation that can be offered for the absence of avian foragers is that a very strong south-easterly wind, at times approaching gale force velocities, blew during the study period. Although wind velocity will undoubtedly influence pollinator activity and efficiency, it seems unlikely that birds will not visit *Poellnitzia* flowers during windy spells. This is especially the case since the plants usually grow in protected habitats, such as north-facing slopes and in the shelter of rocks and woody, xerophytic perennials. Furthermore, high wind velocities favour ornithohpily over entomophily (Rebelo & Jarman 1987). It is noteworthy that malachite sunbirds, which feed on the nectar of a variety species, are captured illegally and sent overseas by smuggling syndicates (Simpson 1991). Although this practice will deplete the number of birds present in any habitat, it does not explain the total absence of birds from *Poellnitzia* localities.

Although ornithophily has not been recorded for *P. rubriflora* in habitat, the species shows distinct flower morphological adaptations which indicate bird pollination. These are: secretion of a plentiful supply of slightly viscous nectar at the base of the perigone tube; large pollen-nectar distance; bright reddish orange flowers; absence of odour and nectar guides; distinctly curved tubular flowers; and secund flower arrangement. Furthermore, the distribution of five avian species which utilize nectar as a major food source overlaps with the restricted distribution of *Poellnitzia* (Table 2; Figure 2). Species of sunbird can gain access to the nectar reward of a number of flowers with intriguing morphologies (Burton & Burton 1970). It is therefore unlikely that they will not be able to unlock the connivent flowers of *Poellnitzia*. Birds have been observed on *P. rubriflora* at the Karoo National Botanic Garden, Worcester, (M.B. Bayer personal communication) where the species is used as a border plant, along with many other aloeoid species. This, however, represents an artificial horticultural situation and the birds could well have been attracted by, amongst other, *Aloe ciliaris* Haw. var. *tidmarshi* Schonl. blooming *en masse*. Clearly, extrapolation of garden observations to the natural habitat should be treated with caution.

[INSERT TABLE 2 & FIGURE 2 NEAR HERE]

Two major classes of bird blossoms, namely the brush and tube type (Faegri & Van der Pijl 1979; Rebelo 1987) are encountered in the Cape Floristic Kingdom, where *P. rubriflora* is a floristic component of the Robertson Karoo vegetation. The tube type is defined as having a narrow tube which excludes most nectar feeding visitors with mouthparts shorter than the effective tube length. In contrast, the brush type of inflorescence is defined as having an external surface of the pollination unit formed by the sexual organs, with the perianth reduced or split into segments interspersed between the sexual organs (Faegri & Van der Pijl 1979). Within the tube type category a further distinction can be made on the ground of anther exposure: those with internal anthers (typical tube) and those with anthers exserted (brush-tube). Clearly, the pollen, but not the nectar, of brush-tube blossoms is accessible to non-avian visitors. Along with, amongst others, *Leonotis leonurus* (L.) R. Br. (Getliffe Norris 1989) and some sections of *Erica* L. (Rebelo 1987), *Poellnitzia* which have included anthers should be classified in the typical tube blossom category. It is hypothesized that pollen can only be effectively removed from flowers with included anthers once a potential pollinator has actively inserted its feeding organ into a fairly narrow perianth tube to reach the nectar reward. In the case of flowers with exserted anthers pollination is possible by casual anemophilous visits or via floral visitors that collect pollen only. Anther inclusion probably represents an adaptation to a specialized pollination syndrome. It is noteworthy that, although *Poellnitzia* has tube flowers (anthers included), pollen does, in fact, accumulate on the margins of the reduplicate-valvate portions of the perigone segments. However, this phenomenon can be attributed primarily to intrafloral microfaunal activity and not to anther exsertion. This over-elaborate and probably ineffective process of making pollen available for dispersal [resource limitation *sensu* Stanton *et al.* (1986)] might well be one of the primary reasons for the comparatively low fruit percentage (*ca.* 40%) in *Poellnitzia*.

The majority of tube-blossom species, such as *Aloe*, have inflorescence peduncles which serve as perches. Although the slender, wiry peduncle of a *Poellnitzia* inflorescence might be an insufficient perch for visitors which can weigh up to 40 g (Rebelo 1987), branches of associated woody species would provide adequate landing platforms for large, perching, avian visitors. However, as in the case of taxa which are primarily pollinated by winged visitors, for example the central-American *Quararibea* Aublet (Bombacaceae) (Alverson 1989), the long peduncles of racemes of *Poellnitzia* hold the flowers sufficiently exposed from the array of foliage and branches of associated vegetation. This provides unobstructed access to flying visitors.

Baker & Baker (1990) have shown that a close relationship exists between the sucrose/(glucose + fructose) ratio of nectar sugars and the type of pollinator that visits the flower. For *Poellnitzia* which has hexose dominated nectar (B-E. van Wyk personal communication), the predictions of Baker & Baker (1990) suggest a passerine bird pollination syndrome, especially when taken in conjunction with the morphology of the flowers and inflorescence.

From the foregoing it is clear that *Poellnitzia* shows distinct trends towards ornithophily. However, if the few-flowered inflorescences of *Poellnitzia* attract only the very occasional avian visitor, the hypothesis that pollinators are preferentially attracted to larger and more conspicuous inflorescences would be supported (Pyke 1981). In such a case it should be clear that the plant cannot rely on ornithophily alone, but would have to exploit divergent pollinator groups to ensure successful pollination under harsh environmental conditions.

Although ants can effectively guard flowers against, amongst others, beetle infestations, they seldom pollinate plants. Usually they only thieve nectar (Whitehead *et al.* 1987) and in some cases they play a role in seed dispersal (myrmecochory) (Midgley & Bond 1990). Plants pollinated by ants produce few, inconspicuous flowers at a time and are usually small, intertwining ground creepers in hot, dry desert areas (Faegri & Van der Pijl 1979). Although these features are in general applicable to *Poellnitzia* and its habitat, several flower characteristics seem to exclude obligatory myrmecophily. These are: production of large quantities of nectar; conspicuously coloured flowers; and the fact that the flowers do not open. In general, ants seldom move between plants when nectar is present in large quantities, thereby limiting cross-pollination (Whitehead *et al.* 1987).

However, it is noteworthy that *Camponotus fulvipilosus* was observed to visit not only the lateral slits (ostioles) in the proximal half of the flowers where nectar is taken, but also the flower apex where pollen accumulates. These formicine ants usually spend equal periods of time at these two sites on the flowers. Since ants are brood-rearing it is likely that they use the pollen as a source of protein (Faegri &

Van der Pijl 1979).

Camponotus cf. *werthi*, the smaller of the two formicine ants collected from *Poellnitzia*, chews away part of the flower apex, thereby destroying the protective function of the connivent perigone segments. Thus, the anthers, stigma and ovary are exposed to parasites such as the drosophilid species, and the high summer temperatures [up to 42°C in December (Weather Bureau 1986)] can result in an increase in the viscosity of the comparatively dilute nectar reward. Apart from these obviously detrimental effects that *C.* cf. *werthi* has on the plant reproductive efforts, it comes into direct contact with both anthers and stigma and is a more likely pollinator of *Poellnitzia* than *C. fulvipilosus*. Although a purely myrmecophilous pollination syndrome is unlikely for *P. rubriflora*, the two species of formicine ant can act as phoretors for the acarine *Adhaerenseius* which, in turn, has been observed to carry sticky pollen of *Poellnitzia* (Smith *et al.* 1989).

The ascid mite, *Adhaerenseius floralis* is by far the most plentiful inhabitant of *Poellnitzia* flowers. In general, the family Ascidae is a large and diverse group which has adapted to a variety of terrestrial and subaquatic habitats, such as coastal and intertidal regions, invertebrate nests and stored food products (Krantz 1978). While most ascids are predatory, a few species have adapted to polleniphagy. Pollen feeding species are, however, not peculiar to the Ascidae. For example, it has been shown that sugars applied to pollen grains during bee processing serve as a feeding stimulus for the polleniphagous *Pneumolaelaps longanalis* (Acari: family Laelapidae). Females of this species of mite are phoretic on queens of bumblebee (*Bombus occidentalis*) (Royce & Krantz 1989). Polleniphagous mites use a number of winged animals for transportation from flower to flower, where some species may also feed on other arthropods. Mite phoretors include moths and other lepidopterans for the genera *Proctolaelaps* and *Lasioseius* (Treat 1975) and hummingbirds for *Rhinoseius* (Rebelo & Jarman 1987). Species of the latter mite genus usually occur wherever the hummingbirds forage.

Mites are also known to live and feed in flowers of species of *Aloe* which are frequently visited by sunbirds (Skead 1967; Rebelo & Jarman 1987; Hoffman 1988). However, hummingbirds are restricted to the New World, ranging from southern Alaska to Tierra del Fuego (Burton & Burton 1969). To the best of my knowledge mites have not been recorded from any of the Old World species of sunbird (Burton & Burton 1970). The larval and protonymph stages of the life-cycle of *Adhaerenseius* have a pair of conspicuous sucker-like structures on the posterior border of the pygidial shield which may indicate that they are phoretically transported to the flowers of *Poellnitzia*. Although transportation by nocturnal lepidopterans cannot be ruled out, it is more likely that either sunbirds or formicine ants serve as phoretors of *Adhaerenseius*.

Representatives of the predacious mite family Phytoseiidae are capable of surviving periods of low prey density by polleniphagy. The movable digit of the chelicera is either edentate or provided with small denticles, while the fixed digit is provided with small, sharp teeth. The chelicera of *A. floralis* has the same shape with an edentate, moveable digit. If, in fact, the species is a predator of phytophagous mites, and there is as yet no proof of this, it is clear that *Poellnitzia* recruits and sustains polleniphagously intrafloral populations of the mite before being attacked. The advantages of such a mutualistic interaction is obvious; the plants obtain bodyguards even before damage is inflicted (Dicke & Sabelis 1988).

The presence of a variety of life history stages of mites (*Adhaerenseius* and *Erevipalpus*) within *Poellnitzia* flowers clearly indicates that these structures act as a shelter for development and reproduction. Mite association with leaf domatia (specialized chambers in the vein axils on the underside of leaves of many plant species) has been known for a long time (O'Dowd & Willson 1989). Leaf domatia are widespread among woody dicotyledonous angiosperms of temperate and tropical regions, but very rare in the monocotyledons, *Dioscorea* L. (Dioscoreaceae) and *Luisia zeylanica* Lindl. (Orchidaceae) being notable exceptions (O'Dowd & Willson 1989). Although foliar domatia have never been reported for representatives of the Alooideae (or any leaf succulent for that matter), it is clear that the connivent flowers of *Poellnitzia* are well-adapted as acarodomatia.

Conclusion

From the foregoing it is clear that *Poellnitzia rubriflora* attracts and sustains a number of diverse microfaunal species, some of which have a detrimental effect on reproductive potency and, ultimately, seed yield. It is also evident that the plant and its potential pollinator(s) and/or bodyguard(s) exist in a finely tuned mutual relationship that influences most aspects of the plant reproductive effort. Furthermore, interactions between plants and their associated animal species are widely considered to have been a driving force in the evolution of angiosperm flowers (Stanton *et al.* 1986 and references therein).

The flower morphology of *Poellnitzia* suggests that unobstructed entry to the flower is possible only for micro-arthropods. A well-developed mutualistic relationship exists between the polleniphagous ascid mite which transports pollen out of the connivent flowers in exchange for shelter, food and breeding space. The morphology of the chelicera of the mite also suggests that it may be predaceous in the presence of plant enemies, such as phytophagous mites. Thus, the results indicate that mite-flower association represents a relationship of comparable scope to mite-foliar domatia associations and therefore extends the plant organs that produce specialized mite chambers to include flowers.

As in the case of *Aloe* (Hoffman 1988) and the Cactaceae (Rowley 1980), the obligatory outbreeding *Poellnitzia* exploits divergent pollinator groups, the relationship having centred on the mite, *Adhaerenseius floralis*, and its hymenopteran and/or avian phoretor.

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Table 1 Microfaunal visitors and inhabitants collected from flowers of *Poellnitzia rubriflora.* Behaviour: I = inhabitant, V = visitor. Frequency: r = rare, o = occasional, c = common, v = very common (see text for explanation)

Taxa	Determination	Voucher specimens	Behaviour	Frequency
Camponotus fulvipilosus (De Geer)[1]	Dr. H.G. Robertson[2]	SAM-HYMC001804[3]	V	c
Camponotus cf. *werthi* Forel[1]	Dr. H.G. Robertson	SAM-HYMC001803[3]	V, I	o
Thripidae (unidentified species)[4]	Prof. P.D. Theron[5]	Personal collection – P.D. Theron	I	c
Drosophilidae (unidentified species)[6]	Prof. P.D. Theron	"	V, I	o
Adhaerenseius floralis Loots & Theron ined.[7]	Proff. G.C. Loots[5] and P.D. Theron	Mite collection of Department of Zoology, PU for CHE[8]	I	v
Brevipalpus species[9]	Prof. P.D. Theron	Personal collection – P.D. Theron	I	r

[1] Insecta: Hymenoptera: Formicidae

[2] Entomological Section, South African Museum, Cape Town.

[3] Reference numbers, Entomological collection, South African Museum.

[4] Insecta: Thysanoptera: Thripidae

[5] Department of Zoology, PU for CHE, Potchefstroom.

[6] Insecta: Diptera: Drosophilidae

[7] Acari: Parasitiformes: Ascidae

[8] Female holotype and *ca.* 30 paratypes are kept as slide mountings in the mite collection of the Department of Zoology, PU for CHE. Two male and two female paratypes are kept in the National Collection of Acari, Plant Protection Research Institute, Pretoria. Several hundred duplicates of all stages of the life cycle of *Adhaerenseius* are preserved in 75% ethanol — personal collection of P.D. Theron.

[9] Acari: Acariformes: Tenuipalpidae

Table 2 Putative avian pollinators of *Poellnitzia rubriflora.* (Adapted from Rebelo 1987). These species of the Nectarinidae are nectarivores and forage on, amongst others, species of *Aloe.* Mean length of the flower tube of *P. rubriflora* is (18-) 20,7 (-24) mm

Species	Common name	Status[1]	Culmen length (mm)
Nectarinia famosa	Malachite Sunbird	common	29–34
Nectarinia chalybea	Lesser Doublecollared Sunbird	common	18–23
Nectarinia afra	Greater Doublecollared Sunbird	common	24–29
Nectarinia fusca	Dusky Sunbird	common	18–22
Nectarinia amethystina	Black Sunbird	present	25–30

[1] In Karroid shrubland

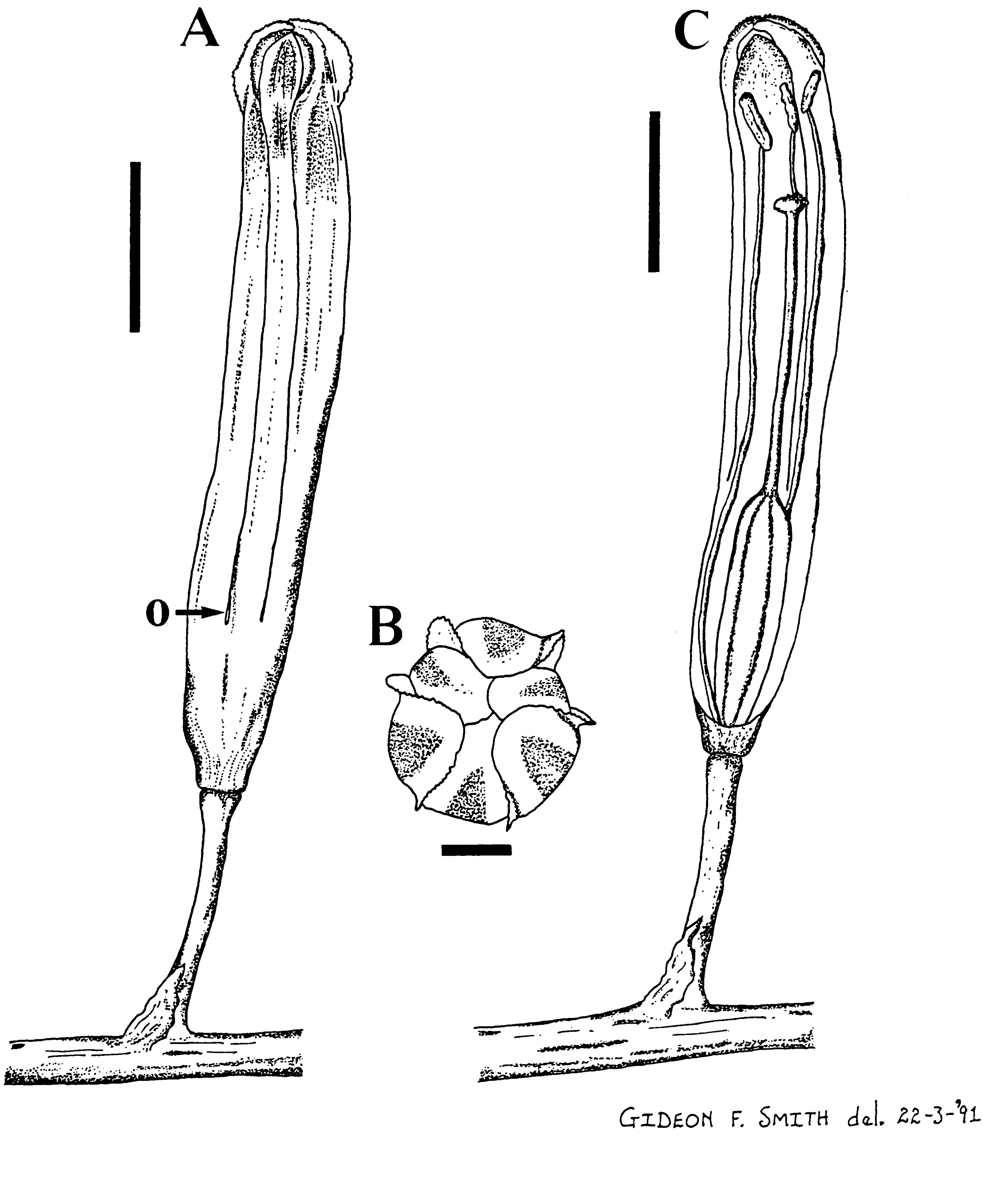

Figure 1 Flowers of *Poellnitzia rubriflora*. A. Lateral view showing angle at which flower is borne secundly on arched raceme; B. Apical view showing connivence of perigone segments; C. Longitudinal section (three stamens removed). All drawings were made from live material of *Smith 174* (PUC). O = ostiole. Scale line = 5 mm in Figure 1A, C and 1 mm in Figure 1B.

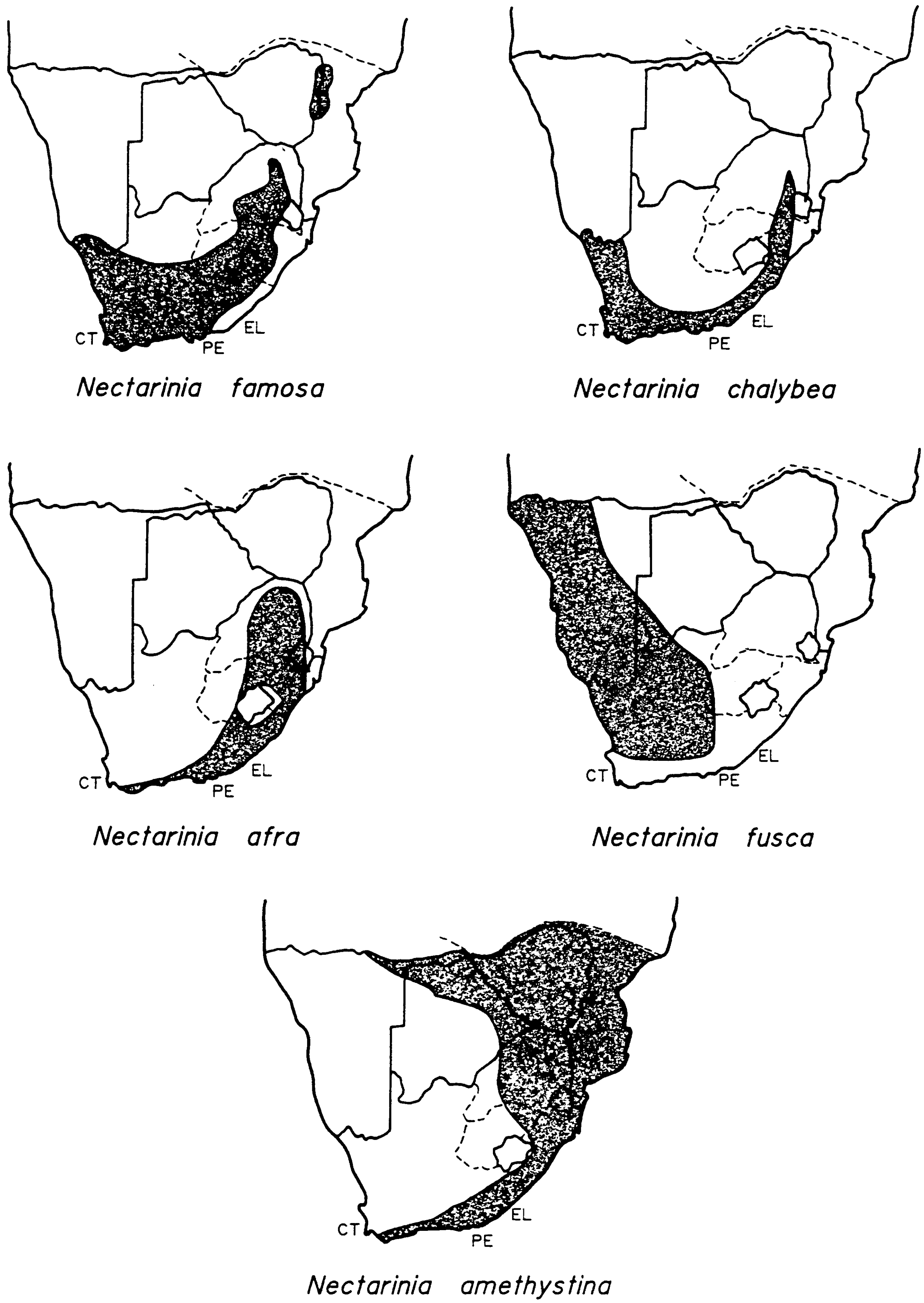

Figure 2 Habitat distribution of five avian nectarivores which occur in the south-western Cape Province. Adapted from Maclean (1985). CT = Cape Town, PE = Port Elizabeth, EL = East London.

CHAPTER 5

LEAF ANATOMY

"From time to time, genera are found which exhibit one or more [anatomical] characters of particular interest. Such is the variability of plant life that a character may be of interest in an individual family or small number of families or genera only. When a genus is found which shows a wide degree of variation, it is often worth spending additional time on it. This is particuarly true if it seems possible that the variable character may be of diagnostic or taxonomic significance."

D.F. Cutler: 1969, remarking
on cuticular markings and
other epidermal features
in *Aloe* leaves.

CONTENTS

CHAPTER 5

LEAF ANATOMY

5.1 INTRODUCTION

5.1.1 Background

The anatomical study of representatives of the Alooideae commenced in the late nineteenth century (Matzke 1947 and references therein). However, it was only by the late 1960's that the taxonomic value of leaf anatomical characters was appreciated, mainly due to the work of Dr. David F. Cutler at the Jodrell Laboratory of the Royal Botanic Gardens, Kew. Apart from a few contributions by, among others, Newton (1972a, b; 1991), most subsequent leaf anatomical studies of the Alooideae have been carried out at the Jodrell Laboratory.

As part of this wider leaf anatomical study of the subfamily currently under way, *Aloe bowiea* (= *Chamaealoe africana*), *Chortolirion* and *Poellnitzia* were examined. The leaf anatomy of these taxa is presented in the form of a manuscript which will be submitted for publication in a suitable journal (Smith & Van Wyk in preparation, see 5.2). Since the results of this investigation is discussed in detail in the manuscript, it will not be repeated here.

5.1.2 Basic features of the epidermis and explanation of terms used in the anatomical description

It is clearly very desirable that there should be uniformity in the descriptive leaf anatomical terminology used during work on a particular group (in this case the Alooideae). For this reason the terminology used here follows that developed by Cutler and co-workers in previous papers (Cutler & Brandham 1977; Brandham & Cutler 1978, 1981; Cutler 1978, 1979, 1982; Cutler *et al.* 1980; Carter *et al.* 1984). However, inclusion of a detailed terminological explanation in Smith & Van Wyk (in preparation) would be inappropriate. For this reason a detailed enumeration is given in the following paragraphs of the terminology used in this chapter for basic features of the epidermis as seen under the scanning electron microscope (SEM) and to a lesser extent, the light microscope (LM). These features have previously been established to be of taxonomic importance (see abovementioned references). Reference to Figure 5.1 will assist in understanding the meaning of the terms used here. Figure 5.1A shows in diagrammatic form the cells associated with a stoma in surface view, and Figure 5.1B the stoma in transverse section. Plates, figures and taxa referred to below are included in the respective literature references cited.

STOMATA

Each stoma(s) (= regulated pore) consists of two guard cells (g). These may be sunken (Cutler 1979, *Aloe dawei,* Plate 5C, D) or superficial (Cutler 1979, *Aloe ciliaris,* Plate 5A, B). When the stomata are deeply sunken it is normally not possible to see the guard cells (Cutler 1978, *Haworthia reinwardtii* var. *chalummensis*, Figure 2), and they have above them a suprastomatal cavity (ssc) (= outer pore) (Brandham & Cutler 1977, Figure 11; Cutler & Brandham 1977).

The four epidermal cells adjacent to a pair of guard cells are regarded as subsidiary cells (su) because they are normally distinct in their morphology from other epidermal cells not associated with stomata. In most species each subsidiary cell produces a more or less well developed lobe (l) on its side next to the guard cells (Cutler 1979, *Aloe dawei*, Plate 5C, D). These lobes make a raised chimney-like structure (ou) (= outermost aperture). The degree to which the lobes overarch the suprastomatal cavity varies and may be of taxonomic significance. In species with superficial stomata the lobes are either absent (Cutler 1982, *A. haemanthifolia* var. *haemanthifolia* and *A. gracilis* var. *decumbens*, Figures 3, 12) or only slightly developed (Cutler 1982, *A. striatula* var. *caesia*, Figure 11). Furthermore, these lobes may be arranged to form a more or less square or rectangular rim; they may be moderately thick or thick and are upright, or overarch, or slope away from the stoma. Four distinct lobes are present in most species of *Aloe* and in a proportion of *Haworthia* species (Cutler 1979, *A. parvula*, Plate 73; *H. coarctata*, Plate 2E). The lobes may be "fused", that is not clearly distinct as separate entities, as in some species of *Haworthia* (Cutler 1979, *H. tenera*, Plate 1D). The lobes are usually of equal length, but the aperture (suprastomatal cavity) which they surround is square if the flanking and polar lobes meet in a "mitre-joint" fashion (Cutler & Brandham 1977, *Gasteria planifolia* x *A. dorotheae*, Plate 5A) or elongated and rectangular if the flanking lobes are inset so that their outer edge is aligned with one end of the polar lobe (Cutler & Brandham 1977, *Gasteria carinata* x *A. antandroi*, Plate 6C).

Below the raised rim formed by the lobes, the flanks of the suprastomatal cavity slope gently towards the cuticular ledges (= rim; = lips; = flanges) (ocl) above the guard cells. Most species have cuticular ledges to the outer side of the guard cells (Brandham & Cutler 1981, *H. glauca* var. *herrei* forma *armstrongii*, Figure 5d). This is most conspicuous in species with superficial stomata. The lip develops from a continuous dome of cuticle; in the juvenile condition this dome is unperforated (Cutler 1979, *A. tenuior*, Plate 43). In mature stomata the dome splits along its long axis. The width of the pore (p) produced by this split, and the thickness and prominence of the cuticular ledge, vary from species to species and are of diagnostic importance. An inner cuticular ledge (icl) may also be developed (Cutler 1979, *A. kedongensis*, Plate 6C; Brandham & Cutler 1981, *H. glauca*, Figure 5g).

EPIDERMAL CELLS

The other features of considerable taxonomic importance can be seen on the outer wall of epidermis cells in surface view. Three orders of sculpturing can be defined with reference to the epidermis cells and associated cuticle (Cutler 1982; Carter *et al.* 1984). First, there is the outline of individual cells (cell shape),also referred to as the primary sculpturing. The outline of epidermal cells is usually 6-sided (markedly hexagonal), but that of occasional cells may be from 3--7-sided. Individual epidermis cells in surface view of the East African shrubby species of *Aloe* are predominantly 4-sided (square to oblong) (Cutler *et al.* 1980). The epidermal cells are normally slightly longer than wide (elongated axially) (Brandham & Cutler 1978; Cutler 1978). Cell boundaries (cb) can usually be distinguished as shallow grooves or channels of various depths and widths lacking ornamentation (Cutler 1978, *H. reinwardtii* var. *chalummensis*, Figure 2). In many other sppecies the cell boundaries are indicated by raised ridges. The ridge may be seen as "double" structures in occasional species. Here the two ridges of adjacent cells are separated by a shallow groove (Cutler 1979, *A. ciliaris*, Plate 4C). The cell boundaries give an indication of the position of the anticlinal cell wall, (acw) i.e. the cell wall perpendicular to the surface of the leaf.

The second order of sculpturing involves the outer (periclinal) wall (pcw) of epidermis cells. The periclinal wall (parallel to the surface to the leaf) may be more or less flat (Cutler 1982, *A. thompsoniae*, Figure 1) or slightly domed (convex) (Cutler 1982, *A. kniphofioides*, Figure 2), strongly domed (convex) (Cutler 1982, *A. wickensii*, Figure 9) or slightly domed with a prominent, usually central papilla (pa) (Cutler 1982, *A. peglerae*, Figure 4; Carter *et al.* 1984, *A. jacksonii*, Plate 23B). Rarely the outer wall of the epidermal cells may be slightly concave (Carter *et al.* 1984, *A. somaliensis* complex, Plate 22C). In species with delicate cuticle and/or walls, concavity may be an artefact, but in aloes in general this is not the case.

Here a papilla (part of secondary sculpturing) is regarded as a conspicuous projection from the cell wall equivalent to at least 1/6 of the width of the cell in diameter. The papilla is usually central and solitary, but other states may be found. A papilla may grade more or less inconspicuously into the domed wall from which it arises, it may arise abruptly, or there may be a constriction between the base of the papilla and the cell wall. The apex of a large papilla may be smooth or irregular (Cutler 1979), and a papilla is normally hemispherical to subspherical in shape.

Tertiary sculpturing is made up of finer structures superimposed on the secondary sculpturing. Most commonly this takes the form of micropapillae (mp), finer in some species than others but usually more pronounced on cells adjacent to stomata (Cutler *et al.* 1980, *A. kedongensis*, Figure 3). Micropapillae can be classified as fine (small) (Cutler 1982, *A. kniphofioides*, Figure 2), moderately coarse (Cutler 1982, *A. arborescens*, *A. comptonii*, Figure 13, 17), or coarse (Cutler 1982, *A.*

striata, Figure 8). Fine ridges or ridges are also classed with the tertiary sculpturing (Cutler 1982, *A. striatula* var. *caesia*, Figure 11), and in some species the micropapillae are fused to form larger structures (Cutler 1982, *A. speciosa*, Figure 16). Micropapillae may also coalesce to form ridge-like structues (Cutler 1982, *A. gracilis* var. *decumbeas*, Figure 12).

WAX

Wax is present on leaves of all species. In the Alooideae wax is remarkably stable, suffering little if any change during the chemical processing of material for study in the SEM. It may be affected by high temperature, when it melts and may recrystallise in a different form. This does not appear to happen at temperatures to which the plants are normally exposed, but may take place in the SEM if a very high keV is used. Sometimes the type of wax crystals is very typical (Cutler 1979, *A. tenuior*, *H. glauca*, Plate 4B, 3C). Thus, no attempt should be made to remove the wax when specimens are prepared for study.

Wax is usually present as a continuous cover of variable thickness, which may not be evident if it does not obscure the three orders of sculpturing. However, wax may obscure epidermal patterns; in such cases it is clearly necessary to look at both untreated and dewaxed preparations. In most Alooideae conspicuous wax particles may be emhedded in or on top of the unpatterned, continuous sheet of wax over the cuticle surface. These wax particles may be evident as a few fine flakes (Cutler 1982, *A. kniphofioides*, Figure 2), a denser cover of more upright flakes (often fused on the raised parts of the cell wall) (Cutler 1982, *A. glauca*, *A. lineata*, Figure 6, 7), or there may be coarse, irregular particles (Cutler 1982, *A. lutescens*, Figure 10). Although density of wax may vary from specimen to specimen within a species, the type is normally constant within a species.

GENERAL

Fragments of foreign matter may occur on some samples, notably spores and fungal hyphae. Removal of such debris is impossible without disturbance of the wax, and should not be attempted during specimen preparation.

Patterns observed on the outer (periclinal) cell walls are made up of both cell wall and overlying cuticle (c). The cuticle is often very thick in *Aloe*, moderately thick in *Gasteria* and relatively thin in *Haworthia* (Cutler & Brandham 1977; Brandham & Cutler 1981). The outer cell wall in *Haworthia* is extensively cutinized, whereas the thinner, inner (anticlinal) part of the cell wall is not impregnated with cutin (Brandham & Cutler 1981).

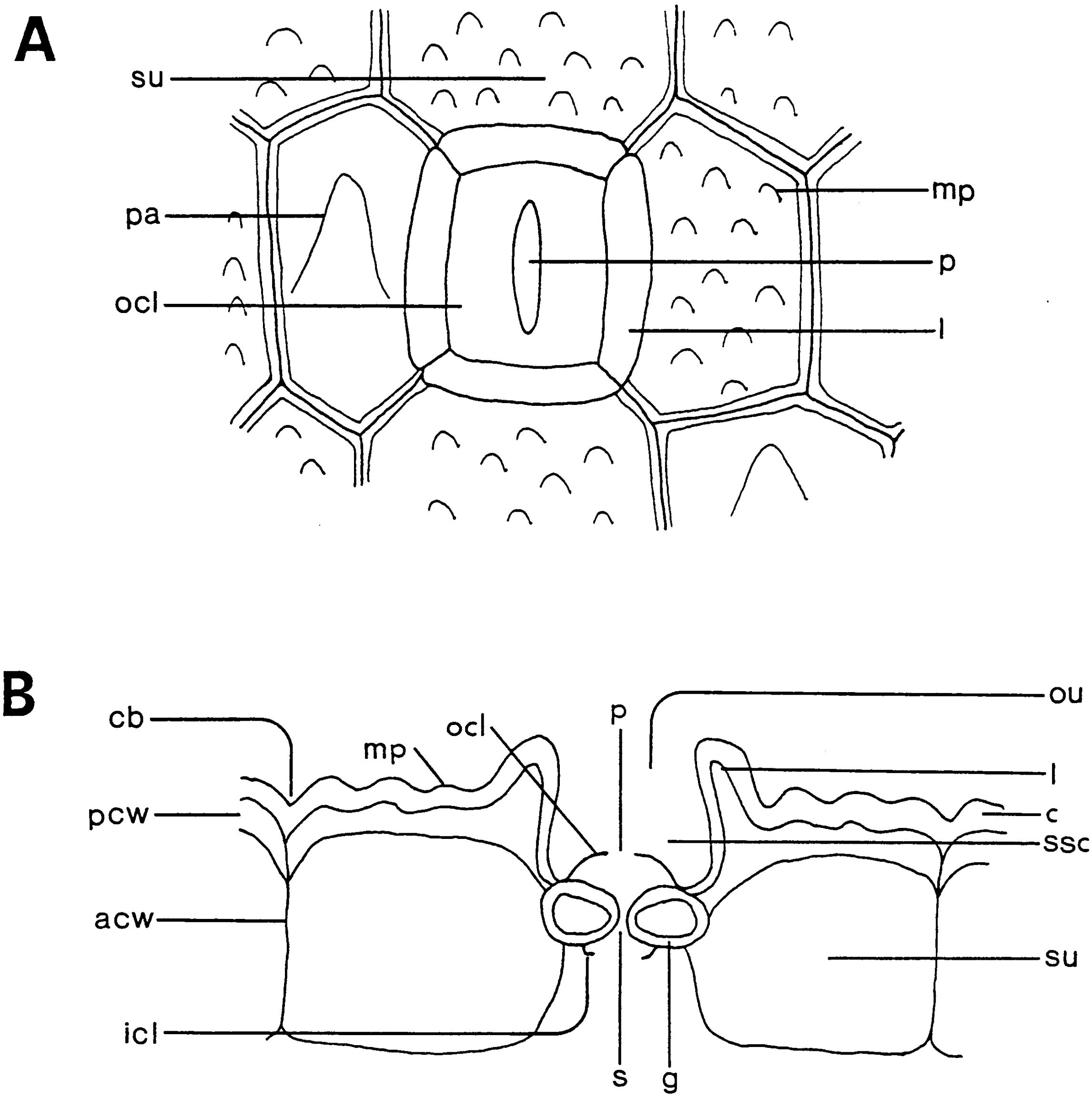

Figure 5.1 Diagrams to show the details of stomata and epidermal cells in the Alooideae. A, surface view [lobes (l) meet in a "mitre"-joint fashion]. B, transverse section. For an explanation see text. Adapted from Brandham & Cutler (1978). acw, Anticlinal cell wall; c, cuticle; cb, cell boundary; g, guard cell; icl, inner cuticular ledge; l, lobe; mp, micropapilla; ocl, outer cuticular ledge; ou, outer aperture; p, pore; pa, papilla; pcw, periclinal cell wall; s, regulated pore (stoma); ssc, suprastomalal cavity; su, subsidiary cell.

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Systematic leaf anatomy of selected genera of southern African Alooideae (Asphodelaceae)

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Abstract

Leaf epidermis/surface patterns [scanning electron microscopy (SEM) and light microscopy (LM)] and internal leaf anatomy (LM) are described in two taxonomically controversial Alooideae genera, Chortolirion Berger and Poellnitzia Uitewaal, and the aberrant Aloe bowiea Schult. & J.H. Schult. [= Chamaealoe africana (Haw.) Berger]. Particular reference is made to the possible value of epidermal characters as an aid to taxonomic studies in the subfamily. Although leaf cuticular sculpturing has previously been shown to be under strong genetic control, and that it is little influenced by local microclimate, some variation in patterning in at least Chortolirion and Aloe bowiea is demonstrated. However, the affinities of representatives of a particular species are normally still evident. Furthermore, SEM of both leaf surfaces is valuable in examining the range of patterns present. In the internal leaf anatomy vascular bundles, presence of thin-walled parenchymatous cells in the inner bundle sheath, presence of palisade cells and location of idioblasts are of particular interest. The data presented here lend support to the maintenance of Chortolirion and Poellnitzia as distinct genera, whereas the leaf anatomy of Aloe bowiea falls well within the range of variation previously reported for the genus.

Uittreksel

Blaarepidermis-/-oppervlakpatrone [skandeerelektronmikroskopie (SEM) en ligmikroskopie (LM)] en die interne blaaranatomie (LM) word beskryf vir twee taksonomies kontroversiële Alooideae-genusse, Chortolirion Berger en Poellnitzia Uitewaal, en die afwykende Aloe bowiea Schult. & J.H. Schult. [= Chamaealoe africana (Haw.) Berger]. Aandag word veral geskenk aan die moontlike nut van anatomiese

kenmerke as 'n hulpmiddel in taksonomiese ondersoeke van die subfamilie. Hoewel daar voorheen bepaal is dat blaarkutikulaskulptuur geneties streng beheer word, en dat dit nie noemenswaardig deur mikroklimaat beïnvloed word nie, is daar in die geval van ten minste Chortolirion en Aloe bowiea wel 'n mate van variasie waargeneem. Die affiniteite van verteenwoordigers van 'n betrokke spesie kan egter normaalweg wel bepaal word. Verder is SEM-ondersoeke van beide blaaroppervlaktes wenslik om sodoende die volle reeks van patrone teenwoordig by 'n spesie vas te stel. In die geval van interne blaaranatomie is die vaatbondels, teenwoordigheid van dunwandige, parenkiemagtige selle in die binneste bondelskede, teenwoordigheid van palissadeselle, en die ligging van idioblaste van besondere belang. Die data wat hier verskaf word, verleen steun aan die behoud van Chortolirion en Poellnitzia as afsonderlike genusse, terwyl die blaaranatomie van Aloe bowiea binne die bestek van variasie val wat voorheen vir die genus vermeld is.

Introduction

According to a recent survey of relationships among aloeoid taxa (Smith & Van Wyk in press), the subfamily Alooideae, Asphodelaceae (sensu Dahlgren et al. 1985) is considered to comprise seven genera. With the exception of the Mascarene Lomatophyllum Willd., all the genera are strongly represented within the Flora of Southern Africa region. Anatomical research in this group by other researchers, mainly Dr. D.F. Cutler and co-workers of the Jodrell Laboratory, Royal Botanic Gardens, Kew, have been concentrated on the principal genera, Aloe L., Gasteria Duval and Haworthia Duval. The latter continuing research programme which was initiated more than 20 years ago has involved, among others, studies on the range of leaf epidermal patterns to be found in the subfamily Alooideae (Brandham & Cutler 1978, 1981). This has revealed that leaf surfaces show a range of cell arrangement, stomatal structure and cuticular sculpturing which, when taken together, are frequently characteristic of a species or closely related species (Cutler 1982; Carter et al. 1984).

Furthermore, Cutler (1972, 1978a), Brandham (1977), Cutler & Brandham (1977) and Cutler et al. (1980) have demonstrated that aspects such as epidermal cell patterns, details of stomatal structure seen on leaf surfaces and even inheritance of leaf pigmentation are under strong genetical control in members of the Alooideae. Since epidermal patterns have been shown to be sufficiently stable and taxon specific (Cutler 1969, 1972), they provide additional taxonomic characters which can aid in the identification of, especially, non-flowering aloeoid plants (Glen & Hardy 1986).

As part of the wider leaf anatomical study of the Alooideae currently under way, the following southern African species are being examined, Aloe bowiea Schult. & J.H. Schult., Chortolirion angolense (Bak.) Berger and Poellnitzia rubriflora (L. Bol.) Uitewaal. Chortolirion Berger and Poellnitzia Uitewaal are here considered to be monotypic genera. The third species, A. bowiea, was previously regarded as the only constituent of Chamaealoe Berger, but the latter genus is now included in the synonymy of Aloe (Smith 1990). The leaf anatomy of these three taxa is presented and its usefulness for diagnostic or taxonomic purposes is considered.

Materials and Methods

Leaf material of all the species was obtained from plants collected in the field and subsequently grown under uniform conditions. As shown previously by Cutler (1978a), glasshouse-grown plants retain their epidermal features unaltered when compared with freshly collected plants. Fully expanded leaves were freshly collected, fixed and stored in formalin-acetic acid-alcohol (FAA) (Johansen 1940). All leaves were examined at a standard level, halfway between the base and apex. Voucher specimens and locality details pertaining to the various samples studied are listed in Table 1.

[INSERT TABLE 1 NEAR HERE]

For light microscopy (LM) small portions of fixed material were dehydrated, infiltrated and embedded according to standard methods in glycol methacrylate (GMA) (Feder & O'Brien 1968). Transverse sections, 1--3 μm thick, were stained with the periodic acid/Schiff's (PAS) reaction, counterstained with toluidine blue (TB) and mounted in Entellan (Feder & O'Brien 1968). For the detection of calcium oxalate crystals, sections were stained with TB and viewed under polarized light. Cuticular preparations were obtained after treatment with Jeffreys' solution, and stained with safranin O (Kiger 1971). To further elucidate epidermal cell shape and stomatal structure, paradermal free-hand sections were prepared and stained with TB or safranin O.

Standard procedures were followed for scanning electron microscopical (SEM) studies of both adaxial and abaxial leaf surfaces. Leaf tissue fixed in FAA was infiltrated with liquid CO_2 and dried in a critical point drier, sputter-coated with gold and viewed with the SEM.

Unless otherwise indicated, the descriptive terminology with regard to epidermal structure proposed for the Alooideae by Cutler and co-workers (Cutler 1982 and references therein) are used. Descriptors to indicate abundance and frequency are based on those proposed by Schmid (1982).

Results

The general distribution of tissues in the leaf is rather similar to that described for other aloeoid genera (Figure 1). However, there are several differences and it is mainly some of these features which will be considered. A summary of the main leaf anatomical differences between the investigated species is given in Table 2. More detailed descriptions follow below.

[INSERT TABLE 2, FIGURE 1, FIGURES 2--10 & FIGURES 11--16 NEAR HERE]

<u>Aloe</u> <u>bowiea</u> (Figures 1B, 2, 5, 8, 11 & 12)

Leaf in transverse section, LM:

Outline crescentiform with a shallow mid-adaxial groove; margins rounded, with scattered prickles. Cuticle relatively thin (± 3 μm), following outline of outer wall of epidermal cells; outer part clear, inner part apparently grading with cutinized outer-most part of epidermal cell wall. Lobes forming the suprastomatal cavity well developed, consisting in part of an extention of the wall of the subsidiary cell. Epidermal cells usually slightly periclinally elongated (rectangular); those on both surfaces similar. Outer periclinal walls moderately cutinized (6 μm thick). Stomata sunken, suprastomatal cavity with parallel or slightly overarching lobes. Guard cell walls slightly and evenly thickened; cuticular ledges bordering outer and inner pore very short and apparently containing some cell wall material (stain dark pinkish purple with PAS/TB). Hypodermis absent. Chlorenchyma several-layered; cells thin-walled; present to inner sides of both surfaces, as well as the margins; cells of 1--3 outermost layer(s) slightly and irregularly radially elongated, but not distinctly palisade-like; those of inner layers ± isodiametric. Vascular bundles arranged ± equidistant from leaf surface at boundary between chlorenchyma and central parenchymatous water storage tissue; more numerous (± 12) abaxially than adaxially (± 5); bundles of roughly equal size; phloem poles directed outwards; no bundles distinctly positioned as groove or marginal ones. Phloem pole ± T-shaped in outline, the stem of the T directed outwards. Sieve tubes and companion cells very narrow. Xylem composed of few (2--6) tracheids of medium width. Bundle sheaths consisting of two layers of parenchyma cells; outer layer sometimes difficult to distinguish from surrounding cells; inner layer forming a conspicuous cap of large, thin-walled cells at the phloem pole; sectional area of cap larger than that of phloem and xylem together. Sclerenchyma absent. Central tissue composed of large parenchymatous cells; ± sharply demarcated from chlorenchyma. Crystals present as raphide bundles in idioblasts; scattered amongst chlorenchyma cells, but not specifically associated with vascular bundles. Silica bodies & tannins not observed.

Leaf epidermis/surface, LM & SEM:

Stomata anomocytic, sunken; lobes ± upright, fused; outer pore ± square, occasionally longer than wide. Primary sculpturing: epidermal cells mostly 5- or 6-sided; as long as wide, or slightly longer; anticlinal walls indistinct or only slightly depressed. Secondary sculpturing: outer periclinal walls of epidermal cells slightly convex; papillae generally absent; a single centrally positioned papilla present on most cells on the abaxial surface of the Kariega collection only. Tertiary sculpturing: micropapillae moderately coarse, many per cell, distributed over entire surface of each cell; those on subsidiary cells more prominent. Wax present as amorphous deposits over entire leaf surface, partly blocking some stomata.

Chortolirion angolense (Figures 1A, 3, 6, 9, 13 & 14).

Leaf in transverse section, LM:

Outline broadly triangular (plano-convex) in transverse section; adaxial surface ± plane; abaxial surface convex; margins rounded, with scattered prickles. Cuticle relatively thin (up to 8 µm), following outline of outer wall of epidermal cells, clear. Lobes forming the suprastomatal cavity well developed, without subsidiary cell wall-extentions. Epidermal cells slightly radially elongated (rectangular); those on both surfaces similar. Outer periclinal walls strongly cutinized (± 9 µm thick), others only slightly so; inner periclinal walls convex. Stomata sunken, suprastomatal cavity with parallel or slightly overarching lobes. Guard cell walls unevenly and heavily thickened, particularly towards supra- and substomatal cavities; inner cuticular ledges minute and darkly stained with PAS/TB, outer ones minute and unstained. Hypodermis absent. Chlorenchyma 1--4-layered; cells thin-walled; present to inner sides of both surfaces, as well as the margins; cells of outermost layer strongly and regularly radially elongated, forming a distinct palisade layer; those of inner layer(s) ± isodiametric. Vascular bundles ± 10, evenly distributed ab- and adaxially, arranged in a single ring, ± equidistant from leaf surface and towards inside of chlorenchyma in central parenchymatous water storage tissue; bundles of alternating large and medium-sized ones; phloem poles directed outwards; no bundles distinctly positioned as "keel" or marginal ones. Phloem pole represented by a single strand, parallel to outer leaf surface. Sieve tubes and companion cells very narrow; medium-sized bundles with few cells only. Xylem composed of few (1--4) tracheids of medium width. Bundle sheaths consisting of 1--2 well defined layers of thin-walled parenchymatous cells; inner layer forming a small cap of parenchymatous cells at the phloem pole; sectional area of cap smaller than that of phloem and xylem together. Sclerenchyma absent. Central tissue composed of large, ± isodiametric parenchymatous cells; merging rather imperceptibly with chlorenchyma. Crystals present as raphide bundles in scattered idioblasts immediately to the inside of the chlorenchyma; not specifically associated with vascular bundles. Silica bodies & tannins not observed.

Leaf epidermis/surface, LM & SEM:

Stomata anomocytic, sunken; lobes ± upright, fused; outer pore ± square. Primary sculpturing: epidermal cells 4-sided; longitudinally elongated (rectangular), or slightly fusiform; longitudinal radial walls distinctly depressed; transverse radial walls obscure.

Secondary sculpturing: outer periclinal walls of epidermal cells plane; papillae 2--4, serially (longitudinally) arranged on each cell of the abaxial surface; adaxially absent. Tertiary sculpturing: micropapillae moderately coarse, many per cell and distributed over entire surface, adaxially coalescing to form low, transverse, ridge-like structures; micropapillae on subsidiary cells more prominent. Wax present as amorphous deposits over entire leaf surface, partly blocking some stomata.

Poellnitzia rubriflora (Figures 1C, 4, 7, 10, 15 & 16)

Leaf in transverse section, LM:

Outline broadly triangular in transverse section, occasionally with an incomplete, obliquely-situated abaxial keel; adaxial surface plane or slightly concave; abaxial surface convex; margins acute, scabrid. Cuticle very thick (up to 70 µm), following outline of outer wall of epidermal cells. Outer part clear, inner part apparently slightly grading with outer-most part of epidermal cell wall. Lobes forming the suprastomatal cavity well developed, with wall of subsidiary cell extending slightly into lobe. Epidermal cells radially elongated and distinctly papillate (strongly convex); those on both surfaces similar. Outer periclinal walls strongly cutinized (up to 20 µm thick), others only slightly so, or not at all. Stomata sunken, suprastomatal cavity with strongly overarching lobes. Guard cell walls unevenly and strongly thickened, particularly the exposed walls; outer and inner cuticular ledges present, without cell wall extensions, hence appearing unstained with PAS/TB. Hypodermis absent. Chlorenchyma usually multi-layered; present to inner sides of both surfaces, though better developed abaxially; cells ± isodiametric, not palisade-like. Vascular bundles relatively large and more numerous abaxially (± 10), smaller and fewer (± 4) adaxially; ± equidistant from leaf surface and on boundary between chlorenchyma and central parenchymatous tissue; phloem poles directed outwards; no bundles distinctly positioned as "keel" or marginal ones. Phloem pole ± T-shaped in outline, the stem of the T directed outwards. Sieve tubes and companion cells very narrow. Xylem composed of usually 1--5 tracheids of small diameter. Bundle sheath(s) consisting of 1 or 2 layers of thin-walled parenchymatous cells; outer layer usually clearly distinguishable from surrounding cells. Bundle caps of large thin-walled cells absent; Sclerenchyma present as a well developed cap (± reniform in transverse section) at the phloem pole; sectional area of cap much larger than xylem and phloem together. Central tissue composed of large parenchymatous cells, merging imperceptibly with chlorenchyma. Crystals present as raphide bundles in idioblasts; relatively few and mainly confined to the chlorenchyma on the adaxial side; not specifically associated with vascular bundles. Silica bodies & tannins not observed.

Leaf epidermis/surface, LM & SEM:

Stomata anomocytic, sunken; lobes strongly overarching, fused; outer pore minute, square or rectangular. Primary sculpturing: epidermal cells (4-) 6-sided in surface view, resulting in a marked "honeycomb" appearance; anticlinal cell walls distinctly grooved. Secondary sculpturing: outer periclinal walls of epidermal cells markedly domed, the latter often grading into a single papilla. Tertiary sculpturing: micropapillae absent. Wax present as amorphous deposits over entire leaf surface, partly blocking some stomata.

Discussion and Conclusions

This investigation of the leaf anatomy of Chortolirion, Poellnitzia and Aloe bowiea has revealed some characters which may be of diagnostic and probably also taxonomic value.

The more significant of these are the presence of chlorenchymatous tissue distinctly differentiated into a palisade layer and isodiametric cells, the inner bundle sheath cap-type, the localization of idioblasts, the cutinized cell wall, and epidermal patterns. These and other leaf anatomical aspects of representatives of the Alooideae are discussed below. A comparison of the taxa under consideration to other aloeoid genera and Kniphofia with regard to selected leaf anatomical characters are given in Table 3.

[INSERT TABLE 3 NEAR HERE]

CHLORENCHYMA

Of all the Alooideae taxa of which leaf transverse sections have been investigated to date, only Chortolirion displays, chlorenchymatous tissue which are distinctly differentiated into a palisade layer (a single layer of cells present adjacent to both the upper and lower surfaces) and more or less isodiametric (spongy) cells (see caption to Table 3 for references). Since the arrangement of cells in the chlorenchyma is under rigid genetical control, this probably represents a diagnostic character for Chortolirion. It also stresses the need for more, wide-ranging studies of leaf transverse sections in the Alooideae, especially the graminoid-leaved species of Aloe and Haworthia.

INNER BUNDLE SHEATH CAPS

This character has been extensively reviewed by Beaumont et al. (1985) and will not be discussed in detail here. However, to date transverse sections of Chortolirion leaves had not been investigated by means of light microscopy (see Table 1 in Beaumont et al. 1985). The present study showed that this genus, too, in common with most other aloeoid taxa including Aloe bowiea has an inner bundle sheath-cap consisting of thin-walled parenchymatous cells. In contrast, the vascular bundles of Poellnitzia have large (sectional area), reniform, inner bundle sheath schlerenchymatous caps. The parenchymatous condition is generally regarded as derived since it is a unique feature in an otherwise advanced group of plants.

LOCALIZATION OF IDIOBLASTS

Very little is known about the localization of idioblasts in the leaves of representatives of the Alooideae, and the type(s) of crystals that they contain. As shown here (Table 2) for Chortolirion idioblasts have not been found in the chlorenchyma, whereas, in the case of Poellnitzia and Aloe bowiea, idioblasts occur scattered in the chlorenchyma. This character, too, requires more detailed investigation in a representative sample of aloeoid taxa.

CUTINIZED WALLS

Although the strongly cutinized outer periclinal cell wall is not unique to the Alooideae, the distribution of this wall structure among the genera Astroloba, Chortolirion, Gasteria, Haworthia and Poellnitzia might be phylogenetically significant (Cutler 1972). Although Baijnath (1980) did not mention this character when he investigated the leaf anatomy of Kniphofia Moench, reference to his Figures 2A and 2C indicate that at least some species of the genus also have thickened outer epidermal cell walls.

In a leaf anatomical study of the monocotyledonous Gloriosa superba L., Littonia modesta Hook., Sandersonia aurantiaca Hook. and Hexacyrtis dickiana Dint. (Iphigenieae:

Colchicaceae), Baijnath (1988) found only the latter species to have markedly thickened outer periclinal epidermal cell walls. It is interesting that, in general, Baijnath (1988) suggested a correlation between the leaf anatomical characters of these species and their growth forms and habitats. Hexacyrtis shares a number of anatomical features with xerophytes and this tends to correlate with its dry, sandy habitats in the Namib Desert (see also Cutler, 1978b, 1982 on the correlation between leaf surface sculpturing and habitat in Aloe and in general).

LEAF EPIDERMAL PATTERNS

The leaf surface sculpturing of Chortolirion angolense has previously been investigated by Cutler (1979; under the name Haworthia angolense). However, our result differ from that of Cutler (1979) in a number of respects. For example, we found the cuticular lobes to be fused (not free), the outline of the suprastomatal chamber to be square (not rectangular), the micropapillae coalescing adaxially to form transverse ridges (not well-spaced), at least the longitudinal radial walls distinctly depressed (not indistinct), and the wax present as amorphous deposits (not flaky particles). These differences show that considerable variation exists in the leaf surface patterns of this aberrant monotype. Clearly, any taxonomic changes proposed for a particular species on the basis of leaf anatomy alone should be based on a rigorous investigation of a representative sample.

The results of the present study, especially in the case of Chortolirion and Aloe bowiea (Kariega specimen; Figure 11), indicated different patterning on the ad- and abaxial leaf surfaces. This certainly emphasizes the need for future routine examination of both surfaces. The "honeycomb" patterning present on both the ad- and abaxial leaf surfaces of

Poellnitzia is very distinctive and should serve to characterise the genus on leaf anatomical grounds. It is quite unlike any pattern previously recorded for representatives of the Alooideae.

STOMATA

The leaves of all the species studied are amphistomatic and the guard cells are very deeply sunken, and more or less overarched by prominent cuticular lobes. In addition the guard cells also have inner and outer cuticular ledges which may (Aloe bowiea; Figure 8) or may not (Chortolirion, Poellnitzia; Figures 9 & 10) contain cell wall extensions. Thus, two extensions of the stomatal pore are delimited: a front (outer) cavity and a back (inner) cavity (Stace 1965).

Morphologically the stomata of representatives of the Alooideae have previously been considered to be tetracytic (four subsidiary cells; two polar and two lateral) (Cutler 1972). However, the present authors are not at all convinced that the epidermal cells bordering the guard cells are in fact significantly different from the epidermal cells which are not in direct contact with guard cells, to warrant referring to them as subsidiary cells. Pending ontogenetic studies of Alooideae stomata, these structures are best referred to as anomocytic. Although in many aloeoid taxa the cells bordering the guard cell pair are furnished with distinctive micropapillae and/or conspicuous lobes, morphologically similar stomatal types can be developmentally dissimilar. Such variable characters obviously cannot be used in taxonomy, since different genetic mechanisms are involved (Tomlinson 1974; Patel 1978).

It is noteworthy that, as is the case with cuticle and epidermal cell wall thickness

(Cutler 1978b), stomatal elevation (sunken vs. superficial) is not a reliable guide to xeromorphy, habitat or climate. For example, Eggli (1984) has shown that in most cases in the highly succulent Cactaceae the stomata are superficial.

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Table 1 Origin of material and list of voucher specimens. All collection numbers are those of the first author. Unless otherwise indicated all specimens are deposited in PUC. One specimen from each locality was studied

Species	Locality number	Locality; grid reference	Collection number	Figure
Aloe bowiea	1	Brakfontein, Kariega; 3325 AC Port Elizabeth	206	11B
	2	Maasward, Coega; 3325 DC Port Elizabeth	173	1B, 2, 5 8, 11A, 12
	3	Jachtvlakte, Uitenhage; 3325 CD Port Elizabeth	1 (PEU)	-
Poellnitzia rubriflora	4	Langverwacht; 3320 CC Montagu	176	7
	5	Sandberg, Robertson; 3319 DD Robertson	184	10
	6	5 km W of Bonnievale; 3320 CC Montagu	9 (PRU)	1C, 4, 15, 16
Chortolirion angolense	7	Cachet railway siding; 2627 CA Potchefstroom	14	1A, 3, 6, 9, 13, 14

Table 2 Summary of salient, mainly leaf anatomical, differences between *Aloe bowiea*, *Chortolirion* and *Poellnitzia*. LM = light microscopy; SEM = scanning electron microscopy

	Aloe bowiea	*Poellnitzia rubriflora*	*Chortolirion angolense*
Geographical distribution	endemic to Uitenhage distric, eastern Cape	endemic to Robertson Karoo, south-western Cape	widespread in central southern Africa
Habitat	subtropical thicket	karroid shrublands	grassland
Habit	acaulescent, rosulate, leaf succulent	caulescent, rosulate, leaf succulent	bulbous plant; leaves weakly succulent
		Leaf anatomy (transverse section; LM)	
Leaf outline	crescentiform	broadly triangular, keeled	broadly triangular
Cuticle	relatively thin	very thick	relatively thin
Cuticular lobes	consisting in part of epidermal cell wall		clear
Epidermal cells	periclinally elongated	radially elongated	
Outer periclinal epidermal cell walls	moderately cutinized	strongly cutinized	
Guard cell walls	evenly thickened	unevenly thickened	
Cuticular ledges	very short; with cell wall extensions	well-developed; without cell wall extensions	minute; unstained
Chlorenchyma	undifferentiated		differentiated into palisade and isodiametric cells
Vascular bundles	at boundary between chlorenchyma and central tissue		in central tissue
Phloem pole	T-shaped		single strand
Inner bundle sheath cap (parenchymatous)	large sectional area	absent	small sectional area
Schlerenchyma	absent	present at phloem pole; very large sectional area	absent
Central tissue	± sharply demarcated	merging with chlorenchyma	
Idioblasts	scattered in chlorenchyma		to inside of chlorenchyma
		Leaf epidermis / surface (LM & SEM)	
Cuticular lobes	± upright	strongly overarching	± upright
Outline of epidermal cells	5- or 6- sided	predominantly 6- sided; leaf surface with "honeycomb" appearance	4- sided; longitudinally elongated
Outer periclinal epidermal cell walls	slightly convex; papillae generally absent	markedly domed; latter often grading into single papilla	plane; papillae present
Micropapillae	moderately coarse	absent	moderately coarse; coalescing adaxially

Table 3 Comparison of selected leaf anatomical character states in related aloeoid taxa and *Kniphofia*. +++ = character state usually present; ++ = character state often present; + = character state occasionally present; - = absent; ? = no data. Data sources: Roberts Reinecke 1965; Cutler 1972; Schneider 1972; Baijnath 1980; Beaumont *et al.* 1985; present study

	Inner bundle sheath cap			Outer periclinal epidermal cell wall		Chlorenchyma	
	Large; parenchym=atous	Small; parenchym=atous	Schleren=chymatous	Strongly cutinized	Weakly cutinized	Palisade present	Undiffer=entiated
Aloe	+++	+	+	+++	+	-	+++
A. bowiea	+++	-	-	++	-	-	+++
Astroloba	+++[1]	-	-	+++	-	-	+++
Gasteria	+++	-	-	+++	-	?	?
Haworthia	+++	+	+	+++	-	-	+++
Lomatophyllum	+++	-	-	?	?	?	?
Chortolirion	-	+++	-	+++	-	+++	-
Poellnitzia	-	-	+++	+++	-	-	+++
Kniphofia	-	-	+++[2]	+++	-	?	?

[1] With scattered fibres

[2] At both xylem and phloem poles

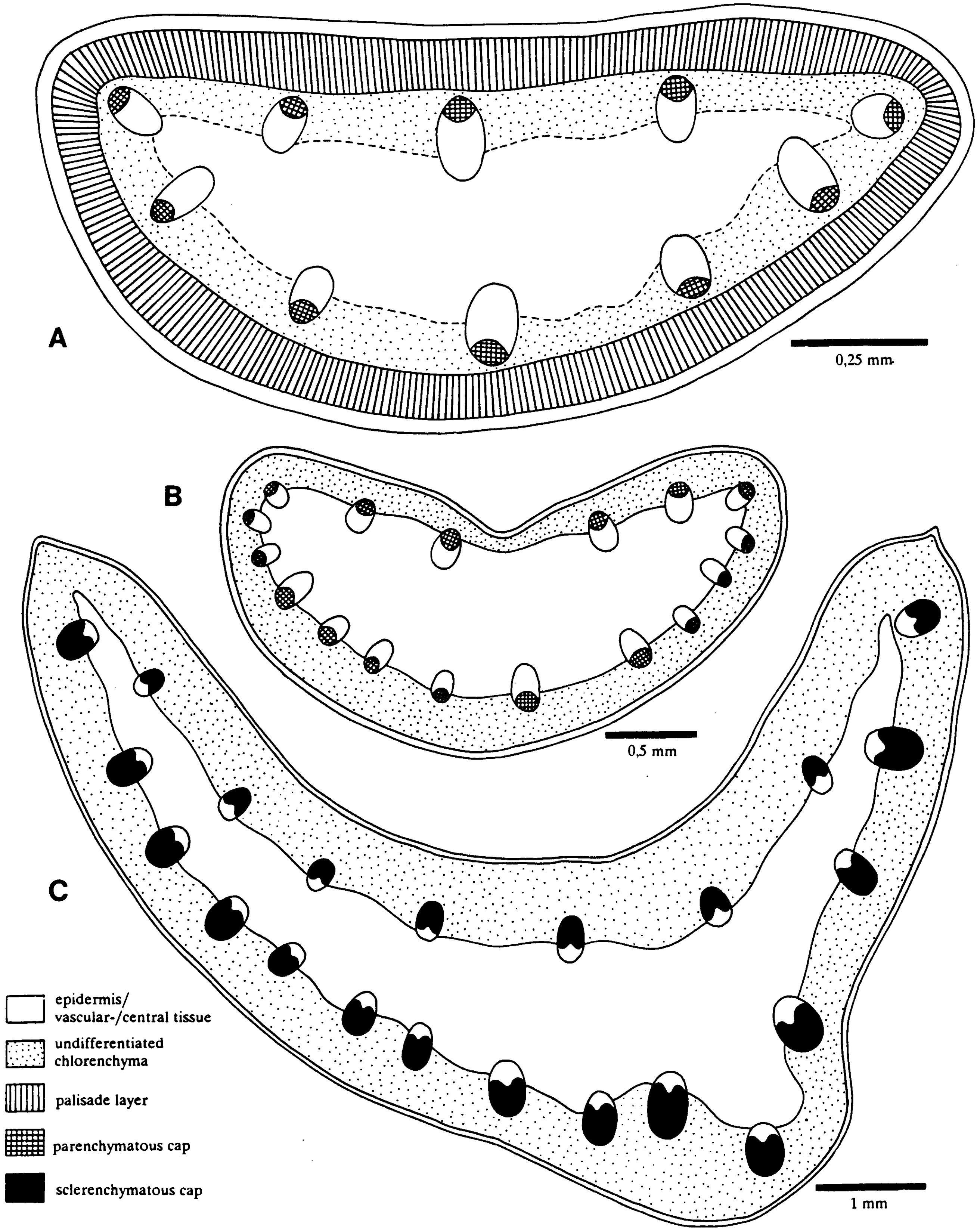
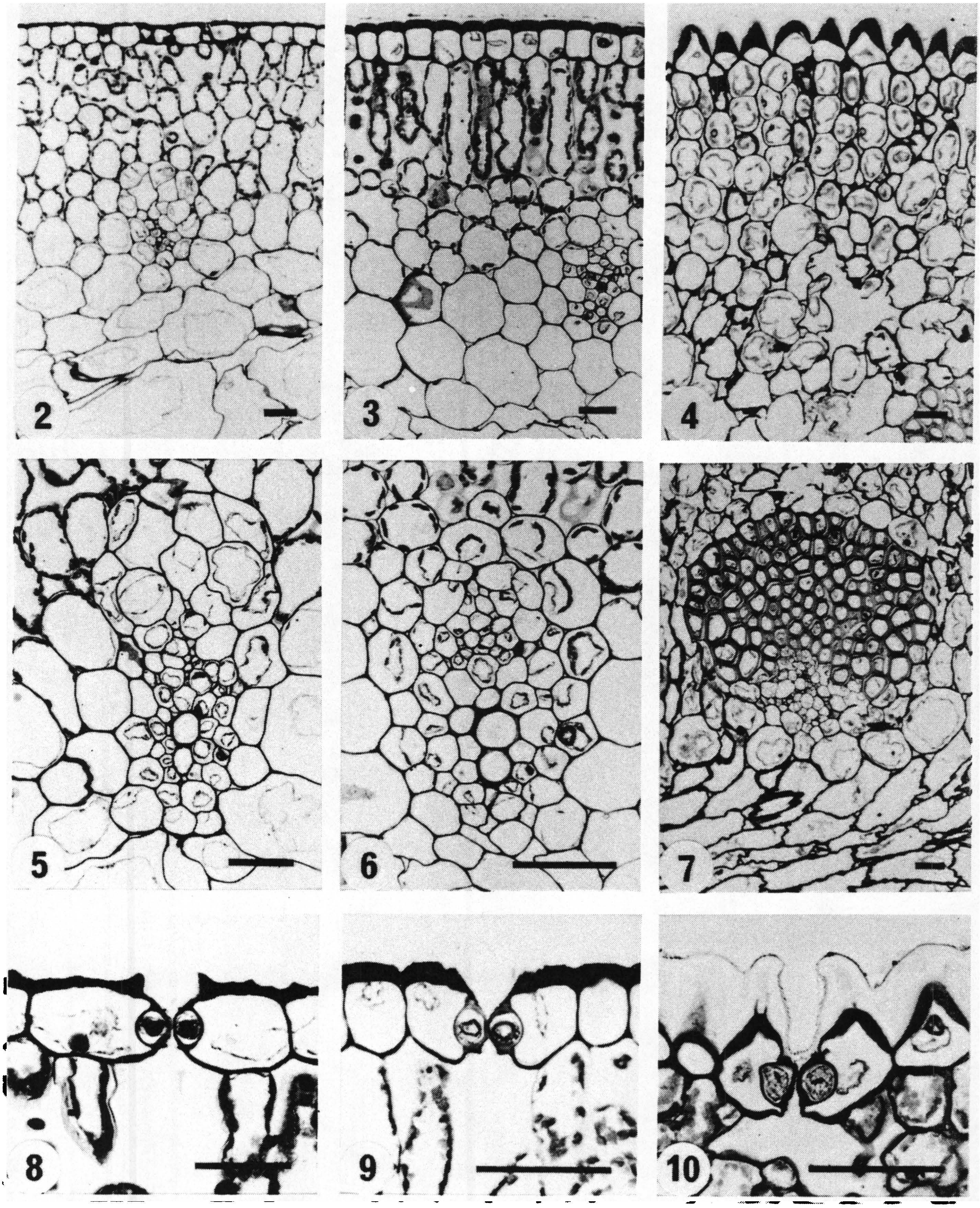
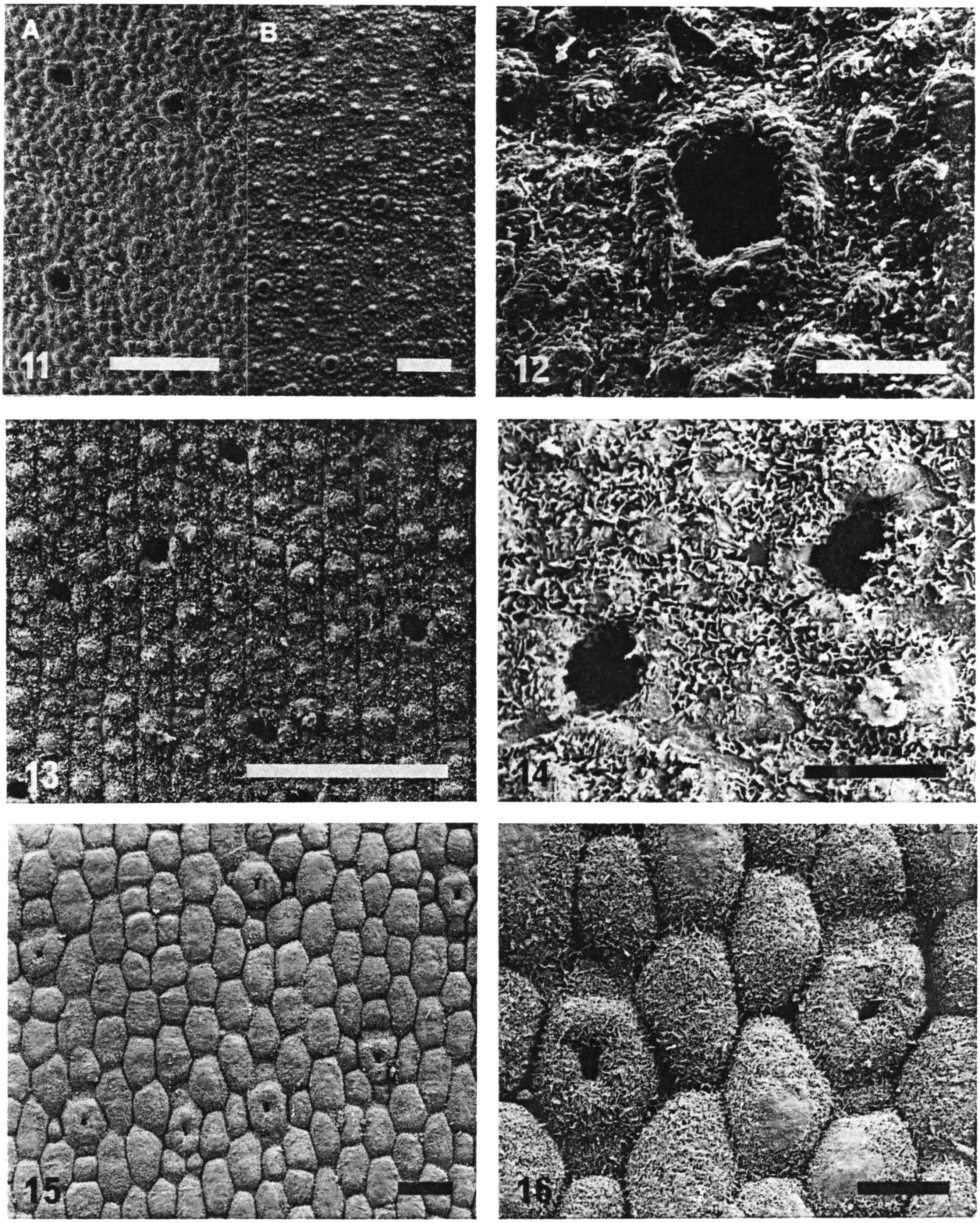


FIGURE 1 Plans of transverse sections of leaves illustrating distribution of tissues in *Chortolirion angolense* (A), *Aloe bowiea* (B) and *Poellnitzia rubriflora* (C). Sources of material are given in Table 1.



FIGURES 2—10 Details of transverse leaf sections in *Aloe bowiea* (2,5,8), *Chortolirion angolense* (3,6,9) ar *Poellnitzia rubriflora* (4,7,10). Sources of material are given in Table 1. Sections of adaxial leaf segments (2—4), vascul bundles from mature leaves (5—7) and adaxial stomata (8—10) are shown. The adaxial leaf surface points towards the tc of the page throughout. Scale bar = 50 µm throughout.



FIGURES 11–16 Scanning electron micrographs of abaxial leaf surfaces of *Aloe bowiea* (11,12), *Chortolirion angolense* (13,14) and *Poellnitzia rubriflora* (15,16). Sources of material are given in Table 1. Long axis of leaves vertical throughout. Scale bar = 100 µm in Figures 11,13 & 15 and 20 µm in Figures 12, 14 & 16.

CHAPTER 6

KARYOLOGY

"Since karyological distinctions doubtlessly are of great evolutionary significance, studies of cytological characteristics have sometimes been regarded as the final solution in the search for methods for a natural classification of genera. It is true that, such differences have been found to be of a great help in many cases, whereas we must observe that other instances have been less promising."

A. Löve: 1963

CONTENTS

CHAPTER 6

KARYOLOGY

6.1 INTRODUCTION

6.1.1 Background

The quoted passage that heads this chapter has been especially chosen since it emphasises the realities of cytogenetical investigations intended for use in taxonomy. I endorse the statement of Löve (1963) and regard as a fallacy the point of view that chromosomal characters are more important than others. The subfamily Alooideae is a case in point since, due to its extreme karyotypic uniformity, a cytogeneticist could be prompted to lump all the genera (some 450 species) into a single, inclusive genus with probably less than 30 species. This would clearly be nonsensical and not in the best interest of the classification of aloeoid taxa. The abovementioned misconception apparently arose because the chromosomes carry the genes, which contain the genetic information expressed in the phenotype.

By no means do I want to play down the role of cytogenetics in taxonomy. Basic evidentiary characters resulting from cytotaxonomic studies are helpful in the resolution of problems of hybridization and of lineages in phylogenetic reconstruction (Brandham 1983). Cytological studies can also be very helpful in understanding the evolutionary history of related taxa, particularly at the infraspecific and specific levels (Brandham & Carter 1990). Characters that can be used include the number, structure, type and meiotic behaviour of chromosomes and ploidy level. However, for classificatory purposes --- and this is very important --- chromosomal evidence is simply another informative data set used in context for a purpose (Radford 1986; Stace 1989).

The Alooideae is almost unique in the plant kingdom in the uniformity of its chromosome pattern. The chromosomes of the vast majority of the members of the subfamily show remarkable similarity and constancy in their markedly bimodal karyotype. Four pairs of chromosomes are long and three pairs are much shorter, about one third of the length of the long ones. The uniformity of the asymmetrical karyotype together with the fact that the chromosomes are few (2n = 14) and large makes the Alooideae ideal for a cytogenetic investigation of, for example, the frequency of spontaneous structural change. For these reasons the Alooideae has been the subject of cytological investigation for almost 80 years [see Riley & Majumdar (1979) for a comprehensive bibliography]. However, for one monotypic genus, *Chortolirion*, basic information of karyotype characteristics is still awaited.

Mutation (occurrence of heritable change in the genotype of an organism that was not inherited from its ancestors) and recombination (reassortment of chromosomes, crossover segments and, by implication, genes that produce new genotypes in sexually reproducing organisms) are the major sources of genetic variation in natural populations. The occurrence of these processes in the Alooideae has been investigated and discussed in some detail by Brandham (1976). The following is a brief summary:

* Inversions (a type of chromosomal mutation) occur frequently in the Alooideae but are always present as heterozygotes (Brandham 1983).
* Symmetrical interchanges (a type of recombination) also takes place in the Alooideae, but these have little effect on the morphology of diploid karyotypes and homozygotes are undetectable in somatic cells (Brandham 1969, 1983).
* Asymmetrical interchanges (a type of recombination) can lead to the establishment of new karyotypes if they become homozygous. However, in this case too, Brandham (1983) has determined that these interchanges are always heterozygous.
* Thus, although structural alteration of the karyotype may take place in the Alooideae they never become established as homozygotes and are evolutionary insignificant (Brandham 1969, 1973). This also applies to phenomena such as the production of iso-chromosomes in somatic cells [cf. Brandham (1970) on hybrid *Haworthia*].

It is therefore clear that interchange homozygotes and chromosomal aberrations in general are eliminated by extreme natural selection. This results in the maintenance of karyotype uniformity in the subfamily (Brandham 1983).

In contrast to the aforementioned phenomena, polyploidy (a type of chromosomal mutation) has played a limited role in speciation in the Alooideae (Brandham & Cutler 1981; Brandham 1982).

The underlying principles of cytogenetics have been established fairly recently in comparison to those of other subdisciplines of botany and numerous excellent texts are currently available on its phylosophy, theory and practise (Dyer 1979; Schulz-Schaeffer 1980; Swanson *et al.* 1981; Snyder *et al.* 1985). Furthermore, a wide range of techniques for cytogenetical investigation have been described in specialist journals, for example La Cour (1941, 1947, *et sequens*), O'Mara (1948), Tsuchiya (1971), Marks (1973) and Gill & Badcock (1990).

This chapter includes contributions on the karyology of *Aloe bowiea*, *Chortolirion* and *Poellnitzia*. The appearance of the somatic chromosomes at mitotic metaphase is termed the karyotype. This phenomenon is usually studied by routine techniques in parts of plants with rapidly dividing cells, such as root tips (Heywood

1979). In the present investigation of the mitotic metaphases of the chromosomes of *Chortolirion* and *Poellnitzia* the Feulgen staining technique as described by Van der Schijff & Robbertse (1976) gave excellent results and was used throughout.

Since chromosome studies have not been reported for *Chortolirion* to date, information included in Smith (1990, 1991) fills a void in our knowledge of the karyology of the Alooideae which has existed ever since its cytogenetical investigation commenced in the early twentieth century [see for example Taylor (1924)]. This gap in our knowledge has become even more apparent after a detailed karyological investigation of the subfamily was started in the late 1960's at the Jodrell Laboratory, Royal Botanic Gardens, Kew, by, amongst others, Prof. Keith Jones, Dr Peter E. Brandham and Ms Margaret A.T. Johnson. The manuscript (Smith 1991) also presents for the first time karyograms and idiograms for *Poellnitzia* (and *Chortolirion*, for that matter). Karyotype variation between observed and published data in *Poellnitzia* is discussed and difficulties encountered in attempting an interpretation of taxa of the Alooideae as either primitive or advanced, based on karyological evidence alone is highlighted. Although there are minor chromosome differences between *Chortolirion* and *Poellnitzia*, the karyotypes of neither genus deviate from the typical Alooideae pattern and as such testify to the widely accepted monophyly of the aloeoid genera (2n = 14; bimodal karyotype, etc.). Attention should therefore not be called to minor chromosomal differences only. From a phylogenetic point of view it is just as important to take note of the considerable and very obvious karyotype similarities which exist amongst the genera of the Alooideae. From the results obtained in the present study it is clear that chromosome morphology and number will not solve taxonomic (classificatory) problems at generic level in the subfamily [but see Brandham (1983) on chromosomal size differences between *Aloe* and *Gasteria*].

Aloe bowiea (as *Chamaealoe africana*) has been included in a number of recent broader cytogenetical surveys of the Alooideae (see 6.2 for references) and for this reason its chromosomes have not been investigated during the present study. Aspects of the chromosomal complement and behaviour of this species are therefore briefly discussed from the literature only (see 6.2). The manuscript on the chromosomes of *Chortolirion* and *Poellnitzia* has been accepted for inclusion in the section "Chromosome studies on African plants", part 9 of which appeared in *Bothalia* 19 (1): 125-132 (May 1989). A brief report (Smith 1990) on the chromosome numbers only of these two genera has been included in part 2 of the series "IOPB Chromosome Data", which is published in the *Newsletter of the International Organization of Plant Biosystematists*. The latter series is a continuation of "Chromosome number reports" (edited by Prof. Askell Löve) which saw 100 appearances between 1964 and 1988 in *Taxon*, journal of the International Association for Plant Taxonomy [for additional information *Taxon* 37 (4): 920 (November 1988) and *IOPB Newsletter* No. 13: 15 (1989) should be consulted].

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6.2 KARYOLOGY OF *ALOE BOWIEA*

6.2.1 Karyotype and hybrids

The chromosomes of *Aloe bowiea* (reported under the name *Chamaealoe africana*) were found to match the markedly bimodal karyotype which has been observed in every species of Alooideae to date. The chromosome complement consists of four pairs of large chromosomes and three pairs of small chromosomes in the diploid. The chromosomes are all more or less acrocentric (Viveiros 1949; Brandham 1971). To date polyploids have not been encountered in *Aloe bowiea* (Riley & Majumdar 1979).

Brandham (1969a) investigated the occurrence of E-type bridges in 163 taxa of the Alooideae, including *Aloe bowiea*. In general an E-type bridge is formed at anaphase I of meiosis by a proximal connection between the long arm of an acrocentric chromosome and the short arm of its homologue. It has been suggested that a high incidence of E-type bridges is indicative of inter-specific hybridity (Brandham 1969a). E-type bridges do not form in *A. bowiea*. Brandham (1971) has, however, determined that U-type bridges are formed at anaphase I of meiosis in *A. bowiea* (frequency of 1 %). The origin of U-type bridges is not yet clear, although an attractive and simple explanation is that errors in normal chiasma formation might produce this type of exhange (cf. Riley & Majumdar 1979). *A. bowiea* also lacks interchange heterozygosity, that is, the occurrence of unequal interchanges between portions of non-homologues (Brandham 1969b). Natural selection acts very strongly against these asymmetrical changes. This maintains the karyotype integrity of the Alooideae (see also 6.1 Introduction).

Especially in cultivation hybridization is extensive amongst taxa of the Alooideae. Consequently hybrids in the subfamily can be synthesized with great ease under artificial conditions (Brandham 1973; Rowley 1982). Although the general ease of hybridization has probably played an evolutionary role in most aloeoid genera, this phenomenon is far less common in nature than this suggests [cf. Bayer (1982) on *Haworthia*]. Numerous nothogeneric names (hybrid-generic names) have been proposed to accommodate the plethora of intergeneric hybrids that have been produced to date (Rowley 1982). *Aloe bowiea* is no exception to this generalization and the names x*Alchamaloe* Rowl. (*Aloe* x *Chamaealoe*), x*Chamaeleptaloe* Rowl. (*Chamaealoe* x *Leptaloe*), x*Chamaeteria* Cumming (*Chamaealoe* x *Gasteria*) and x*Chamaeloba* Cumming (*Chamaealoe* x *Astroloba*) have all been proposed at one time or another for hybrids between *Aloe bowiea* (clearly under the name *Chamaealoe*) and species of other Alooideae genera (Jacobsen & Rowley 1973; Rowley 1982). The first two of the above-mentioned nothogeneric names are currently regarded as refering to interspecific hybrids in *Aloe* whereas the last two are included in the synonymy of x*Gasteraloe* Guill. and x*Aloloba* Rowl., respectively. Hybrids between *Aloe bowiea* and *A. humilis* (L.) Mill., *A. parvula* Berger and *A. ballii* Reynolds have been positively identified and documented, the latter under the cultivar name x*Alchamaloe* 'Marianne North' (Brandham 1973; Graf 1980).

Although the occurrence of intergeneric hybrids in the Alooideae throw some doubt on the validity of the generic concept, there can be little doubt that the genera upheld in this investigation are more or less distinct entities in terms of both reproductive and vegetative morphology, perhaps with the exception of the diverse *Aloe*. A lack of generic separation by reproductive barriers should not be regarded as sufficient evidence to lump all the species of the subfamily into one vast genus.

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THE CHROMOSOMES OF *CHORTOLIRION* AND *POELLNITZIA* (ASPHODELACEAE: ALOOIDEAE)

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Key words: Asphodelaceae, Alooideae, *Chortolirion angolense,* chromosome number, karyotype, *Poellnitzia rubriflora*

ABSTRACT

The somatic chromosomes of *Chortolirion angolense* (Baker) A. Berger and *Poellnitzia rubriflora* (L. Bol.) Uitewaal have been studied. Both taxa are monotypic genera in the subfamily Alooideae of the Asphodelaceae. Prior to this study *Chortolirion* had not been cytologically examined, while karyograms and idiograms have never been presented for *Poellnitzia*. *Chortolirion* and *Poellnitzia* are diploid with 2n = 14 chromosomes and with a bimodal karyotype typical of the entire subfamily, comprising four pairs of long chromosomes and three pairs of short chromosomes. For *Poellnitzia* minute structural differences in karyotype morphology were noted between observed and published data, especially with regard to the presence of satellites.

UITTREKSEL

Die somatiese chromosome van *Chortolirion angolense* (Baker) A. Berger en *Poellnitzia rubriflora* (L. Bol.) Uitewaal is bestudeer. Beide taksons is monotipiese genusse in die subfamilie Alooideae van die Asphodelaceae. *Chortolirion* is nog nooit voorheen sitologies ondersoek nie, terwyl kariogramme en idiogramme van *Poellnitzia* nog nie voorheen aangebied is nie. *Chortolirion* en *Poellnitzia* is beide diploïed met 2n = 14 chromosome en elk beskik oor 'n bimodale kariotipe wat uit vier pare lang en drie pare kort chromosome bestaan. Hierdie kariotipe is soortgelyk aan dié van die oorgrote meerderheid taksons in die Alooideae. Veral ten opsigte van die teenwoordigheid van satelliete bestaan daar by *Poellnitzia* fyn, strukturele verskille in kariotipe-morfologie tussen waargenome en gepubliseerde data.

INTRODUCTION

The subfamily Alooideae of the Asphodelaceae (*sensu* Dahlgren *et al.* 1985) includes about seven genera and more than 450 species. Most Alooideae taxa are found in sub-Saharan Africa, with a marked concentration of species and genera in southern Africa. All species of Alooideae are petaloid, succulent-leaved, rosulate or distichous perennials. They differ in size from miniatures barely 10 mm high (*Haworthia parksiana* Von Poellnitz) to trees of massive bulk up to 20 m tall (*Aloe bainesii* Thiselton-Dyer). In spite of this notable morphological variation the Alooideae is reasonably homogeneous in an evolutionary sense, unifying characters being the widespread occurrence of secondary thickening growth, leaf succulence, usually tubular petaline flowers and fusion of the perianth segments. Furthermore, in the entire subfamily the basic diploid karyotype (2n = 14; four pairs of long chromosomes and three pairs much shorter) is only very rarely altered (Brandham 1969).

The majority of species of Alooideae has been investigated cytologically. These studies were initiated early in the 20th century and have resulted in an extensive bibliography on the cytology of this group (for reviews see Muller 1941; Riley 1959a,b,c; Brandham 1971, 1983; Riley & Majumdar 1979). The intention of the present paper is to contribute to the cytotaxonomic knowledge of the Alooideae by the chromosome complement analysis of *Chortolirion* Berger and *Poellnitzia* Uitewaal, two monotypic genera. Chromosome studies have not been reported for *Chortolirion* to date and for *Poellnitzia* only four previous counts have been published, one of which is not readily accessible (Majumdar 1968 quoted by Riley & Majumdar 1979). The previous cytological observations of *Poellnitzia* were all made on specimens cultivated in botanic gardens (Resende 1937; Viveiros 1949; Majumdar & Riley 1972). These early cytological studies therefore had no connection with natural populations. Problems which arise from such a practice have been discussed by Riley & Majumdar (1979).

C. angolense (Baker) A. Berger is a perennial, deciduous herb with a subterranean bulb and is widely distributed in the summer rainfall region of southern Africa. With short, annual, succulent shoots arising from the bulb in early spring, *C. angolense* presents a combination of geophytic and succulent habits (Figure 1). *P. rubriflora* (L. Bol.) Uitewaal is a low-growing, caulescent, succulent herb. Stems are up to 250 mm long and densely leaved. The ovate leaves are pungent-acuminate and up to 40 mm long (Figure 2). *P. rubriflora* has a restricted distribution in the south-western Cape Province of South Africa. This region receives its precipitation mainly during the winter months.

[INSERT FIGURE 1 NEAR HERE]

Chortolirion and *Poellnitzia* have been the subject of taxonomic confusion (Bayer 1974; *cf.* Smith 1988). A revision of the smaller genera of Alooideae currently under way has shown that both taxa warrant recognition as monotypic genera.

[INSERT FIGURE 2 NEAR HERE]

MATERIAL AND METHODS

The origin of the material of C. *angolense* studied is:
TRANSVAAL. -- 2528 (Pretoria): in habitat in the Botanic Garden of the National Botanical Institute, Brummeria (-CB), *Smith 8* (PRU).

Material of *P. rubriflora* was collected at:
CAPE. -- 3320 (Montagu): southern side of farm 'Langverwagt 169', 5 km W of Bonnievale (-CC), *Stayner s.n.* sub *Smith 9* (PRU).

Plants for cytological study were grown in the greenhouse of the Department of Botany, University of Pretoria. Somatic chromosomes were studied in root tips collected during late winter/early spring from vigorously growing potted plants. Actively elongating root tips (2--5 mm) were collected at 14:00 and pre-treated with freshly prepared colchicine (0,05% in distilled water) for 2h and fixed in Pienaar's (1955) fixative (methanol: chloroform: propionic acid in the ratio 6:3:2) for 16h. Root tips were hydrolysed for 12 minutes in a 1M hydrochloric acid solution kept at 60°C and stained in Feulgen for 2,5 h. Squash preparations were made using a standard technique (Van der Schijff & Robberste 1976). Photographs were taken with a Nikon FX 35A microscope fitted with a Nikon Optiphot camera. Measurements were made directly from mitotic preparations using an eyepiece micrometer. For chromosome nomenclature, the terminology introduced by Levan *et al.* (1964) has been followed. The karyograms (Figures 3B; 4B) and idiograms (Figures 3C; 4C) are arranged according to chromosome length.

RESULTS

General.
In *Chortolirion* and *Poellnitzia* the somatic chromosome number 2n = 14 was constant in all metaphases with karyotypes as in Figure 3B (*Chortolirion*) and Figure 4B (*Poellnitzia*). For both genera the haploid set is asymmetrical, producing a distinctly bimodal karyotype which consists of four long and three short chromosomes. No major chromosomal differences between *Chortolirion* and *Poellnitzia* could be detected. Furthermore, no marked size variation was encountered within the sets of long and short chromosomes in the respective

genera.

Karyotype of *C. angolense*.

Each of the long chromosomes (I-IV) is of the st type, while all the short chromosomes (V-VII) are of the sm type (Figure 3C). Satellites were detected at the ends of the short arms of the shortest long chromosome (IV) (Figure 3A, B). Secondary chromosome constrictions are absent from the long arms of the short chromosomes (V-VII). Such constrictions occur widespread in taxa of the Alooideae (Brandham 1971).

One chromosome I has a short arm much smaller than that of the other (Figure 3A, B). Since this phenomenon was not encountered consistently, it is probably not associated with an interchange or a deletion, but rather due to the orientation of the chromosome on the slide.

[INSERT FIGURE 3 NEAR HERE]

Karyotype of *P. rubriflora*.

The longest long chromosome (I) is of the sm type while the three other long chromosomes (II-IV) are of the st type. The longest short chromosome (V) is of the m type and the two remaining short chromosomes (VI-VII) are of the sm type (Figure 4C). Satellites were not detected on any of the chromosomes (Figure 4A, B). Secondary constrictions of unknown nature were observed on the short arms of the long chromosomes (except I) and the long arms of all the short chromosomes.

[INSERT FIGURE 4 NEAR HERE]

DISCUSSION

The chromosomes of all plants studied were found to match the markedly bimodal karyotype which has been observed in every species of Alooideae to date. The basic number is x = 7 and comprises four long and three short chromosomes. To date a large number of intra- and intergeneric hybrids produced in the Alooideae have been described and figured (Riley 1948; Jacobsen & Rowley 1955, 1973; Rowley 1968, 1976; Graf 1980). Although some of the hybrids are sterile, others are fully fertile (Brandham 1973). This testifies to the close cytogenetical relationship which exists amongst taxa of the Alooideae (Rollins 1953). *Chortolirion* and *Poellnitzia* are no exceptions to this rule, *Chortolirion* having been crossed successfully with *Aloe* and *Poellnitzia* with *Gasteria* (Rowley 1980, 1982; Brandham 1990).

Both *Chortolirion* and *Poellnitzia* are diploid with 2n = 14 chromosomes, in common with the great majority of species in the subfamily Alooideae as a whole.

Although *Aloe*, *Gasteria* and *Haworthia* are known to include a variety of polyploids (Riley & Majumdar 1965; Brandham & Johnson 1977a, 1982; Cutler *et al.* 1980; Brandham 1982; Motohashi *et al.* 1985), none of the individuals included in the present study contained different levels of ploidy. In the Alooideae polyploidy can give rise to local bursts of speciation (Brandham & Cutler 1981; Cutler *et al.* 1980).

Some authors have previously established a nomenclature for the chromosomes of taxa of the Alooideae (L1 through L4 for the long chromosomes and S1 through S3 for the short chromosomes) (Snoad 1951; Riley & Majumdar 1966; cf. Brandham 1971 for an explanation; Brandham & Johnson 1977b; Brandham & Cutler 1978, 1981). However, the identification of individual chromosomes (especially the short chromosomes) and their subsequent classification is very difficult and no attempt was made to do so here. Brandham (1983) eventually concluded that only L1 (long chromosome with longest short arm) could be identified with certainty in somatic and meiotic cells. However, recognition even of the L1 chromosome, which usually is the only submetacentric long chromosome, can occasionally yield difficulties as is evidenced by reports of Mogford & Rautenbach (1981), Vosa & Bayer (1981) and Vosa & Mogford (1981). In *Chortolirion* chromosome II is clearly the L1 and chromosome I is the L2, which is often longer than the L1 (Figure 3C). In *Poellnitzia* chromosome I is the L1 (Figure 4C).

In the case of *Poellnitzia* the short arms of the long chromosomes, with the exception of the longest long chromosome (I), and the long arms of the short chromosomes appeared to be thinner in their mid-region than at either end (Figure 4). These thin regions [secondary constrictions *sensu* Sharma & Mallick (1966)] have been used as basis for the establishment of a number of different types of chromosomes (Sharma & Mallick 1966). As Brandham (1971) justifiably remarks the constrictions could possibly be due to variations in the degree of coiling of the chromatids and are structurally insignificant. Thinner regions on the chromosomes were virtually absent from *Chortolirion*, with the exception of satellites present on the short arms of the two shortest long chromosomes (IV) (Figure 3).

The chromosome count of *Poellnitzia* agrees with that reported by Resende (1937), Viveiros (1949), Riley (1961) and Majumdar & Riley (1972), but the chromosome morphology differs in that the latter workers reported satellites as being present on the long arms of two long chromosomes [L1 and L4 *sensu* Majumdar & Riley (1972)]. In the present study no satellites were observed in *Poellnitzia* (Figure 4). The difference in karyotype between published and observed data indicate the existence of chromosomal variability in *Poellnitzia*. It is noteworthy that considerable variation in the number and position of satellites has also been reported for other species of Alooideae genera (Brandham 1971; Spies & Hardy 1983). This karyotype character therefore appears to be taxonomically insignificant.

Knowledge of chromosome morphology in closely related taxa is of primary importance in biosystematic and taxonomic studies. In the Alooideae studies of karyotypes are particularly informative, where the asymmetry in size within complements can assist in determining the progress of chromosome alteration and its consequences. However, some doubt still exists with regard to the phylogenetical significance of certain karyological aspects, such as overall size of chromosomes. Majumdar & Riley (1972) have, for example, suggested that in the species of the various genera of Alooideae reduction in chromosome size is paralleled by a reduction in size and specialization of the plant. In contrast, Brandham (1983) has shown that, at least in *Aloe*, there is a gradation from smaller chromosomes in primitive species to larger ones in advanced species. The latter are often highly adapted miniatures. Similarly, the chromosomes of *Gasteria* are larger than those of *Aloe* (Brandham 1990). *Gasteria* is generally regarded as phylogenetically more advanced than *Aloe* (Van Jaarsveld 1989). The karyotypes of species of *Gasteria* are also more acutely bimodal than those of species of the more primitive *Aloe*. Based on chromosome size and increased bimodality *Poellnitzia* would therefore appear to be more advanced than *Chortolirion*. However, the complexity of interpreting taxa of the Alooideae as either primitive or advanced is illustrated by the suggestion of Hayashi (1987), based on callus characteristics, that *Poellnitzia* is a relict of early Alooideae. For *Chortolirion* a close affinity was suggested with *Haworthia* subgenus *Haworthia*, a derived group. It is therefore clear that a multidisciplinary approach should be followed when drawing conclusions regarding phylogenetical position of Alooideae taxa. In such studies wide ranging karyological analyses will be of crucial importance (cf. Carter *et al.* 1984).

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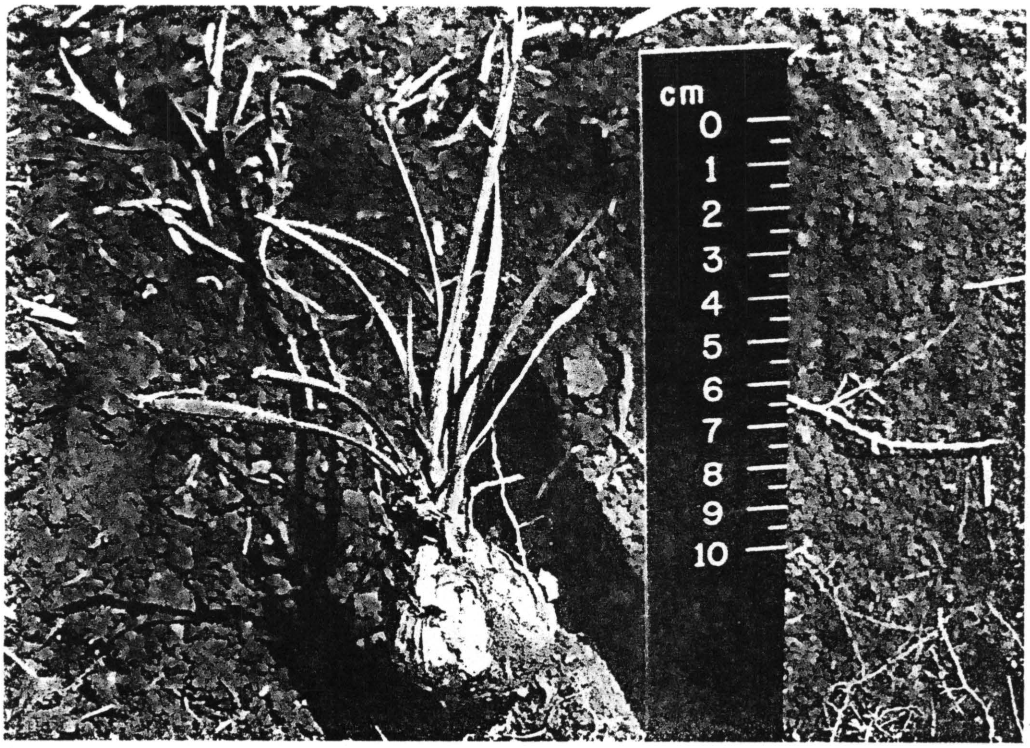

FIGURE 1. --- Growth form of *Chortolirion angolense* in habitat in grassland at Potchefstroom, south-western Transvaal, South Africa. The soil has been removed to show the bulb and narrowly linear leaves.

FIGURE 2. --- *Poellnitzia rubriflora* (arrowed) in habitat at Langverwacht near Bonnievale, south-western Cape Province, South Africa. The species usually grows in association with sclerophyllous xerophytes.

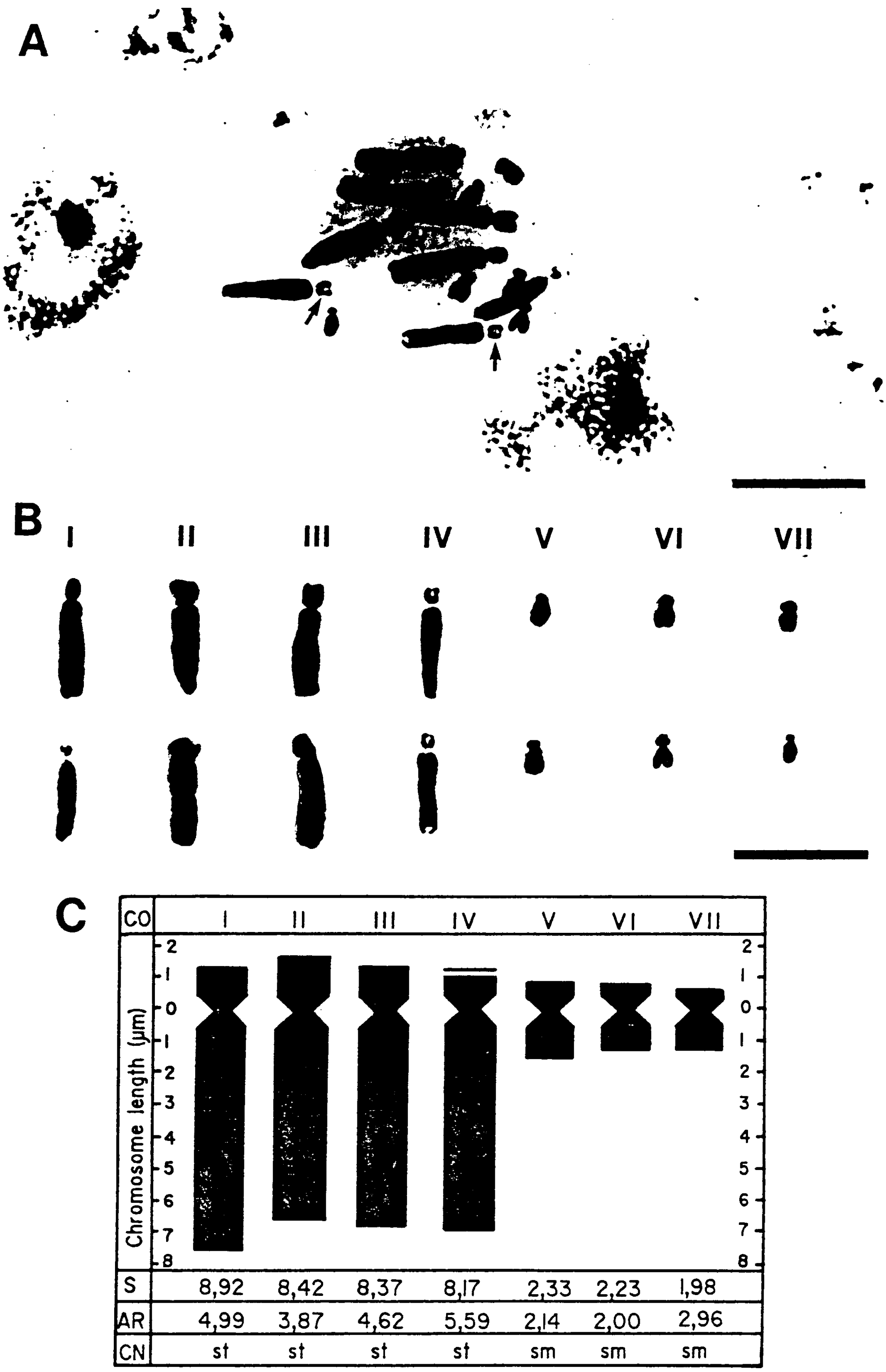

FIGURE 3. --- *Chortolirion angolense*. A, Mitotic metaphase; arrows indicate satellites. B, Karyogram. C, Idiogram. CO, chromosome ordering (overall length); S, chromosome size; AR, arm ratio (= long arm/short arm); CN, chromosome nomenclature after Levan *et al.* (1964). Chromosome II is clearly the L1 (long chromosome with longest short arm) and chromosome I is the L2, which is often longer than the L1.

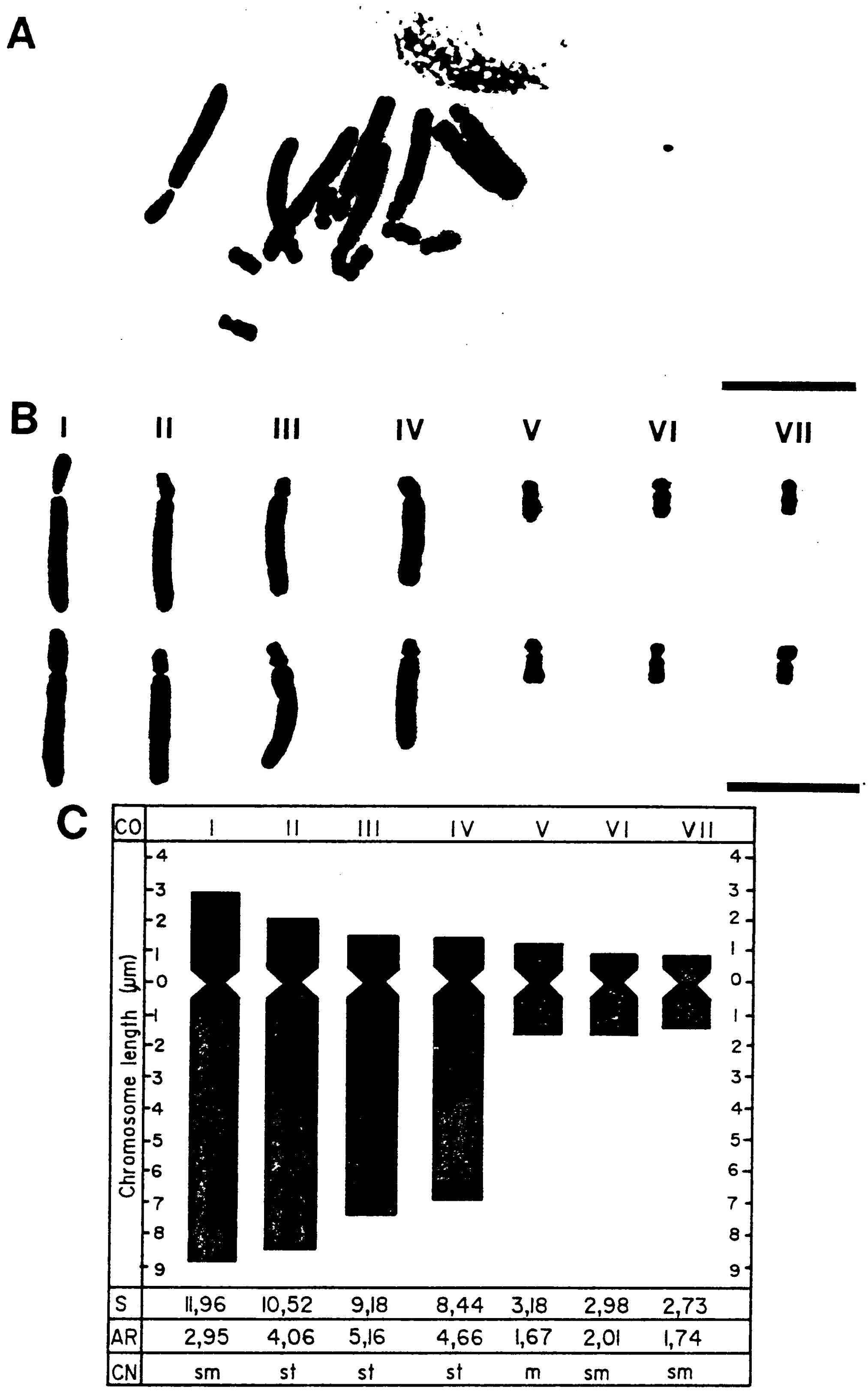

FIGURE 4. --- *Poellnitzia rubriflora*. A, Mitotic metaphase. B, Karyogram. C, Idiogram; symbols as in Figure 3.

6.3.2 SMITH, G.F. 1990. IOPB chromosome data 2. Liliaceae: *Chortolirion angolense, Poellnitzia rubriflora. Newsletter of the International Organization of Plant Biosystematists* No. 15: 15 218

International Organization of Plant Biosystematists

Newsletter No. 15

4. IOPB Chromosome Data 2

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LILIACEAE
Chortolirion angolense (Baker) A. Berger 2n=14. South Africa: C. Transvaal: Brummeria N. of Pretoria, Smith 8.
Poellnitzia rubriflora (L. Bolus) Uitewaal 2n=14. South Africa: S.W. Cape: 5 km W. of Bonnievale, Smith 9.

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CHAPTER 7
ECOLOGY AND CONSERVATION

" ... the rapid extinction of species is the folly for which our descendants will be least likely to forgive us."

Professor Edward Wilson,
Harvard University's Museum
of Comparative Zoology,
in conversation with
C. Joyce: 1986

CONTENTS

CHAPTER 7

ECOLOGY AND CONSERVATION

7.1 INTRODUCTION

7.1.1 Background

The Republic of South Africa is fortunate in that it is relatively large (surface area of 1 123 226 km^2, excluding the republics of Transkei, Bophuthatswana, Venda and Ciskei), has a rich and diverse natural resource base (both abiotic and biotic) and an unsurpassed scenic beauty (Anonymous 1987). The coastline is approximately 3 000 km long, from the Mocambique border in the east to the mouth of the Orange River in the west. The country is lapped by the Indian Ocean in the east and the Atlantic Ocean in the west. The coastline is swept by the warm Mocambique-Agulhas Current which flows southwards along the east coast and westwards along the south coast as far as Cape Point, and the cold Benguela Current which flows northwards along the west coast as far as Angola. The general topography comprises a coastal belt bordered by a more or less continuous range of mountains on the edge of a vast interior plateau with an average elevation of 1 200 m [cf. Partridge & Maud (1987) for a discussion of the geomorphic evolution of the Great Escarpment]. The location, ocean currents and topography account for the fact that South Africa probably is climatologically least typical of all African countries. Since southern Africa is host to a variety of major climatic, topographical, geological and pedological transition zones, a wide variety of ecological niches are available for plant colonization, often over short distances. These selection pressures, amongst others, have acted to produce a flora unsurpassed in the world in terms of species/area ratios (0,0081 species/km^2 overall). Even when the Cape Floral Kingdom, which is known to be extremely rich in species [and endemic taxa, for that matter (cf. Dahlgren & Van Wyk 1988)], is excluded from calculation, the figure for the rest of the southern African flora (0,0061) is still considerably higher than that of the humid tropics (0,0044 for Brazil) (Gibbs Russell 1985, 1987). This exceptional southern African floral wealth has been known internationlly since the early seventeenth century (Smith 1990).

The large variety of vegetation types (Acocks 1988) and their respective floristic compositions (and the consequent scenic beauty which is of considerable importance to the southern African tourist industry) has its origins in the ancient geological and gravitational forces which shaped and honed the great southern continent of Gondwana. This continent split, resulting in landmasses drifting apart and then reshaping under the influences of rising and falling sea-levels, of ocean currents and a multitude of successive climatological events (Raven 1983). These processes are on-going and our present situation represents but a brief moment in time. With the unsurpassed mineral and natural historical wealth of South Africa necessarily comes demanding conservation responsibility. It is therefore clear that the seriousness of the present efforts to protect our floral heritage cannot be doubted.

After the Anglo-Boer War (1899--1902) the responsibility for wildlife protection was accepted by the four provinces. With the establishment of the Union of South Africa (1910), this condition was confirmed (Section 85, Paragraph 10 of the South Africa Act, 1909) and it has remained virtually unchanged since then. In the Republic of South Africa there are currently at least 590 protected areas of which 547 are terrestrial and 43 are marine and island reserves. The terrestrial component comprises an area of 7 277 109 ha which represents 6,5 % of the total land area of the Republic (Cohen 1989; cf. also Greyling & Huntley 1984). However, the preponderance of conservation effort is more or less concentrated in the veld types (*sensu* Acocks 1988) of the eastern and southern parts of South Africa. In contrast, almost negligible conservation is found in the semi-arid and arid western parts of the country (Scheepers 1983; Palmer 1990). It is therefore clear that the conservation status of the southern African flora and vegetation is still deficient in a number of respects. The position in regard to the conservation of specific threatened plant species also gives cause for concern. The lists of threatened plant species which have been published recently (Hall *et al.* 1980; Hall & Veldhuis 1985) are essentially first drafts and much more research is required before the conservation of threatened species can be put into practice on a scientific basis.

It is becoming increasingly evident that no single theory, hypothesis or definition is sufficient to describe and understand the concept of rarity in plant species (Fiedler 1986). The International Union for the Conservation of Nature and Natural Resources (IUCN) have, however, developed standard categories which attempt to apply concepts of static and dynamic rarity to threatened taxa. Although these codes of rarity and endangeredness have been criticized in the past (Stirton 1990), the utility value of an international system should not be underestimated. This system is used widely in southern Africa and, for the sake of uniformity, I have used the IUCN categories as guidelines for assessing the conservation status of *Aloe bowiea* (Smith 1989; Smith & Van Wyk 1990), *Chortolirion* and *Poellnitzia*. These categories are as follows (cf. Hall & Veldhuis 1985):

Extinct: Taxa which no longer exist in the wild: not found in repeated searches of all known and likely areas. This category is also used for a taxon which no longer occurs in the wild but survives in at least some form in cultivation, probably so genetically impoverished or altered as to make it impossible to return it to a natural habitat.

Endangered: In immediate danger of extinction if the factors causing decline continue operating. Included here are taxa whose numbers of individuals have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction.

Vulnerable: Taxa believed likely to move into the Endangered category in the near future if the factors causing decline continue operating. Included here are taxa of which most or all of the populations are decreasing because of over-exploitation, extensive destruction of habitat or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security is not yet assured; and taxa with populations that are still abundant but are under threat from serious adverse factors throughout their range.

Critically Rare: Taxa with small world populations that are not at present Endangered or Vulnerable, but are at risk as some unexpected threat could easily cause a critical decline. These taxa are usually localized within restricted geographical areas or habitats or are thinly scattered over a more extensive range. The category is termed Critically Rare to distinguish it from the more generally used word 'rare'.

Indeterminate: Taxa temporarily grouped here are awaiting placing in one of the above categories when further information becomes available.

Uncertain: Taxa temporarily grouped here are those for which reasonably good but unconfirmed grounds exist for believing the plant to be in one of the above categories, as well as being taxonomically distinct.

Not Threatened: This is used for taxa which are no longer in one of the above categories due to an increase in population sizes or to subsequent discoveries of more individuals or populations. Unlike a previous report (Hall *et al.* 1980) there are no cases in which the plant is threatened within the region under study but Not Threatened elsewhere.

All three taxa (*A. bowiea, Chortolirion* and *Poellnitzia*) that this study is primarily concerned with, occur in the Cape Province. In the province the protection of these taxa is governed by Ordinance 19 of 1974 (Appendix 3: Threatened flora and Appendix 4: Protected flora). *Aloe pillansii, A. buhrii* and *A. erinacea* are listed as threatened while all the other species of *Aloe* (except *A. ferox*) are treated as protected flora, along with *Gasteria beckeri* and all the species of *Haworthia* and *Kniphofia* (for complete lists see Le Roux & Schelpe 1981, Moriarty 1982 and Kidd 1983). The Ordinance on Nature Conservation of the Orange Free State makes provision for the protection of all 11 species of *Aloe* (including *A. ferox*) and all species of *Kniphofia* which occur in the province (Anonymous no date). The genus *Chortolirion* is protected in the Transvaal along with all the species of *Gasteria, Haworthia* and *Kniphofia* (Nature Conservation Ordinance 17 of 1967, Article 76, Appendix 7; cf. Onderstall 1984). All the species of *Aloe* indigenous to the Transvaal are also protected, with the exception of *A. aculeata, A. ammophila, A. barbertoniae, A. castanea, A. davyana, A. globuligemma, A. grandidentata, A.*

lutescens, A. marlothii, A. mutans, A. parvibracteata, A. transvaalensis and *A. wickensii*. A protected or threatened plant, or part thereof may be picked or removed by the landowner, his family or employees only, and then only on land that is needed for farming or development purposes. The landowner may donate such plants to outsiders but then these plants have to be accompanied by a donation letter in which the plant species and numbers, as well as the names and addresses and signatures of both the donator and recipient, are noted. All plants growing in the strip which encloses 100 m on both sides of the road, are protected and nobody may tamper with them. These strips, apart from the fact that the indigenous plant life remains intact, act as seed reservoirs for neighbouring fields (Milton & Dean 1987).

Although we are today approaching the point where many South Africans regard the flora of the country as a national asset of enormous value, few people are actively involved in nature conservation. One still gets the impression that today's materialistic wants and needs are far more important than treating environmental resources with the respect they deserve and demand. In itself development (of whatever kind) is not evil --- provided it is measured in quality and not in quantity. We must realise the necessity of environmental awareness [more recently referred to as "maintaining biodiversity"; see, for example, Correspondence: In defence of taxonomy, *Nature* 347: 222-224 (20 September 1990)] and the obligation of every human being to act in a responsible way that will ensure the survival of our planet and its resources.

The population of southern Africa is growing more quickly than almost any other area in the world (Hall 1978; Sadie 1978). To make this fact even more serious, southern Africa has an erratic and unequally distributed rainfall (Weather Bureau 1984). To the question whether this situation will worsen, the answer has to be yes. Even if droughts would cease, the population continues to grow. This escalation brings with it the need for more industry, more forestry and increases the requirements for more food production. More land would therefore have to be cleared and cultivated. The solution to this problem is complex and a long road of educating people lies ahead. It first must be centred on a commitment to educate and implement population control measures for all the peoples of southern Africa. It also implies the development of an increased environmental awareness, and the conservation of the flora which is one of our most precious natural resources. Calculations concerning the state of equilibrium between man and his environment contain many imponderable factors. The most important is the alarmingly rapid deterioration of the environment as man's numbers increases (Huntley *et al.* 1989).

Even to the uninitiated it should be clear that flora conservation is the real issue. For example, carnivores are linked through predation to herbivores, which are, in turn, linked to each other through competition and the plant communities by their foraging. Does this intricately woven webb of matual dependence only apply to the African elephant, rhinoceros, spotted cats and majestic birds of prey? What about inconspicuous, low-growing species of succulent plants? In some instances farmers and agriculturists regard indigenous succulents as a nuisance to man, for example *Euphorbia aggregata* Berger in the Grahamstown district of the eastern Cape and a species of *Astroloba* in the Willowmore district, southern Cape. Do we therefore only conserve those species that are (at least at the moment) of value to man? Do we allow the rest to slip quietly into extinction? Surely it is up to man to foresee and forestall the consequences of his actions. Due to the destruction of South Africa's flora, traditional medicinal healers already have to face the fact that the supply of medicinal herbs is dwindling alarmingly. Apart from their medicinal value, traditional mutis are often believed to have magical powers and are usually preferred to the White man's medicines. Although the tribal ways of the Blacks have changed with urbanization, there is still a great demand for traditional medicine and large quantities of plants are being illegally taken to cities such as Soweto where it is in huge demand (Cunningham 1987, 1988).

The slogan "Survival is **YOUR CHOICE**" [my emphasis] was used in 1986 during a special environmental awareness campaign launched by the Department of Environment Affairs. Indeed, everyone should be brought to the realisation that harmony between man and environment can only be accomplished by the actions and sacrifices of individuals. We should not be trying to persuade someone else to engage in conservation matters if we are not prepared to act ourselves; complaining about others salves the conscience, but it does not improve the relationship between man and environment. With rare exceptions (see for example Jacot Guillarmod 1989) individuals are unaware of their vital role in preserving and improving the environment of our country. Everyone has the responsibility of creating an environmentally conscious population consisting of responsible planners, educationists, scientists and technicians. Clearly we need an integrated approach if we are to achieve the sustainable utilisation of our resources for the benefit of all people. Unless action is taken now, we will only have ourselves to blame for the loss of natural habitats, for surely that will be the result of our inactivity. Only a change in attitude on the part of the entire community can ensure the survival of, amongst others, our indigenous succulents, as individuals and as populations.

The message is clear --- unless something is done, whole ecosystems and their constituent species will suffer and eventually disappear. In fact, at the present rate of mankind's continuous rush in disrupting the earth's natural resources, a great many species will be extinct by the turn of the century (Simon 1986). Although conservation of our flora cannot be accomplished solely by the setting aside of specially protected areas by some conservation agency, it should be clear that every last hectare which can be protected, does matter. At any rate, *ex situ* conservation only should not be regarded as sufficient in assuring the survival of threatened species (Hall *et al.* 1980; Jain & Sastry 1984). To succeed, conservation must be practised in all places and at all times --- conservation must be a way of life.

Sound conservation and management of our floristic heritage is a matter of highest priority and mistakes of the past must not be perpertuated [cf. Phillipson (1990) on exotic weeds]. A good example of a previous error is the misguided introduction to South Africa of the Mexican *Opuntia ficus-indica* (L.) Mill. (Henderson & Musil 1987). Since 1750 the species has become one of the most serious threats to the vegetation of the eastern Cape and cactus eradication and biological control have already cost the taxpayer millions of rands (Stirton 1983; Ferrar & Kruger 1983; Henderson *et al.* 1987). Although it is a pity that the awareness of the need for this approach did not arise many years earlier, this problem appears insignificant in the light of global environmental problems. Threats such as the depletion of the ozone layer and atmospheric pollution, the greenhouse effect, water pollution, species extinction, in short, the degradation of the natural environment, cannot simply be postponed - it is a responsibility to be dealt with now. In no way can we justify our inability to manage resources judiciously. Why then, one must ask, are most South Africans sitting idly on their hands?

Although aloeoid species are protected by legislation in all the provinces of the Republic of South Africa (references given above), very little information is available on the conservation status of individual species, *Aloe polyphylla* being a notable exception (Beverly 1978, 1979, 1980; Jacot Guillarmod 1969, 1975; Kofler 1966; Smith 1986; Talukdar 1983). In Chapter 7 detailed notes are provided on the ecology and conservation status of *Aloe bowiea* (Smith 1989; Smith & Van Wyk 1990). The wild country of the eastern Cape Province of South Africa where the species is endemic is dissected by great rivers including the Sundays and Gamtoos. Inhospitable habitats such as this one and, amongst others, the Richtersveld, have always fascinated man and are being increasingly exploited for recreational purposes (Castle 1990), making it a high priority conservation area. The subtropical transitional thicket which occur in this region is unique even by world standards (Smith & Marx 1990). But even now land surrounding Port Elizabeth, the eastern Cape capital, is being threatened by, amongst others, urban development (Peckover 1990). Consequently the region is host to several threatened taxa of succulent plants. For this reason the conservation status of two more species of Alooideae endemic to the eastern Cape, *Aloe microcantha* Haw. and *Haworthia fasciata* (Willd.) Haw., are discussed (Smith 1991a, b). Brief reports on the conservation status of *Chortolirion* and *Poellnitzia* are also included. These genera are fortunately not as threatened as the species of Alooideae which occur in the eastern Cape.

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Notes on the vegetation and succulent flora of the eastern Cape Province, South Africa

Gideon F Smith* and Gerhard Marx**

Abstract

The physiography and climate of the eastern Cape are briefly discussed to provide a scenario for the discussion of the subtropical thicket vegetation types which are dominated by succulents and spinescent species. Endemic geophytic and succulent plant taxa are enumerated and a bibliography of botanical research in the eastern Cape is provided. In this region a wide range of habitats are present over short distances. As a result of considerable variation in climate, edaphic factors, landscape and prevailing rainfall regimes, the eastern Cape has a great variety of niches available for occupation by floristic elements of the four phytochoria (Tongaland–Pondoland forest and thicket; succulent and dwarf shrublands of the Karoo–Namib Region; Afromontane elements and Fynbos taxa of the Cape region) converging in this area. This region exhibits lower levels of endemic plants than the Cape flora, but two centres of endemism, one for Cape taxa and one for karroid and subtropical taxa have been recognized in the eastern Cape.

Introduction

The southern African subregion is generally recognised as one of the richest known succulent areas in the world (Court [1981]; Van Jaarsveld [1987]; Roberts [1989a,b]). Of the approximately 10 000 plant taxa in the world loosely referred to as succulents, more than 36% originate from Africa south of Angola, Zambia, Zimbabwe and Mocambique (Van Jaarsveld [1987]). Succulents occur throughout southern Africa (for example *Peperomia tetraphylla* (G. Forst.) Hook. & Arn., Piperaceae, which is indigenous to the forests of southern Africa (Batten & Bokelmann [1966]; Moriarty [1982]), and large numbers of succulents have been reported from five geographical regions of this subcontinent. These are: (1) the western Cape, (2) the southern Cape, (3) the eastern Cape, (4) Transkei and Natal and (5) the eastern Transvaal and Swaziland (cf. Van Jaarsveld [1987] for the circumscription of these areas).

The eastern Cape is a major climatic, topographical, geological and pedological transition zone and consequently supports a diverse flora, including many succulents (Everard [1985]; Lubke et al. [1986]). For this reason synoptic discussions of the geographical situation and climate are provided. The vegetation is dealt with in more detail, with special reference to endemism in the succulent flora. A brief bibliography of recent research on the vegetation is also given.

Botanical exploration of this region commenced in the mid-1750's and plants collected in the eastern Cape reached Europe shortly afterwards (Britten [1908, 1920]; Hilliard & Burt [1971]; Gunn & Codd [1981]). The eastern Cape was traversed by many well-known explorers, plant collectors and botanists, including Carl Peter Thunberg, generally referred to as "the father of South African Botany", William John Burchell, Christian Frederick Ecklon, Carl Ludwig Philip Zeyher, Johann Franz Drège, James Bowie and many more (MacOwan [1887]; Verduyn den Boer [1929]; Hutchinson [1946]; Dubovsky [1985]; Forbes [1986]).

Geographical situation

In the past, the eastern Cape has been variously demarcated by different research workers (cf. Everard [1985] for references). In accordance with a recent proposal of Lubke et al. [1986], the eastern Cape is here defined as the area south of 31° S and between 24° E in the west and the Great Kei River and the Transkei boundary in the east (Fig. 1). As natural boundaries this region therefore has the Sneeuberg–Winterberg–Stormberg escarpment in the north, the Great Kei River in the east and the Kromme and Gamtoos Rivers in the west (Everard [1987]).

The eastern Cape is thus approximately 80 000 km^2 in extent and is topographically variable. The land rises from sea level to about 2 000 m in the north-east (Stormberg Range: Dordrecht), 1 900 m in central-eastern Cape (Winterberg Range: north of Adelaide) and 2 100 m in the north-west (Sneeuberg Range: north-west of Graaff-Reinet). Many rivers drain into the Indian Ocean along the eastern Cape coast and little flat country remains (Gibbs Russell & Robinson [1981]).

Climatic characteristics

Any discussion of climate should take a number of environmental variables into account. These include seasonal climatic controls, cloud cover and frequency, solar radiation, wind speed and direction, rainfall and temperature. The climate of the eastern Cape in general and of specific localities in this region has been discussed by many authors, including Gibbs Russell & Robinson [1981], Cowling [1984], Everard [1985, 1987] and Kopke [1988]. This article does not attempt to offer a complex description of this region's climate and previous detailed discussions will not be repeated here. However, temperature and

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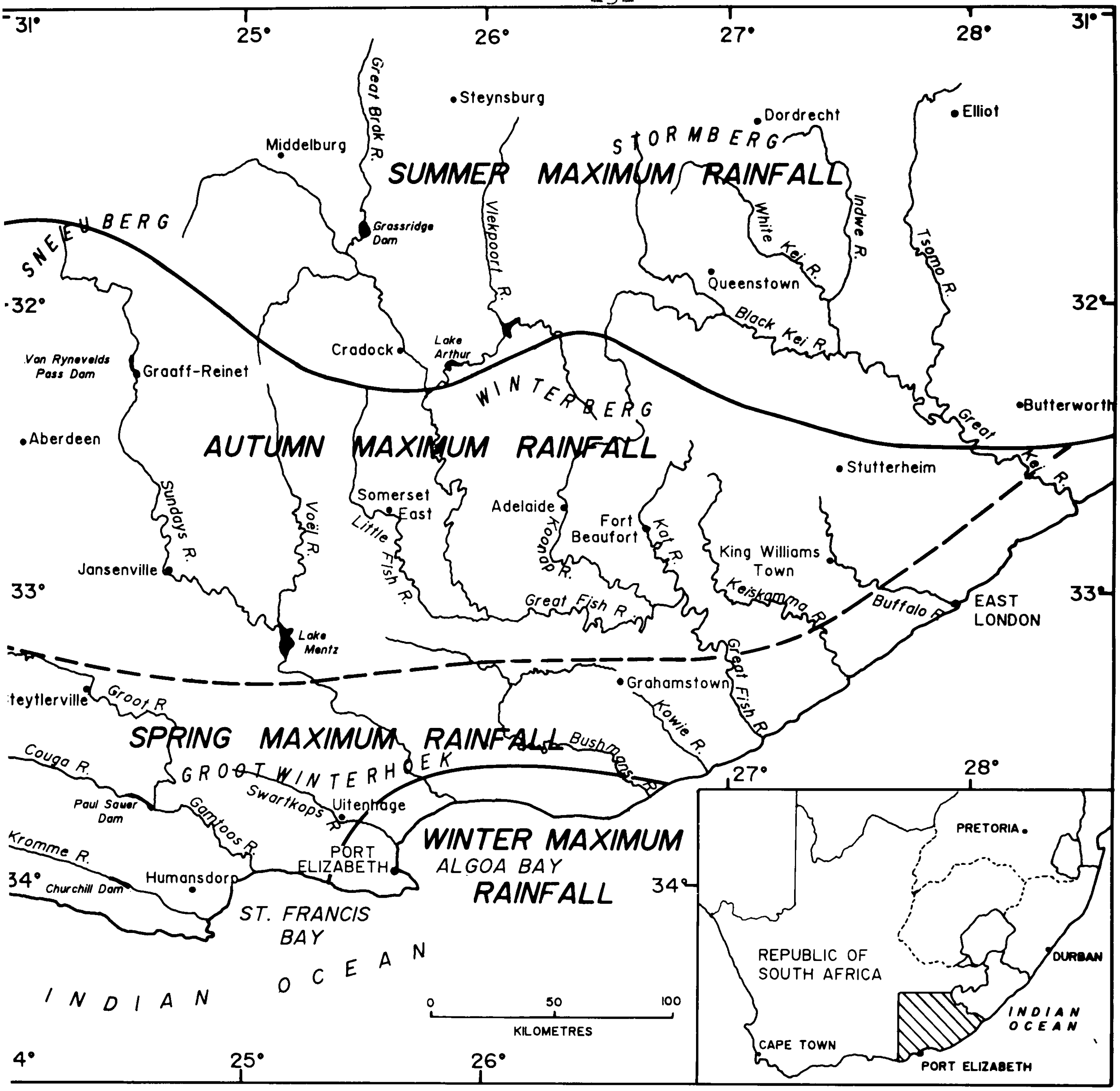

ure 1. Map showing the regional limits of the eastern Cape (after Lubke et al. [1986]). Seasonal distribution of rainfall after ɔke [1988].

nfall play an important role in determining the tribution of succulents, and are briefly discussed ow.

Rainfall varies considerably in amount and a large t of the eastern Cape is semi-arid. Generally the ount of rainfall decreases from the coast inland l from east to west. Due to the unreliability of nfall, droughts are not uncommon. Rainfall also ies seasonally, with regions receiving maximum nfall in spring, summer, autumn and winter be- encountered in the eastern Cape (Gibbs Russell Robinson [1981]; Kopke [1988]) (Fig. 1). The gest portion of the eastern Cape has a pronounced nodal distribution of rain with maximum rainfall ng recorded in spring and autumn and dry periods mid-summer and mid-winter (Weather Bureau 34]). As is the case elsewhere in southern Africa, topography also plays a major part in the distribution of rain, rainfall totals and by producing significant local rainfall variations.

The greater portion of the eastern Cape experiences warm summers and mild winters with occasional frost. In the mountainous regions temperatures are modified by altitude, and local winds often cause a drop in average daily temperatures. The Karoo and the region north of the Winterberg escarpment (summer maximum rainfall area) are characterized by hot summers and cold winters. The coastal zone is mild throughout the year. In general temperatures vary from the coast inland with more extreme temperatures occurring in the north and west of the region.

Climate diagrams of selected stations are shown in Fig. 2.

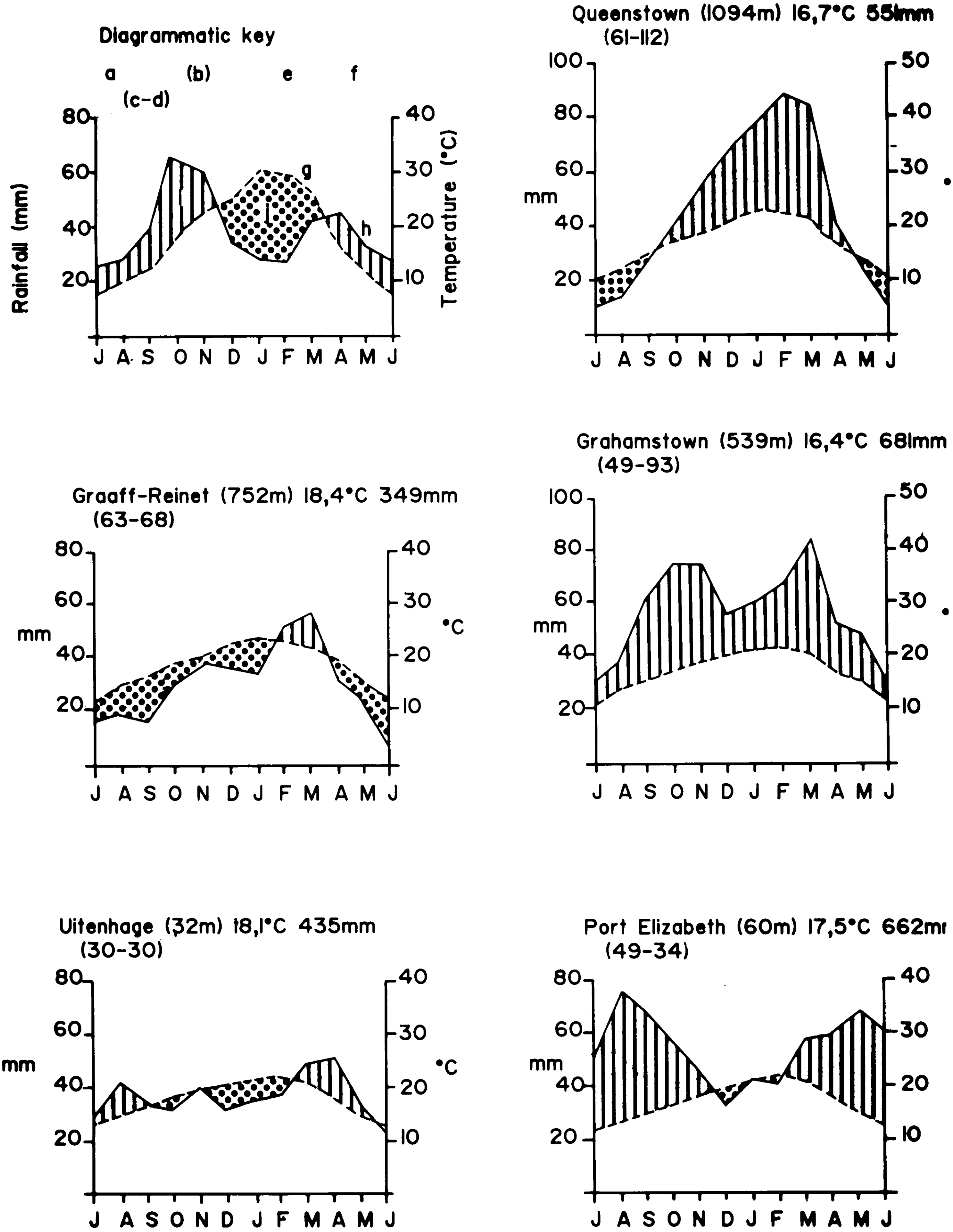

Figure 2. Walter–Lieth climate diagrams of selected stations in the eastern Cape. Diagrammatic key: (a) Station name; (b) altitu (c–d) number of recording years (temperature–rainfall); (e) mean annual temperature; (f) mean annual rainfall; (g) curve of m monthly temperature; (h) curve of mean monthly rainfall; (i) wet season; (j) dry season. Data from Weather Bureau [1984].

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his benchmark publication on the ecology of south- Africa, Acocks [1988] developed the so-called veld e concept. He defined this unit of vegetation as "... whose range of variation is small enough permit the whole of it to have the same farming tentialities." This definition is therefore based both the floristic composition and the agronomic tential of a given vegetation type. Of the 70 d types which Acocks [1988] recognised, 21 are resented in the eastern Cape (Gibbs Russell & binson [1981]). This region has more veld types in any other region of comparable area in southern rica and reflects the diversity of the eastern Cape getation.

The criteria which Acocks [1988] used for dis- guishing veld types (plant communities or ag- gations of communities sensu Gibbs Russell & binson [1981]) are, however, criticised by some thors (Cowling [1984]; Lubke et al. [1986], but see ll [1986] for a discussion of veld types versus the me concept). This is especially the case in the stern Cape where four major phytochoria converge owling [1983a, b]). These are the Tongaland– ndoland dwarf forest or thicket which penetrates area from the east and extends up the river leys, succulent shrublands of the Karoo–Namib ion which extend down the river valleys from the d inland, Afromontane forest and grassland vegeta- n which extend from the mountainous areas to sea- el, and elements of the Cape fynbos which enter the stern Cape from the south-western Cape (Lubke et [1986]). The consequent structural and floristic ersity encountered in the eastern Cape vegetation re discussed by numerous authors, including Gibbs ssell & Robinson [1981] and Olivier [1981]. As a ult, subsequent research workers have attempted refine Acocks's veld type concept, as applied in eastern Cape.

Lubke et al. [1986] took a step in this direction d produced a revised vegetation map of the eastern pe in which they reclassified the vegetation types a biome-type hierarchy. They recognized the lowing eight major vegetation classes in the eastern pe: Cape Fynbos Shrublands, Cape Transitional rublands, Subtropical Thicket, Karoo (subdesert), acia Savanna, Afromontane Forest, Grasslands and toral Strand Vegetation. To a greater or lesser gree succulents occur in all these vegetation classes. wever, especially the Subtropical Thicket is rich succulent plant taxa in that the arid and semi- d river valleys have provided suitable habitats for ny taxa of karroid affinity (Cowling [1983a, b]; ffman [1989]). Four types of Subtropical Thicket recognized in the eastern Cape. These include ocks's [1988] veld type 23 (Valley Bushveld), veld e 24 (Noorsveld) and veld type 25 (Succulent untain Scrub or Spekboomveld). Together these ee veld types once covered approximately 30% of eastern Cape (Hoffman & Everard [1987]). Valley shveld currently covers only about 15% of this gion (Everard [1987]). Along the dunes and at v altitudes along the coastal strip a fourth non-succulent Subtropical Thicket type can be distinguished, namely Dune Thicket (Lubke et al. [1986]). In general thicket is an impenetrable vegetation type with a closed canopy consisting mostly of shade-intolerant species (Cowling & Pierce [1985]; Lubke et al. [1986]). The three Subtropical Thicket types which host large numbers of succulent plant species are briefly enumerated below.

Valley Bushveld

In the eastern Cape Valley Bushveld (sensu Acocks [1988]) is one of the most widespread vegetation types. In general, succulents and thorny plants (for example *Azima tetracantha* Lam., Salvadoraceae) are of great importance in this veld type. The vegetation type is a dense thicket confined mainly to the valleys of rivers which flow east and drain into the Indian Ocean. These valleys are relatively hot and dry in comparison to the intervening ridges. Acocks [1988] regarded this veld type as having had a Karoo–Karroid origin and subdivided it as follows:

(a) Valley Bushveld proper, northern variation, extending as far south as the Great Kei Valley;
(b) Valley Bushveld proper, southern variation, from the Great Kei to the Kabeljauw's Valley;
(c) The Fish River Scrub, in the Lower Great Fish River Valley;
(d) (i) The Addo Bush, and
 (ii) The Sundays River Scrub, in the wide, flat Lower Sunday's River Valley;
(e) The Gouritz River Scrub.

Valley Bushveld sensu Acocks [1988] is therefore not restricted to the eastern Cape, but enters this region from Natal in the east and extends westwards into the southern Cape. The Addo Elephant National Park with an area of 8 879 ha is situated in this veld type. This park was established on 17 June 1931 and hosts a remnant population of the African elephant *Loxodonta africana* (Greyling & Huntley [1984]).

For the purpose of describing the major vegetation categories in and adjacent to the Fynbos biome, which closely approximates the geographic area of the Cape Floristic Kingdom (Takhtajan [1969]; Goldblatt [1978]), Moll et al. [1984] accepted Acocks's [1988] definition and subdivisions of Valley Bushveld. In contrast to Acocks [1988], who postulated that Valley Bushveld had a karroid origin, Rutherford & Westfall [1986] suggested that Valley Bushveld lies within the savanna biome. More recently it has been proposed that it represents a transitional vegetation type linking Subtropical and Afromontane forest to fynbos, karoo and grassland vegetation (Cowling [1984]; Everard [1987]). Although the use of the descriptive term Valley Bushveld for the eastern Cape thickets can now be safely regarded as inappropriate and confusing, this name has become deeply entrenched in popular parlance and will not be discarded in the near future.

Noorsveld

Although Acocks [1988] included Noorsveld in his Karoo/karroid veld types, it is more recently regarded as a type of subtropical thicket (Lubke et al. [1986]).

Noorsveld is centred on Jansenville, the main body of this veld type being situated in a low lying, hot, dry basin in what is essentially a rain shadow valley (middle part of the Sunday's River Valley). The vegetation is a scrub of more or less uniform height (1–2 m) with *Euphorbia coerulescens* Haw. (English: sweet noors; Afrikaans: soetnoors) being dominant amongst scattered small trees (Roux [1953]).

The specific epithet of this *Euphorbia* species whence the name of the veld type is derived alludes to the peculiar blue-green colour of its constricted branches (De Graaf [1983]). The vernacular name "noorsdoring" is applied to a number of succulent, spiny species of *Euphorbia.* The suffix "noors" is added to the common names of a number of other *Euphorbia* species, such as suurnoors (English: sour noors) for *E. ledienii* Berger and gifnoors (English: poison noors) for *E. virosa* Willd. The word "noors" (modern Afrikaans: nors) refers to the surly appearance of these spiny shrubs. Like many other species of *Euphorbia, E. coerulescens* contains a corrosive latex and even honey produced from the nectar of noors flowers contains an irritant compound (Smith [1966]).

Sweet noors has long been recognized as a valuable stockfeed. Branches of plants are chopped with a long knife into small pieces (about 7 cm long) and these are left to dry in the sun for two to five days before it is utilised by stock. Domestic live stock which pick up sweet noors cuttings includes Persian and Merino sheep, boer and Angora goats and cattle. Because farm live stock will eat chopped sweet noors, there has been overutilization of large areas of this veld type.

Succulent Mountain Scrub or Spekboomveld

Spekboomveld is typically a dense scrub dominated by *Portulacaria afra.* The Afrikaans vernacular name of *P. afra* is "spekboom", a direct translation of which would be "pork tree" or "bacon tree". This name alludes to the succulent nature of the stems and leaves of this species. Spekboomveld usually lacks the general thorniness of, for example, Valley Bushveld, with which it merges towards its eastern distribution between Cradock and Cookhouse. In the Graaff-Reinet area it merges upwards into Karroid Broken Veld and in the Jansenville region it merges downwards into Noorsveld (Acocks [1979, 1988]). In dense Spekboomveld karroid shrubs are absent and the bush and tree cover form a more or less closed canopy from one to four metres above ground level (Archibald [1954]; Penzhorn & Olivier [1974]).

P. afra is an important fodder plant and is extensively utilized by game and stock. Consequently, Spekboomveld has suffered from overbrowsing over large tracts. Fortunately pockets of Spekboomveld are conserved in the Zuurberg National Park (Van Wyk [1988a, b]).

Endemism in the flora of the eastern Cape Province

Species diversity in the eastern Cape compares well with that of, for example, Natal (Gibbs Russell & Robinson [1981]; Ross [1972]). However, for an area which hosts such a diverse flora, the easte Cape has relatively few endemic taxa. Accordi to Gibbs Russell & Robinson [1981] this indicat that the floristic diversity in the eastern Cape is d to species from different phytochoria (Afromontai Cape, Tongaland–Pondoland and Karoo–Nami meeting at the ends of their ranges and not a result local speciation. They further postulate that this l incidence of endemism in the eastern Cape is du firstly, to selection pressures, particularly clima instability, having acted to produce a flora in whi "generalist" genotypes predominate and, secondly, the close proximity of divergent phytochoria whi ensures that a variety of species are already availal to fill, by migration, any niche which may becor available. Endemism is, however, not uniformly l throughout this region. Cowling [1983b] recogni two centres of endemicity in this region, one Cape taxa, the other for succulents of karroid a subtropical affinity. For the latter he recognises t Kaffrarian Transition Zone.

Everard [1987] classified the subtropical tran tional thickets of the eastern Cape into syntax nomic units which comply with those of Cowli [1984]. Within this class of vegetation he recognis two orders, one of them being Kaffrarian Succule Thicket which corresponds to the Kaffrarian Succ lent Thicket of Cowling [1984]. Within the vario thicket types endemism is determined largely by t contribution of karroid elements. The Kaffrarian Su culent Thicket has the largest karroid component an within it, the Mesic Succulent Thicket formation h the highest percentage of endemism (9,2%) (Evera [1987]). Xeric Succulent Thicket is also rich in karro elements and is relatively rich in endemics (7,3 (Cowling [1983b]; Everard [1987]).

Figure 3. *Pachypodium succulentum* (L.f.) Sweet growing the Grahamstown district, eastern Cape.

To assess the validity of the statement of Cowling [1983b] and Everard [1987] regarding succulent plant endemism in the eastern Cape, the distributions of approximately 1 700 species belonging to geophytic and succulent plant genera were analysed. Several revisions of geophytic and succulent plant taxa have appeared since the publication of Cowling's [1982, 1983b] analysis of endemism in the eastern Cape. For comparative purposes some succulent plant genera which are absent from the eastern Cape or which do not have endemics in this region [for example *Pachypodium* Lindl. (Fig. 3)] have also been incorporated into this study (Table 1). Southern Africa is here defined as the area south of Angola, Zambia, Zimbabwe and Mocambique. The dicotyledonous families included in this survey are arranged according to the classsification system of Cronquist [1981], while the monocotyledonous families are arranged after Dahlgren et al. [1985]. Within the families the genera are given alphabetically.

Succulent plant families are well represented in the eastern Cape and with the exception of a few minor families, such as the Moringaceae, most of the families mentioned by Van Jaarsveld [1987] occur in this region. The large succulent plant families (in terms of numbers of species included) which have a high percentage of endemism in the eastern Cape are the Asclepiadaceae (Fig. 4) (*Brachystelma*, *Stapelia*, *Tridentea*), Crassulaceae (*Adromischus*, *Cotyledon*), Euphorbiaceae (Figs 5–8) (*Euphorbia*), Mesembryanthemaceae (various genera) and Asphodelaceae (Figs 9–11), (*Gasteria*, *Haworthia*). With the exception of *Cyrtanthus* and, to a lesser extent *Crinum*, the eastern Cape does not represent a centre of endemisim for the geophytic genera included in this survey. The results of this examination of patterns of endemism in the eastern Cape confirm Cowling's [1982, 1983b] earlier reports that the semi-arid river valleys and inland basins of the eastern Cape represents an important centre of endemism for succulent plants. Evolution usually takes place at a faster rate in arid climates (Stebbins [1952]; Axelrod [1972]; Speirs [1980]), the local terrain diversity and relatively dry climate of the eastern Cape therefore providing the scenario for present-day speciation in numerous succulent plant taxa.

The discrepancies in the literature with regard to the number of succulent plant taxa indigenous or endemic to the eastern Cape (Holland [1978]; Gibbs Russell & Robinson [1981]; Cowling [1982,1983b]; Everard [1985]), can be explained mainly by two factors, the most obvious being the different delimitation of the eastern Cape by the different authors. The second and most important reason is that for many taxa, such as some genera of the Mesembryanthemaceae, no satisfactory taxonomic treatment exists. Many succulent plant genera are taxonomically difficult, for example *Bulbine* Wolf. This problem is also illustrated by the percentage taxa endemic to the eastern Cape and percentage of taxa indigenous to the eastern Cape obtained for *Haworthia* and *Astroloba*, respectively, if recent revisions which differ markedly are analysed (Table 1).

Figure 4. *Huernia brevirostris* N.E. Br. growing in the vicinity of Riebeek-Oos, eastern Cape.

Figure 10. *Aloe microcantha* Haw. photographed at Humansdorp where it grows in grassy Fynbos.

Table 1. Patterns of endemism of a selection of geophytic and succulent plant genera in the eastern Cape Province. Centres of diversity given for the large genera (10 taxa or more) are after Gibbs Russell [1987]. Figures which appear in brackets in columns three and five refer to southern African representatives of the genera.

Taxon (Family Genus)	Centre of diversity	Number of species in: genus	Number of species in: eastern Cape	% of total in genus in eastern Cape	No. of species endemic to eastern Cape	% endemism in eastern Cape	Data source
Cactaceae							
Rhipsalis Gaertn.	New World	50 (1)	1	2,0 (100)	0	0	Obermeyer [1976]
Moringaceae							
Moringa Adans.	Savanna	12 (1)	0	0	0	0	Leistner [1970]
Crassulaceae							
Adromischus Lem.	Fynbos	27 (27)	6	22,2 (22,2)	5	83,3	Tölken [1985]
Crassula L.	Fynbos	ca.300 (149)	61	20,3 (40,9)	7	11,5	Tölken [1985]
Cotyledon L.	Savanna & Fynbos	11 (9)	7	63,6 (77,8)	2	28,6	Tölken [1985]
Kalanchoe Adans.	Savanna	ca.200 (13)	3	1,5 (23,1)	0	0	Tölken [1985]
Tylecodon Toelken	Succulent Karoo	27 (27)	1	3,7 (3,7)	0	0	Tölken [1985]
Euphorbiaceae							
Euphorbia L.	Savanna	ca.2000 (280)	75	3,8 (26,8)	33	44,0	White *et al.* [1941]
Geraniaceae							
Pelargonium L'Herit.	Fynbos	232 (200)	45	19,4 (22,5)	3	6,7	Van der Walt [1977]; Van der Walt & Vorster [1981,1988]
Sarcocaulon Sweet	Succulent Karoo & Nama–Karoo	14 (14)	2	14,3 (14,3)	1	50	Moffett [1979]
Apocynaceae							
Adenium R. & S.	Savanna	ca.14 (4)	0	0	0	0	Codd [1963] but see Rowley [1983]
Pachypodium Lindl.	Savanna	ca.14 (5)	2	14,3 (40)	0	0	Codd [1963]; Vorster & Vorster [1973]
Asclepiadaceae							
Brachystelma R.Br.	Savanna & Grassland	ca.100 (69)	17	17,0 (24,6)	14	82,4	Dyer [1980,1983]
Ceropegia L.	Savanna	ca.160 (51)	17	10,6 (33,3)	2	11,8	Dyer [1980,1983]
Huernia R.Br.	Savanna	64 (38)	12	18,8 (31,6)	3	25	Leach [1988]
Orbea Haw.	Fynbos & Savanna	20 (18)	5	25,0 (27,8)	1	20,0	Leach [1978]
Orbeopsis Leach	Savanna	2 (2)	0	0	0	0	Leach [1978]
Pachycymbium Leach	Savanna	3 (2)	0	0	0	0	Leach [1978]
Riocreuxia Decne.	Savanna & Grassland	10 (8)	4	40,0 (50,0)	0	0	Dyer [1980,1983]
Stapelia L.	No apparent centre of diversity	43 (42)	8	18,6 (19,0)	4	50,0	Leach [1985]
Tridentea Haw.	Succulent–Karoo & Nama–Karoo	17 (17)	3	17,6 (17,6)	2	66,7	Leach [1980]
Lamiaceae							
Plectranthus L'Herit.	Savanna & Grassland	ca.350 (42)	15	4,3 (35,7)	0	0	Codd [1985]
Asphodelaceae							
Aloe L.	No apparent centre of diversity	333 (148)	28	8,4 (18,9)	4	14,3	Reynolds [1966,1982]
Astroloba Uitew. (1)	Fynbos & Succulent Karoo	7 (7)	1	14,3 (14,3)	0	0	Roberts Reinecke [1965]
Astroloba Uitew. (2)	Fynbos & Succulent Karoo	4 (4)	1	25,0 (25,0)	0	0	Groen [1987]
Gasteria Duv.	Fynbos	14 (14)	6	42,9 (42,9)	5	83,3	E.J. van Jaarsveld [pers. com.]
Haworthia Duv. (1)	Fynbos	68 (68)	24	35,3 (35,3)	15	62,5	Bayer [1982]
Haworthia Duv. (2)	Fynbos	88 (88)	32	36,4 (36,4)	26	81,2	Scott [1985]
Hyacinthaceae							
Ornithogalum L.	Fynbos	ca.200 (54)	12	6,0 (22,2)	0	0	Obermeyer [1978]
Amaryllidaceae							
Crinum L.	Savanna	ca.130 (21)	3	2,3 (14,3)	2	66,7	Verdoorn [1973]
Cyrtanthus L.f.	Grassland	ca.60 (50)	25	41,7 (50,0)	12	48,0	Reid & Dyer [1984]
Haemanthus L.	Fynbos & Succulent Karoo	21 (21)	6	28,6 (28,6)	0	0	Snijman [1984]
Iridaceae							
Moraea Mill.	Fynbos	119 (101)	14	11,8 (13,9)	0	0	Goldblatt [1986]
Syringodea Hook.f.	Fynbos & Nama–Karoo	8 (8)	4	50,0 (50,0)	2	50,0	De Vos [1983]
Watsonia Mill.	Fynbos	52 (52)	6	11,5 (11,5)	0	0	Goldblatt [1989]
Commelinaceae							
Commelina L.	Savanna & Grassland	170 (16)	6	3,5 (37,5)	0	0	Obermeyer & Faden [1985]

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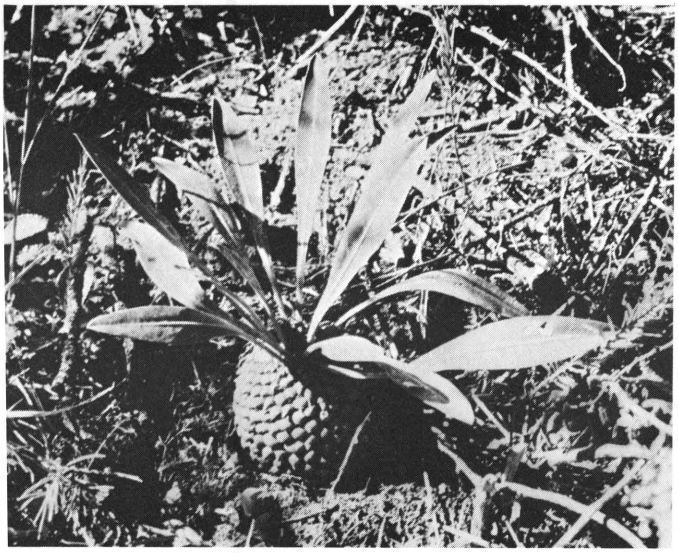


'igure 5. *Euphorbia bupleurifolia* Jacq. growing in Grahams-
own.

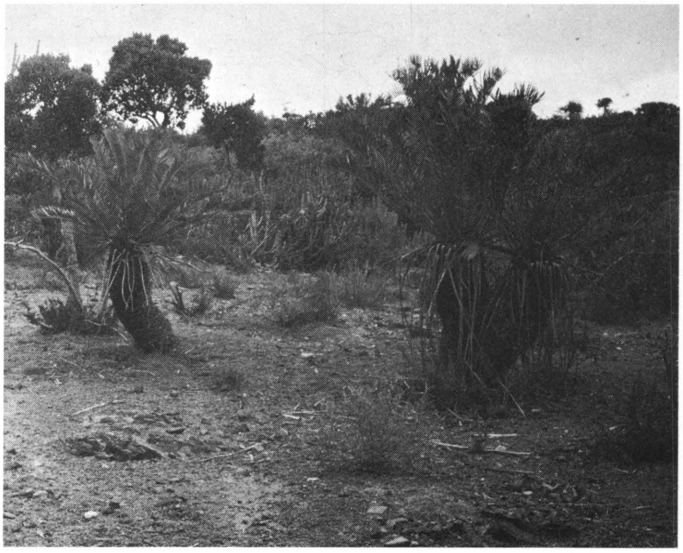
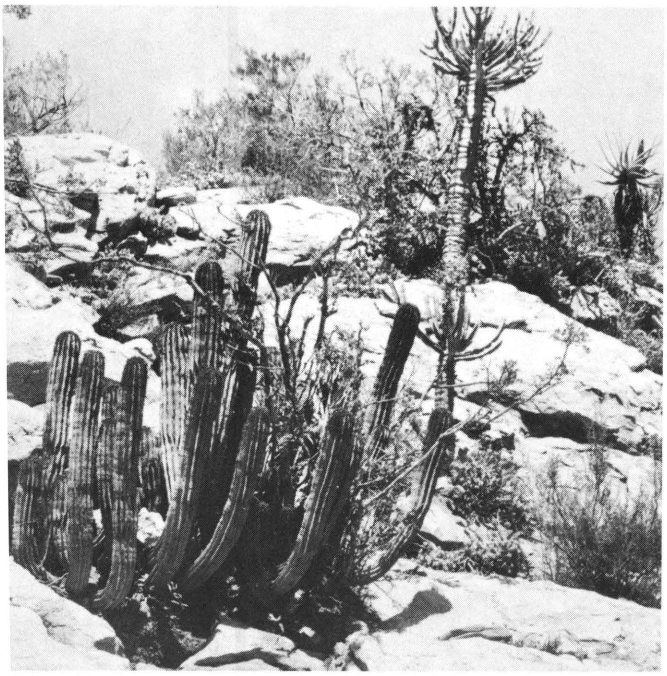


Figure 6. *Encephalartos lehmanii* Lehm. growing in the Steytlerville district in Noorsveld (*Euphorbia coerulescens* **Haw.** dominant).



gure 7. *Euphorbia polygona* Haw. (foreground) and *E. tetra-*
na Haw. growing in Helspoort.

Figure 8. A female specimen of *Euphorbia meloformis* Ait. photographed at Coega, Port Elizabeth.

ure 9. A specimen of *Gasteria maculata* (Thunb.) Haw.
ich grows in Valley Bushveld near Coega.

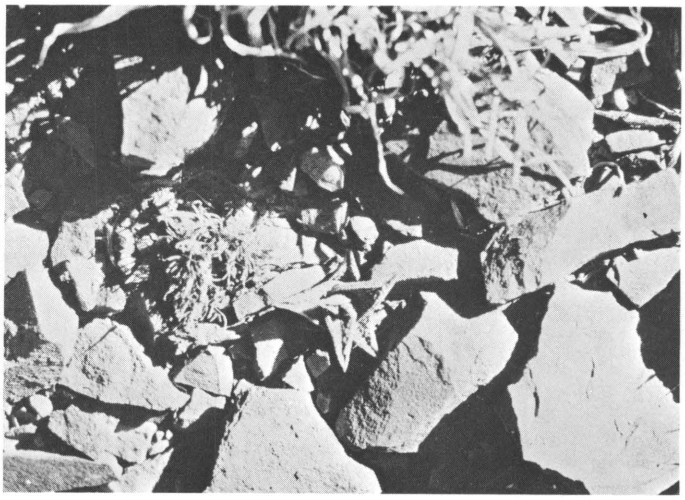


Figure 11. A comparatively stemless form of *Haworthia nigra* (Haw.) Bak. growing in dark brown shale near Fort Brown, Grahamstown.

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It is therefore obvious that much remains to be learned about taxon delimitation in many succulent groups. In many cases we cannot possibly deduce whether taxonomic confusion in some groups is due to evolution in progress, hybridisation and introgression or a combination of these processess (cf. Leach [1986/1987] on *Huernia*). Our understanding of species distribution in the southern Africa flora and the biomes of this region is, in many cases, still very poor. Consequently, information of endemic and endangered plant species, historical relationships amongst vegetation units, selective pressures which govern species distribution and vegetation dynamics in the eastern Cape is fragmentary and incomplete. Despite an increasing interest in the thicket vegetation of the eastern Cape (Bruton & Gess [1988]; Lubke et al. [1988a]), much more taxonomic and vegetation information is needed for the area.

A preliminary bibliography of botanical research in the eastern Cape

For many years floristic, phytosociological, biogeographical, phenological and conservation biological studies in the eastern Cape were few and far between. This general research neglect also exists in the fields of vegetation dynamics and systematics (cf. Cowling [1983b] and Hoffman & Everard [1987]). However, since the late 1970's there has been a surge in the interest in the vegetation of this region. Although a detailed discussion of the respective research topics and their results would fall outside the limited scope of the present article, some of the studies which should be consulted by interested research workers are given below. Additional relevant literature are included in the lists of cited references of these papers. More complete bibliographies of vegetation research in the eastern Cape are generally given in theses and dissertations which were carried out in this region. However, these works are usually unpublished and not readily available. The following bibliography was drawn from diverse sources and includes contributions mainly on research done on terrestrial ecosystems and taxa. These are, alphabetically: Baird et al. [1988]; Batten & Bokelmann [1966]; Bond & Goldblatt [1984]; Bruton & Gess [1988]; Comins [1962]; Court [1988]; Cowling [1982, 1983a, b, 1984, 1986]; Cowling & Campbell [1983, 1984]; Cowling et al. [1986]; Cowling & Pierce [1985]; Cowling & Roux [1987]; Deacon [1983]; Drège [1913]; Dyer [1937]; Ecklon [1830]; Everard [1985, 1987, 1988]; Fourcade [1940]; Gibbs Russell & Robinson [1981]; Gledhill [1981]; Hall & Veldhuis [1985]; Hoffman [1989]; Hoffman & Everard [1987]; Jacot Guillarmod [1985, 1988]; Jessop & Jacot Guillarmod [1969]; Lubke [1983]; Lubke & Avis [1986]; Lubke et al. [1986; 1988a, b]; Lubke & Van Wijk [1988]; Midgley [1990]; Moll et al. [1984]; Moriarty [1982]; Novellie [1988]; Olivier [1977, 1981, 1983, 1986]; Palmer [1982, 1989a, b]; Palmer et al. [1988]; Phillipson [1987]; Pierce & Cowling [1984a, b]; Raven [1983]; Schonland [1919, 1927]; Story [1952]; Taylor & Morris [1981]; Urton [1949]; Van Wyk et al. [1988a, b].

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7.2.2 SMITH, G.F. & VAN WYK, A.E. 1990. Notes on the distribution and habitat of *Aloe bowiea* (Liliaceae/Asphodelaceae: Alooideae), an endangered and little known species from the eastern Cape. In: Miscellaneous note. *Bothalia* 20: 123-125. 243

Bothalia 20,1: 123–125 (1990)

Miscellaneous note

VARIOUS AUTHORS

NOTES ON THE DISTRIBUTION AND HABITAT OF *ALOE BOWIEA* (LILIACEAE/ASPHODELACEAE: ALOOIDEAE), AN ENDANGERED AND LITTLE KNOWN SPECIES FROM THE EASTERN CAPE

A. bowiea is an extremely rare species only known from a limited area in the eastern Cape. Under conditions of normal rainfall it is a dwarf rosulate leaf succulent (sensu Newton 1974), reaching a height of 300 mm at the flowering stage.

Morphologically and taxonomically *A. bowiea* is insufficiently known. A study on these aspects is in progress and will be reported elsewhere.

HABITAT

Geographical situation

Aloe bowiea is known only from the three study sites discussed below (Figure 1). Locality 1 is located south of Uitenhage, between Uitenhage and Despatch, on the farm 'Jachtvlakte'. Locality 2 is situated at Coega, approximately 25 km east of Uitenhage, on 'Maasward', a private nature reserve bordering the Uitenhage–Sundays River mouth road. Locality 3 is on the farm 'Brakkefontein', 20 km from the Kirkwood turn-off on the Uitenhage–Jansenville road. These localities will subsequently be referred to as Uitenhage, Coega and Kariega, respectively. Although the population of *A. bowiea* at Uitenhage, still thriving in 1983, is now considered extinct, this locality will be included in this paper. Hitherto this species was only known from the latter locality.

Climate

The climate at the three study sites is warm temperate and conforms to the semi-arid valley climate recognized by Cowling (1983a) for the river valleys of the south-eastern Cape.

At Uitenhage the average annual rainfall is 435 mm with monthly maxima in April, August and November and minima in the summer and winter months. Temperatures are moderate with all months being between 13° and 23°C. Coega and Kariega (Figure 2: Hermitage and Hillside Farm respectively) experience a warmer and more arid

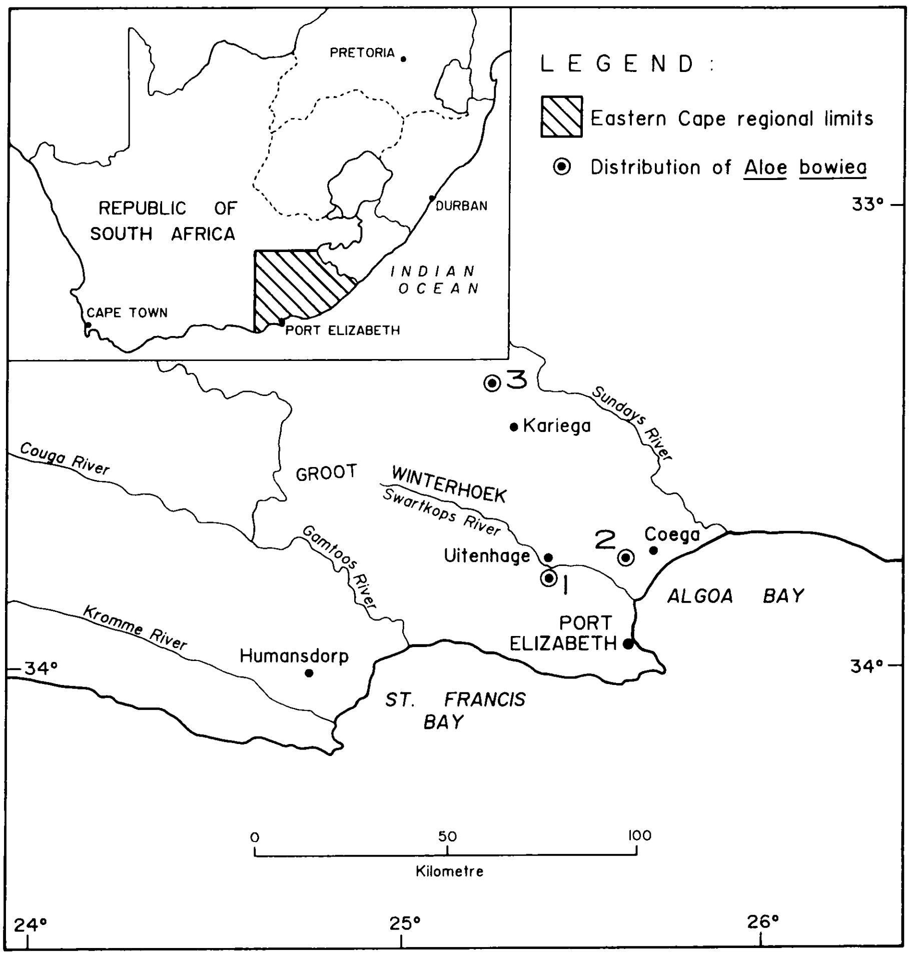

FIGURE 1.—Map showing the regional limits of the eastern Cape (after Lubke *et al.* 1986) and the three known localities of *Aloe bowiea*. In recent years the species has become extinct at locality 1.

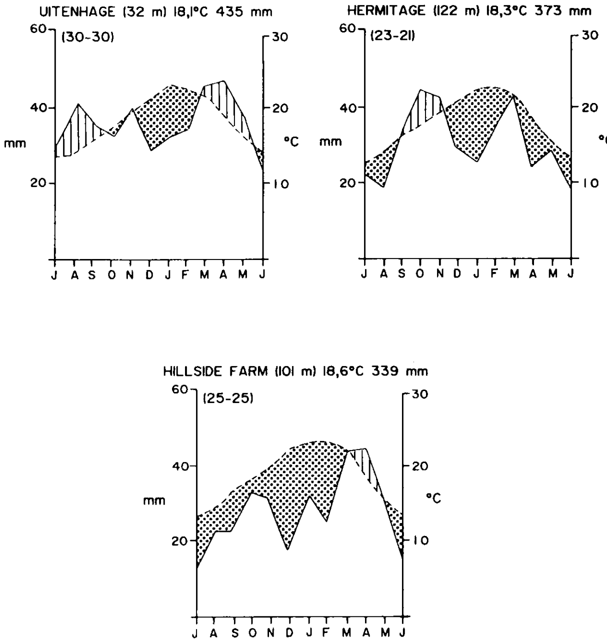

FIGURE 2.—Walter-Lieth climate diagrams of selected stations. Data from Weather Bureau (1984).

climate. Rainfall is generally erratic with an average annual figure of 373 mm at Hermitage and 339 mm at Hillside Farm. Both sites have a bimodal distribution of rain, with peaks in autumn and late spring. At these sites the mean monthly temperatures show a slightly greater range (13–24°C) with maximum temperatures exceeding 40°C and minima dropping below 0°C.

Vegetation

Field observations at all the localities have shown that *Aloe bowiea* is restricted to the Sundays River Scrub variation of Valley Bushveld [Veld Type 23 sensu Acocks 1988)] of the Uitenhage, Coega and Kariega regions in the south-eastern Cape. Acocks (1988) did not specifically mention the vegetation surrounding Uitenhage, Coega and Kariega, but at all localities it would, on the ground of shared *Euphorbia* species, fit into his Sundays River Scrub variation. On the map which accompanied Acocks (1988) the vegetation of this area is given as Valley Bushveld. Other authors have referred as follows to the vegetation with which *A. bowiea* is associated: Thicket (Jessop & Jacot Guillarmod 1969), Addo Bush (Penzhorn & Olivier 1974), Valley Bushveld (sensu Olivier 1977, 1981; Moll *et al.* 1984), Subtropical Transitional Thicket (Cowling 1984; Everard 1987), Subtropical Transitional Thicket, including Valley Bushveld (sensu Lubke *et al.* 1986) and Subtropical Thicket (Van Wyk *et al.* 1988a, 1988b). This vegetation type is confined mainly to the valleys of rivers which flow east and drain into the Indian Ocean, and currently covers approximately 15% of the eastern Cape (Everard 1987). These valleys are relatively hot and dry in comparison to the intervening ridges.

The Valley Bushveld vegetation at both the Uitenhage and Coega localities included in the present study forms a dense and, where undisturbed, almost impenetrable thicket. It agrees with the differentiating characters given by Everard (1987) for Mesic Succulent Thicket in having a mean total cover of about 90%, an average canopy height of about 2,5 m and a large proportion of succulents (more than 20%). At the Kariega locality the vegetation is less dense (average total cover of approximately 60%) with a slightly lower shrub canopy (2,0–2,5 m) and succulents comprise about 30% of the species. This locality falls within the Xeric Succulent Thicket suborder. Succulents associated with *A. bowiea* include, at Uitenhage: *Aloe africana* Mill., *A. striata* Haw., *Bulbine caulescens* L., *B. latifolia* Roem. & Schult., *Euphorbia stellata* Willd., *E. meloformis* Ait., *E. globosa* (Haw.) Sims and *Pachypodium succulentum* (L. f.) A. DC.; at Coega: *Aloe ferox* Mill., *Gasteria maculata* (Thunb.) Haw., *Haworthia xiphiophylla* Bak., *Euphorbia meloformis, E. clava* Jacq., *E. ledienii* Berger and *Pachypodium succulentum* and at Kariega: *Bulbine latifolia, Haworthia sordida* Haw. (M.B. Bayer pers. comm.), and *Haworthia* sp. cf. *cooperi* Bak. At all three localities species of *Cotyledon* L., *Crassula* L. and the Mesembryanthemaceae occur in large numbers.

Although the vegetation at the three localities where *Aloe bowiea* is known to occur can be broadly classified as thicket, plants of this species have never been encountered in the shade of surrounding vegetation. It seems to be restricted to ecological niches where the valley bush opens up naturally to form a less dense karroid/grass community. These breaks in the canopy layer do not appear to be man-induced (at least in recent times) since they also occur in nature reserves which lie within valley bush, such as Springs Reserve at Uitenhage and Maasward Private Nature Reserve at Coega. As a result of litter decomposition the soils on which thicket occurs usually contain high levels of organic matter. *Aloe bowiea* was not recorded from these humic soils.

ENDEMISM

Everard (1985) lists only three species of *Aloe* as being endemic to the eastern Cape, namely, *A. africana, A. tidmarshii* and *A. bowiea*. On the other hand Cowling (1982, 1983b) states that five of the 25 species of *Aloe* indigenous to the eastern Cape are endemic to this region. For *A. bowiea* Cowling (1982, 1983b) prefers to uphold the name *Chamaealoe africana*. The discrepancies in the literature with regard to the number of *Aloe* taxa indigenous or endemic to the eastern Cape (Cowling 1982, 1983b; Everard 1985; Gibbs Russell & Robinson 1981; Holland 1978) can be explained by the different delimitation of the eastern Cape by the different authors.

CONSERVATION

According to Everard (1985) the eastern Cape currently has 662 threatened taxa. Of these, 485 are listed in the category **uncertain whether safe or not**. This conservation status category is defined as one for plants that are so little known that there is an even chance that they could prove to be safe. Everard (1985) listed *Aloe bowiea* in this category. Field observations during recent years have, however, revealed only three localities for this species. Moreover, the population of *A. bowiea* at Uitenhage is now extinct and at both Coega and Kariega the populations are vulnerable and declining. With the exception of the Coega locality, where *A. bowiea* occurs in a privately owned nature reserve, none of the known populations are conserved. This species takes readily to cultivation, but it is horticulturally unattractive and poorly represented in succulent plant collections. The distribution of known populations of *A. bowiea* is shrinking fast. For example, whereas in 1983 the population at Uitenhage comprised 141 individuals, no plants could be found at this locality in 1988.

CONCLUSION

Recent field observations have shown that *Aloe bowiea* has a very limited geographical distribution and that it is now extinct at Uitenhage, the only previously known locality. At the other two localities, Coega and Kariega, the populations of *A. bowiea* are endangered and should be added as such to the list published by Everard (1988).

It is recommended that populations be securely fenced to prevent game animals and domestic stock from grazing individuals of this species. This would allow plants to flower and set seed and could ultimately lead to the expansion of existing populations and the establishment of new ones. Unless immediate action in the form of land acquisition and the education of land owners are taken, this unique and localized species of the karroid vegetation of Valley Bushveld may soon be extinct in nature.

ACKNOWLEDGEMENTS

Discussions with Prof. G.J. Bredenkamp contributed substantially to the formulation of a conceptual basis for this paper. Many of the observations reported here were made while the first author was an undergraduate student at the University of Port Elizabeth and he therefore makes acknowledgement to this institution.

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THE DESTRUCTION OF THE NATURAL HABITAT OF ALOE BOWIEA (ASPHODELACEAE: ALOOIDEAE)

by Gideon F.Smith

Abstract

Aloe bowiea, previously known as *Chamaealoe africana*, is one of the smallest species currently recognized in the genus *Aloe*. It appears to have specific habitat requirements and is known at only two localities in the eastern Cape. It has disappeared from a third. It is suggested that *Aloe bowiea* should immediately be added to the list of threatened plants of southern Africa in the "endangered" category.

Introduction

The "Flora of southern Africa" research programme was initiated by the Botanical Research Institute, Pretoria, more than twenty years ago in order to arrive at a taxonomic account of all known indigenous and naturalized plant taxa of the subcontinent south of Angola, Zambia, Zimbabwe and Mocambique (Anonymous 1986). Currently, as part of this programme, the author is carrying out a detailed taxonomic investigation of the genera *Chamaealoe* Berger, *Chortolirion* Berger and *Poellnitzia* Uitewaal. One of the aims of this project is to establish the conservation status and viability of the known populations of *Aloe bowiea* (= *Chamaealoe africana*). Since the author has visited the then known localities of this species five years ago (1983), he is in a good position to evaluate the factors influencing its conservation status and viability and, if need be, to make suggestions as to alternative management practises which will assure its long term survival in habitat. The aim of this paper is to highlight the inadequate conservation status of this species in its natural habitat. An account of recent syntaxonomic and synecological interpretations of the vegetation of the known localities of *A.bowiea* is given and the phylogenetic affinities of this species and possible reasons for its restricted distribution are also briefly discussed.

In a rearrangement of the family Liliaceae Dahlgren *et al.* (1985) reinstated the family Asphodelaceae. Within the latter taxon two subfamilies, namely, Asphodeloideae and Alooideae are recognised.

The Alooideae constitutes a natural assemblage of more or less succulent-leaved taxa which were previously placed in the tribe Aloineae, one of 28 recognised by Hutchinson (1959) in the family Liliaceae (*sensu lato*). According to Rowley (1976) twenty-seven generic names are available for taxa currently classified in the subfamily Alooideae. However, only seven genera enjoy general recognition, namely, *Aloe* L., *Astroloba* Uitewaal, *Chortolirion* Berger, *Gasteria* Duval, *Haworthia* Duval, *Lomatophyllum* Willd. and *Poellnitzia* Uitewaal. Of these *Chortolirion* and *Poellnitzia* warrant monotypic generic status (Bayer 1972; Smith 1985, 1988), but are included under *Haworthia* by Obermeyer (1973) and Dyer (1976).

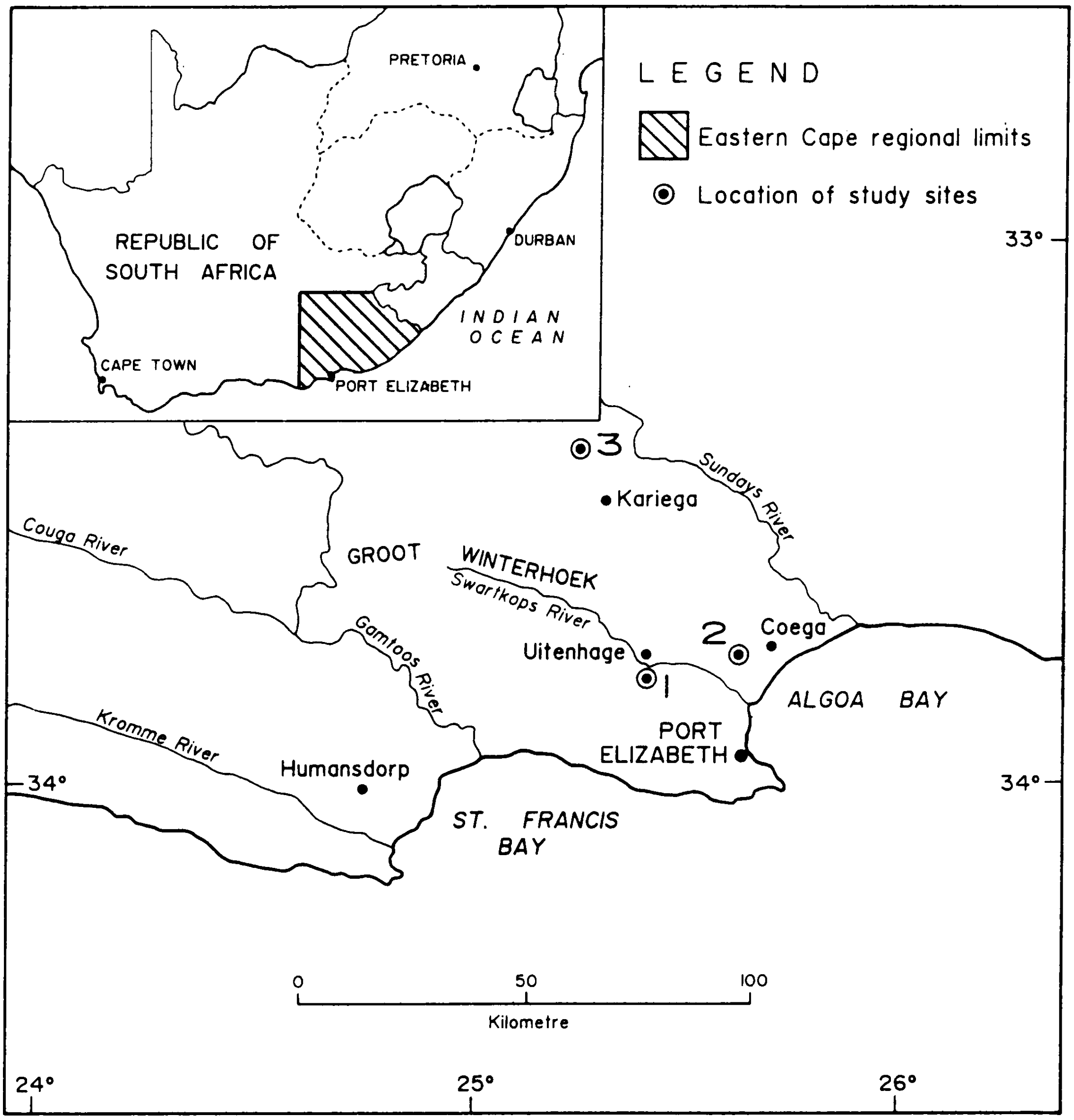
Chamaealoe Berger, one of the genera no longer upheld, was previously recognized as a monotypic entity in the tribe Aloineae (Berger 1905). This taxon has been plagued by taxonomic confusion, originally having been described as a species of *Bowiea* Haworth (1824) non W.H.Harvey ex J.D.Hooker (1867). In accordance with recent proposals by Obermeyer (1973) and Smith (1983) the correct name of the species is *Aloe bowiea* Schult. et J.H.Schult. *A.bowiea* is an acaulescent low-growing rosulate succulent. Its leaves are linear - subulate and have small white spots scattered on the abaxial surfaces. The margins of the pale green leaves are armed with soft, white prickles.

The inflorescence, produced throughout the year, is a laxly-flowered raceme with small greenish-white flowers.

The study area

This species is restricted to three localities in the eastern Cape, the latter region being defined as the area south of 31°S and between 24°E in the west and the Great Kei River and the Transkei boundary in the east (Lubke *et al.* 1986) (Fig.1). The climate of this area is warm temperate and closely approximates the semi-arid valley climate prevalent in the river valleys of the south-eastern Cape (Cowling 1983). Rainfall is generally erratic and low, all the localities having a bimodal distribution of rain with peaks in autumn and late spring. Temperatures are moderate with all months between 13 and 24°C. Maximum temperatures exceed 40°C and, during winter, minima drop below 0°C (Weather Bureau 1984).

Fig. 1 Map showing the regional limits of the eastern Cape (after Lubke et al. 1986) and the locations of the three study sites.



Phytosociology

South African ecologists and botanists in general are fortunate in having a standard guide (Acocks 1975) at their disposal for most vegetation studies. In this reference work Acocks (1975) developed the so-called veld type concept. He defined this unit of vegetation as one "... whose range of variation is small enough to permit the whole of it to have the same farming potentialities." This unit was thus arrived at after considering both the floristic composition and the agronomic potential of a given vegetation type.

Aloe bowiea is restricted to the Sundays River Scrub variation of Valley Bushveld (Veld Type 23 d ii *sensu* Acocks (1975)) of the Uitenhage, Coega and Kariega regions in the south-eastern Cape. This vegetation type is a dense thicket confined mainly to the valleys of rivers which flow east and drain into the Indian Ocean. These valleys are relatively hot and dry in comparison to the intervening ridges. Acocks regarded this veld type as having had a karroid origin. In contrast to this point of view, Rutherford & Westfall (1986) suggested that Valley Bushveld lies within the savanna biome. For the purpose of describing the major vegetation categories in and adjacent to the Fynbos biome, Moll *et al.* (1984) accepted Acock's definition and subdivisions of Valley Bushveld.

The criteria which Acocks (1975) used for distinguishing veld types are, however, often unsound and ill-defined (Cowling 1984; Lubke *et al.* 1986). This is especially the case in the eastern Cape where four major phytochoria (Tongaland-Pondoland forest and thicket; succulent and dwarf shrublands of the Karoo-Namib Region; Afromontane elements and Fynbos taxa of the Cape region) converge to form a complex mosaic of vegetation types. The floristic and structural diversity existing within the eastern Cape was also recognised and discussed by Gibbs Russell & Robinson (1981). As a result subsequent workers have attempted to refine Acocks's veld type concept as applied in the eastern Cape. The interpretations of these authors of the thicket vegetation of this area are discussed below.

Whilst compiling an annotated check list of the Spermatophyta of the Springs Reserve, situated 8 kilometers north of Uitenhage on the Jansenville road, Olivier (1981) recognised the heterogeneity of valley bushveld thicket and distinguished two well-defined communities in this reserve. The first, valley bush *sensu* Olivier (1981), is restricted to low lying areas whereas the second, referred to as the karroid shrub and grass community, occupies the higher elevations outside the valley bush.

To conform more closely to the biome viewpoint, Lubke *et al.* (1986) produced a revised vegetation map for the eastern Cape. Within their Subtropical Thicket class these authors recognised four vegetation types, one of them being Valley Bushveld. The latter equates to Acocks's interpretation of the river valley vegetation dominated by succulents. In contrast Cowling (1984) proposed a hierarchical syntaxonomic classification of the vegetation in the Humansdorp region of the eastern Cape. Within the class Subtropical Transitional Thicket two orders are recognised. The order Kaffrarian Succulent Thicket is structurally characterized as being a Tall (Mid-high) Closed (Mid-dense) Large-leaved and Succulent Shrubland and, with the exception of the northern variation of Valley Bushveld (Veld Type 23 (a) *sensu* Acocks (1975)), includes all the subdivisions of this veld type.

Everard (1987) classified Subtropical Transitional Thicket sensu Cowling (1984) into syntaxonomic and structural units. Within the class Subtropical Transitional Thicket he recognised two orders of vegetation, one of them being Kaffrarian Succulent Thicket. This order of vegetation occurs in dry areas and has a high proportion of succulents. The three localities comprising the present study area fall within the limits of this order. For Kaffrarian Succulent Thicket Everard (1987) recognised two suborders of thicket, namely Mesic Succulent Thicket and Xeric Succulent Thicket. The latter interpretation is in large part supported by Van Wyk *et al.* (1988a, 1988b). The vegetation at both the Uitenhage and Coega localities included in the present study can be classified as Mesic Succulent Thicket (*sensu* Everard 1987). It represents a dense and, where undisturbed, almost impenetrable thicket and more than 20% of the species are succulents. At the Kariega locality the vegetation is less dense and succulents comprise about 30% of the species. This locality falls within the Xeric Succulent Thicket suborder (sensu Everard 1987).

The eastern Cape Subtropical Thickets, which includes Acocks's (1975) Noorsveld, Spekboomveld and Valley Bushveld once covered approximately 30% of the eastern Cape (Hoffman

& Everard 1987). The latter veld type currently covers only about 15% of this region (Everard 1987).

The conservation status of Aloe bowiea - 1983

As recently as 1983 herbarium records showed that *Aloe bowiea* was known from only two accessions from Uitenhage in the south-eastern Cape. The locality data recorded on the herbarium sheets were, however, inadequate and the existence of these populations could not be substantiated. Whilst involved in a preliminary investigation of the taxonomic status of this taxon, intensive field work was carried out to ascertain whether this species was as rare as was generally considered or whether its apparent restricted distribution could be attributed to inadequate collecting. The field work was duly rewarded when a viable population of *A.bowiea* was discovered in the Uitenhage-Despatch area (Fig.1*). This population consisted of four groups of plants, numbering, respectively, 30, 32, 39 and 40 individuals. These groups were dispersed in an area of approximately 75 m^2. A thorough investigation of the surrounding area for more individuals of *A.bowiea* proved fruitless.

Dr.W.R.Branch of the Port Elizabeth Museum reported another population of this plant species from Coega, approximately 30 km east of Uitenhage. Shortly afterwards the author visited this locality in the company of Dr.Branch and Dr.Ria Olivier, then taxonomist in the Department of Botany, University of Port Elizabeth. At this locality, too, a small but viable population of *A.bowiea* was come across. Approximately 250 individuals of this species were scattered amongst other succulent species including *Euphorbia ledienii* Berger, *E.meloformis* Ait., *Gasteria maculata* (Thunb.) Haw., *Haworthia xiphiophylla* Bak. and numerous representatives of the Crassulaceae and Mesembryanthemaceae. This locality is on a private game reserve around which a game fence has been erected. The field trips to the Uitenhage and Coega sites were undertaken during January and February 1983, one of the driest periods in recorded history in the south-eastern Cape. Consequently, the vegetation at these localities were severely overgrazed and badly trampled by domestic stock and game. *A.bowiea* did not escape the foragers and at both Uitenhage and Coega individuals of this species were grazed off at soil level.

This apparently did not pose a threat to the survival of any of the existing colonies since the swollen leaf bases of the plants together with their contractile roots no doubt enabled them to survive through periods of drought and the accompanying overgrazing by small animals. However, indiscriminate foraging would definitely hamper the development of inflorescences and thus subsequent seedset. Under these circumstances the expansion of existing colonies and the establishment of new ones are out of the question. Both Bond & Goldblatt (1984) and Jeppe (1977) list the peak flowering time of *Aloe bowiea* as March to October. In habitat I have, however, encountered flowering specimens of this species throughout the year. Although this ability to flower at any time of year affords it a survival benefit, it might not be sufficient to contribute to the long term *in situ* survival of small populations during extensive droughts.

The conservation status of Aloe bowiea - 1988

During January 1988 the author, in the company of Prof. George Bredenkamp, a colleague from the Department of Plant Sciences, Potchefstroom University for Christian Higher Education, revisited the Uitenhage and Coega localities as well as a third newly discovered locality of *A.bowiea* at Kariega, west of Kirkwood. The existence of the latter locality was brought to our attention by Mr.M.B.Bayer. The results of this field work were alarming. The population which the author discovered at Uitenhage during 1983 is now extinct. The Coega locality is vulnerable because of its small size whilst so few individuals were found at the Kariega locality that it, too, should be considered endangered. The population of *A.bowiea* at Kariega fortunately occurs on the farm of a conservation conscious land owner. At this locality a few hundred individuals of this species were located on a south-west facing slope. The vegetation at this locality can be broadly classified as thicket, but *A.bowiea* seems to be restricted to areas where the valley bush opens up naturally to form a less dense karroid community. These breaks in the canopy layer are not man-induced since they also occur in nature reserves which lie within valley bush, such as Springs Reserve at Uitenhage.

At the Uitenhage locality we spent more than five hours practically on all fours searching for

*For fear of further exploitation of the natural habitat of *Aloe bowiea* exact localities cannot be disclosed. Consequently, all kilometric distances are rounded-off approximations only.

individuals of *A.bowiea*, but to no avail. This area is once again subjected to a severe drought but this time not even the protruding leaf bases of plants grazed off at soil level could be found. At this locality *A.bowiea* has simply been exterminated. Two pairs of trained eyes would not have missed the distinct shape and size of the leaves, leaf bases or inflorescences of this species. Equally alarming was the disappearance of literally hundreds of individuals of all ages of *Euphorbia meloformis* which had been observed there in 1983. This species is said to form part of the diet of donkeys and are considered to be good fattening fodder for goats (Smith 1966; White *et al.* 1941). Watt & Breyer-Brandwijk (1962), although omitting *E.meloformis*, lists the closely related *E.obesa* as being eaten by stock. However, it is more likely that commercial collecting could account for the disappearance of both species.

The taxonomic and phylogenetic affinities of Aloe bowiea

One of the plant species indigenous to southern Africa and in critical need of conservation is *Aloe bowiea*. Although recent commentators are not unanimous with respect to the inclusion of this taxon in *Aloe* (Court 1981; Ginns 1974), sufficient evidence exists which indicates a close enough affinity with other species of *Aloe* to warrant its inclusion in this genus (Dyer 1976; Smith 1983). *Aloe bowiea*, which is endemic to the south-eastern Cape, should best be regarded as a unique entity in *Aloe* and warrants monotypic subsectional status in Reynolds (1950) key to this genus.

It is noteworthy that a striking resemblance exists between *A.bowiea* and a X *Gasterhaworthia* cultivar of unknown parentage obtained from Mr.O.Fritz of Heidelberg, Transvaal. The hybrid is remarkably similar to *A.bowiea* in leaf colouration and shape, floral morphology and the much-exserted stamens. It only differs from *A.bowiea* in the perianth having a reddish tint and in being more robust in all respects. Many species of both *Gasteria* and *Haworthia* occur in the eastern Cape, and, with the exception of *Haworthia limifolia* which has been reported from Mocambique, both genera are endemic to southern Africa (Bayer 1962; Pilbeam 1983). It is, however, extremely unlikely that *A.bowiea* has originated as an intergeneric hybrid (*Gasteria* x *Haworthia*) and has since become established as a selfperpetuating species within *Aloe*. Although purely speculative, the similarities between *A.bowiea* and a X *Gasterhaworthia* cultivar would rather implicate the former as an old taxon within the Alooideae with strong affinities with the progenitor of this natural group. As far as size is concerned, this species meets the requirements set out by Kamstra (1975) for it being an old taxon in the Alooideae. If *A.bowiea* is ancestral to the Alooideae - and there is no proof of this - its restricted distribution would be indicative of palaeoendemism.

In the eastern Cape there is, however, evidence of the occurence of recent hybridization and the presence of neoendemic taxa, for example, the *Euphorbia bothae* complex which occurs in the Grahamstown area (White *et al.* 1941). According to Cowling (1983) this species represents a hybrid complex resulting from crossing and recrossing between *E.coerulescens, E.triangularis* and *E.tetragona* and is a product of a relatively ancient centre of succulent karroid taxa in the eastern Cape. Evolution usually takes place at a faster rate in more arid climates (Axelrod 1972; Speirs 1980; Stebbins 1952). The relatively dry climate and local terrain diversity in the eastern Cape thus provide the scenario for present-day speciation. Along with species of the genera of the Mesembryanthemaceae (*Faucaria* Schwant., *Bergeranthus* Schwant., *Glottiphylum* N.E.Br.), Asphodelaceae (*Bulbine* Willd., *Gasteria* Duv., *Haworthia* Duv.), Crassulaceae (*Crassula* L.) (Van Jaarsveld 1987) and Euphorbiaceae (*Euphorbia* L.) (White *et al.* 1941), *Aloe bowiea* is most likely a neoendemic and a product of recent speciation in the eastern Cape.

The inadequate conservation status of Aloe bowiea

The need to conserve natural habitats in general and those of southern Africa in particular have been stressed many times before. This has resulted in an exhaustive bibliography on areas and taxa worthy of conservation and, no less so, has the need to conserve the unique and precious flora of southern Africa been emphasized (Bayer 1984; Bruton 1988; Cowling & Pierce 1985; Greyling & Huntley 1984; Hall 1978, 1984; Joyce 1986; Lubke *et al.* 1988; Lubke & Van Wijk 1988; Lyons 1972, 1976; Rowley 1973; Teague 1988). However, as illustrated by Simon (1986) extrapolations into the future of rates of species extinction are often on shaky ground. This should by no means deter conservationists from sounding the alarm. Where needed, attention should be drawn to the lack of conservation of regions or taxa, but this should be based on careful and wide ranging analysis.

The taxonomic and phylogenetic affinities of *A.bowiea* are still open to conjecture and yet this species is hovering on the brink of extinction. Even more disturbing is the fact that Valley Bushveld Thicket, the only veld type in which *A.bowiea* occurs, has rapidly deteriorated over the last few decades, 30% having been coverted to wheatlands or wastelands by overgrazing (Everard 1987). Although there are 90 conservation areas in the eastern Cape, covering 3,04% of this region (Everard 1985), only 1,21% of Valley Bushveld currently enjoys some form of conservation (Lubke *et al.* 1986; Olivier 1986). Valley Bushveld is not an homogeneous vegetation type and a wide range of habitats is produced over short distances. Whilst involved in drawing up an annotated systematic check list of the Spermatophyta of the Springs Reserve, Uitenhage, Olivier (1981) recognized this heterogeneity and was able to distinguish two well defined vegetation communities in this area. Although the vegetation at the localities where *A.bowiea* is known to occur can be broadly classified as thicket, this species is restricted to ecological niches where the valley bush opens up naturally to form a less dense karroid/grass community. In the eastern Cape Valley Bushveld *A.bowiea* is not the only species of *Aloe* which occurs in vegetation with a lower, more open physiognomy and a high cover of succulents and grasses. It is, however, specific in that it favours habitats with these characteristics.

The natural habitat of *A.bowiea* is currently subjected to numerous threat factors which might lead to the extinction of this species. These pressures include, amongst others, agronomic mismanagement, for example, the overstocking of veld which can only carry a certain number of stock units. Overgrazing during times of drought can have catastrophic effects on the vegetation. Bad grazing management inevitably leads to deterioration of the structure and vigour of natural veld. This process usually culminates in the desertification and denudation of the land and erosion of the soil. Furthermore, the clearing of non-arable thicket for crop cultivation is not uncommon in the eastern Cape (Cowling 1984). At the Uitenhage locality industrial expansion, urban development, road construction and unauthorized collecting by succulent plant enthusiasts are further factors which have lead to the ultimate extinguishing of the populations of *A.bowiea* known from this area. Although to a lesser extent, these factors are also present at the Coega locality.

Another major threat to the survival of *A.bowiea* in habitat is the uncontrolled encroachment of exotic plant species on localities where this species occurs. Everard (1985) and Jacot Guillarmod (1988) list exotic species which menace eastern Cape vegetation and of these four have been encountered in close proximity to the populations of *A.bowiea* at Uitenhage and Coega, namely *Opuntia ficus-indica* (L.) Mill., *O.aurantiaca* Lindl., *Acacia cyclops* A.Cunn. ex G.Don. and *A.saligna* (Labill.) Wendl. If allowed to spread unchecked these species constitute a major threat, not only to *Aloe bowiea*, but to the whole of the indigenous southern African flora.

The only real solution to the threats currently imposed on *A.bowiea* seems to be the immediate acquisition of land and the education of land owners with respect to the vulnerability of our natural habitats. The conservation of only a single population of *A.bowiea* would not suffice. Nature conservation should have a policy to protect and conserve not only limited and restricted populations of endangered species as in the case of, for example, *Aloe thorncroftii* (Hardy 1984), but should include the whole range of a species. Although specimens of *A.bowiea* are regularly differentiated on reproductive characteristics, it exhibits considerable vegetative variation in habitat. Individuals from the three known localities differ to such an extent that the newly discovered population at Kariega might well warrant formal infraspecific recognition. Such a decision is not taken lightly and pends further investigation. However, *Aloe bowiea* must immediately be added to the list of threatened plants of southern Africa. This species is not included in the recent lists of threatened taxa provided by either Hall *et al.* (1980), Hall & Veldhuis (1985) or Everard (1988). Field investigations have shown that the population at Uitenhage is extinct and that both the Coega and Kariega populations are endangered. The latter conservation status category is used for taxa in immediate danger of extinction if the causal factors continue operating. Included are taxa whose populations are so critically reduced, that a breeding collapse due to a lack of genetic diversity becomes possible, whether or not they are threatened by human activity (Hall *et al.* 1980).

With regard to the occurrence and distribution of

Aloe species in the eastern Cape Province, Urton (1949) stated that "We are indeed fortunate in that so far these members of our rich South African floral heritage are in no apparent danger of extinction, but flourish in spite of droughts and the ruthless hand of man." For *Aloe bowiea* this is no longer the case.

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NOTES ON THE TAXONOMIC AND CONSERVATION STATUS OF *ALOE MICROCANTHA* (ASPHODELACEAE: ALOOIDEAE)

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Abstract

Aloe microcantha is a little known and inconspicuous species of *Aloe* which is classified in the section *Leptoaloe* of this genus. The South African species of *Leptoaloe* are widely distributed in the eastern and south-eastern regions of the subcontinent and is usually encountered in grassland which receives relatively high rainfall. *A. microcantha* occurs in scattered colonies from Uniondale in the west to Grahamstown in the east. It has also been reported from the Port Elizabeth metropolitan area. However, the known localities of this species in the latter region are disappearing rapidly mainly because of urban expansion and public ignorance. Any taxonomic research should take the entire range of variation of a species into account. If the known populations of *A. microcantha* in the Port Elizabeth area are not conserved immediately, they too, like many other succulent species, could become extinct in this region.

Introduction

Reynolds (1950) divided the southern African representatives of the genus *Aloe* into ten sections. In order to facilitate the identification of undetermined specimens of *Aloe,* the sections were, where applicable, divided into subsections and the subsections into series. In cases where some of these infrageneric entities warranted further subdivision (but not formal hierarchical categorization), Reynolds (1950) merely referred to them as "groups". In, for example, Section 3 *Leptoaloe* of *Aloe* four such groups were distinguished mainly on the basis of leave arrangement, degree of leaf succulence and perianth colour. The infrageneric key to the genus *Aloe* which Reynolds (1950) founded was mostly based on macromorphology and growth habit and, according to Holland (1978), provides a fairly accurate reflection of the phylogeny within this natural group currently classified in the family Asphodelaceae (Dahlgren *et al.* 1985).

In the companion volume of the abovementioned monograph (Reynolds 1966), a slightly different format was followed in that the tropical African and Madagascan species of *Aloe* were classified into 20 and nine so-called GROUPS, respectively. Some of these GROUPS are equivalent to formal nomenclatural categories that were recognized within the southern African species of *Aloe* (Reynolds 1950). The delimition of GROUP 6 of tropical African aloes is, for example, equivalent to that of section (4) *Aloe* [*Eualoe sensu* Berger (1908)] subsection (B) *Humiles* series (10) *Saponariae* of the southern African species of *Aloe.* In other cases the tropical African GROUPS of species of *Aloe* form assemblages quite distinct from any of the southern African infrageneric categories, GROUP 4: "Plants with striped perianth" being a good example. Southern Africa is here defined as the region south of, but excluding, Angola, Zambia, Zimbabwe and Mocambique.

An attempt by Jacobsen (1977) to rationalize these two "systems" of *Aloe* classification (Reynolds 1950, 1966) has resulted in closely related taxa being grouped in divergent categories. Carter *et al.* (1984), for example, provided conclusive evidence that both *A. hemmingii* and *A. somaliensis* var. *marmorata* are in fact synonyms of *A. somaliensis.* However, Jacobsen (1977) placed these two species, and the closely related *A. jacksonii* and *A. jucunda,* in four separate subsections (Table 1).

The use of two classification systems for a single genus poses a major identification problem to both layman and professional taxonomist alike since it implies that one should be familiar with the geographic origin of an unknown plant before attempting to name it. Although this information is usually fundamental to the use of a plant identification key, it is often not available, especially in the case of garden plants (Gillet 1967).

One of the infraspecific taxa of *Aloe* which is clearly circumscribed in the case of both southern African and tropical African taxa, is the section *Leptoaloe* Berger. This section consists of both southern African and tropical African representatives (Reynolds 1950, 1966). Since the publication of the latter two monographs a number of new species and infraspecific taxa have been published in this section. These include *A. modesta* Reynolds (1956) (Van der Riet 1977), *A. soutpansbergensis* Verdoorn (1962), *A. fouriei* Hardy & Glen (1987) and *A. cooperi*

TABLE 1. A comparison of the classification systems proposed by Reynolds (1966) and Jacobsen (1977) for four tropical African species of *Aloe*.

Classification *sensu* Reynolds (1966)	Species		Classification *sensu* Jacobsen (1977)
GROUP 4 Small plants with ± striped flowers	*A. jucunda*	→	sect. *Aloe* subsect. *Humiles* series *Proliferae*
	A. jacksonii	→	sect. *Aloe* subsect. *Grandes* series *Aethiopicae*
	A. hemmingii	→	sect. *Aloe* subsect. *Parvae* series *Longistyla*
	A. somaliensis	→	sect. *Aloe* subsect. *Grandes* series *Tropicales*

Baker subsp. *pulchra* Glen & Hardy (1987a). For recent nomenclatural changes in the section *Leptoaloe,* Glen and Hardy (1987b) should be consulted. Within *Aloe* the section *Leptoaloe* is most closely related to the grass aloes (section *Graminialoe* Reynolds). It, however, differs from the latter section mainly in that its constituent taxa are more robust in all respects. *Aloe microcantha,* one of the southern African species of the section *Leptoaloe,* forms the basis of the present article. This species is described and its taxonomic history, geographical distribution and conservation status are discussed.

Taxonomic history

Live specimens of the taxon currently known as *A. microcantha* (Fig. 1) were introduced to Kew in 1819. These specimens, like many other succulent plant species were collected at the then Cape of Good Hope and sent to Kew by James Bowie (ca. 1789–1869) (Pole-Evans 1919). Although Bowie did not publish much on his plant collections or collecting trips into the southern African interior, his interest in succulents led to the introduction into European horticulture of many species new to science [*cf.* Smith and Van Wyk (1989) for additional information on Bowie's collecting activities]. As Reynolds (1950) surmises the most likely type locality of *A. microcantha* is the vicinity of Uniondale, Cape Province, a natural habitat of this species. The first herbarium specimens of this species were, however, prepared by W.J. Burchell (1781–1863) five years before it was collected by Bowie. These specimens, which are housed at Kew herbarium, were collected by Burchell on 27 January 1814 and 5 February 1814 in the vicinity of Algoa Bay (Port Elizabeth) (Reynolds 1950). The two specimens, *Burchell 4482* and *Burchell 4564,* are mounted on the same herbarium sheet (Prof. G.Ll. Lucas personal communication).

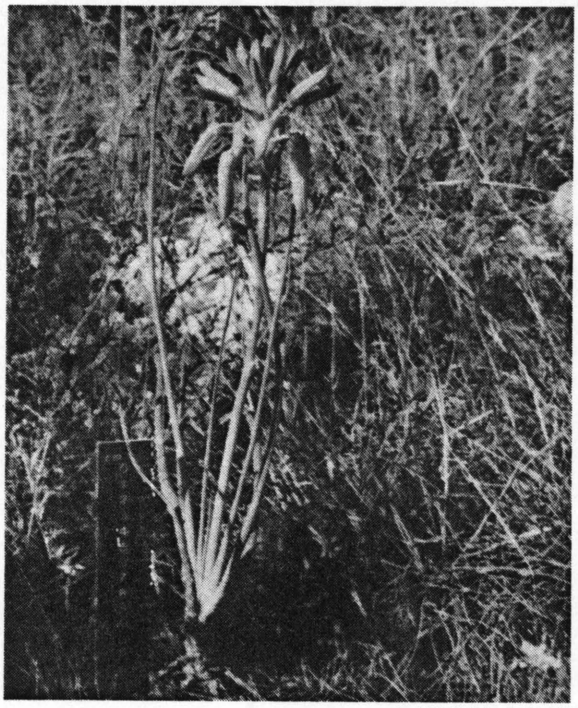

Fig. 1. *Aloe microcantha* Haworth in habitat in Port Elizabeth. Photographed on 24 February 1983. This population has since been destroyed.

As was the case with most of the novelties introduced to Kew by Bowie, *A. microcantha* was described by Adrian Hardy Haworth (1768–1833) (Haworth 1819). There is also an unpublished, unnumbered drawing of this species at Kew, tentatively attributed to Franz Andreas Bauer (1758–1840) (Stafleu and Cowan 1976). Although Reynolds (1950) claims that it bears the date "August 1829", Hunt (1988) suggests that the rather illegible date could be "August 1819", that is, the year of publication of the name *A. microcantha.* However, one of the first figures of this species to appear in print was that of Salm-Dyck (1840).

Various authors have treated this species under the name *"A. micracantha"* [*cf.* Reynolds (1950) for references]. This, however, constitutes an illegitimate orthographic variant of *A. microcantha.* Haworth (1819) clearly published the specific epithet as *"microcantha"*, alluding to the relatively small teeth present on the leaf margins of this species. Regarding the author citation of the name *A. microcantha,* Groenewald (1941) contains an anomaly. On p. 11 of this publication he lists the author of this species name as James Bowie (who introduced living specimens to Kew) whereas, on p. 39, it is correctly ascribed to Haworth. Although *A. microcantha* is a distinctive species of *Leptoaloe,* it has sometimes been confused with *A. boylei* Baker (Anonymous 1923). These two species are easily separable on vegetative morphological grounds in that the leaves of *A. boylei* are up to 90 mm broad, in comparison to the leaves of *A. microcantha* which are only about 30 mm broad.

Apart from the abovementioned nomenclatural inaccuracies and taxonomic confusion, *A. microcantha* has been correctly treated by most recent authors, such as Reynolds (1950 and later editions), Bornman and Hardy (1971), Judd (1972) and Jeppe (1977).

Description

The following description is based on flowering plants collected in the Port Elizabeth metropolitan area.

Aloe microcantha Haworth in Supplementum plantarum succulentarum 105 (1819). For species synonymy, literature references, taxonomy and key to *Aloe* section *Leptoaloe* see Reynolds (1950 and later editions).

Herbaceous perennial; acaulescent or shortly caulescent, usually solitary, with thick fusiform roots. *Leaves* ± 15, dense, multifarious, rigid, tapering gradually, linear-lanceolate, straight, ± 450 mm long, ± 30 mm broad at the base, green to yellowish green; *upper surface* canaliculate; *lower surface* convex, both surfaces copiously spotted with white, the spots subtuberculate on the lower surface; *margins* cartilaginous, minutely denticulate near apex, teeth ± 2 mm long towards leaf base, down-curved. *Inflorescence(s)* 1 -- 2, simple, capitate, ± 450 mm tall; *peduncle* simple, up to 370 mm long, sterile bracteate in upper half; *raceme* up to 90 mm long, densely capitate, young buds erect, open flowers pendulous; *bracts* ovate, as long as or slightly shorter than their pedicels; *pedicels* lowest ± 30 mm long, ascending. *Perianth* dull-orange to salmon-pink, ± 37 mm long, straight, cylindrical, slightly constricted above ovary, the mouth open, basally rounded, stipitate; *outer segments* free to base, apically acute; *inner segments* free, apically sub-acute, *stamens* 6, inserted within the perianth tube, 35 mm long, included or very slightly exserted; *ovary* 6 mm long, diameter 3 mm; *style* straight, capitate, 28 mm long. *Chromosome number* $2n = 14$ [*cf.* Muller 1941)]. Figure 2.

Flowers mainly from December to February.

Fig. 2. Capitate raceme of *Aloe microcantha* Haworth. Photographed on 18 January 1988 in habitat in Rowallan Park, one of the last remaining populations of this species in urban Port Elizabeth.

Distribution and conservation status

The South African species of *Aloe* section *Leptoaloe* are widely distributed in the eastern and south-eastern regions of the subcontinent. It is usually encountered in grassland which receives relatively high rainfall (Laubscher 1973a, b). *Aloe microcantha* is confined to the eastern Cape from Uniondale to Grahamstown where rainfall occurs throughout the year, with peaks in autumn and late spring (southern hemisphere). It grows in grassland in open, sandy places, usually in hilly and mountainous areas (Fig. 3).

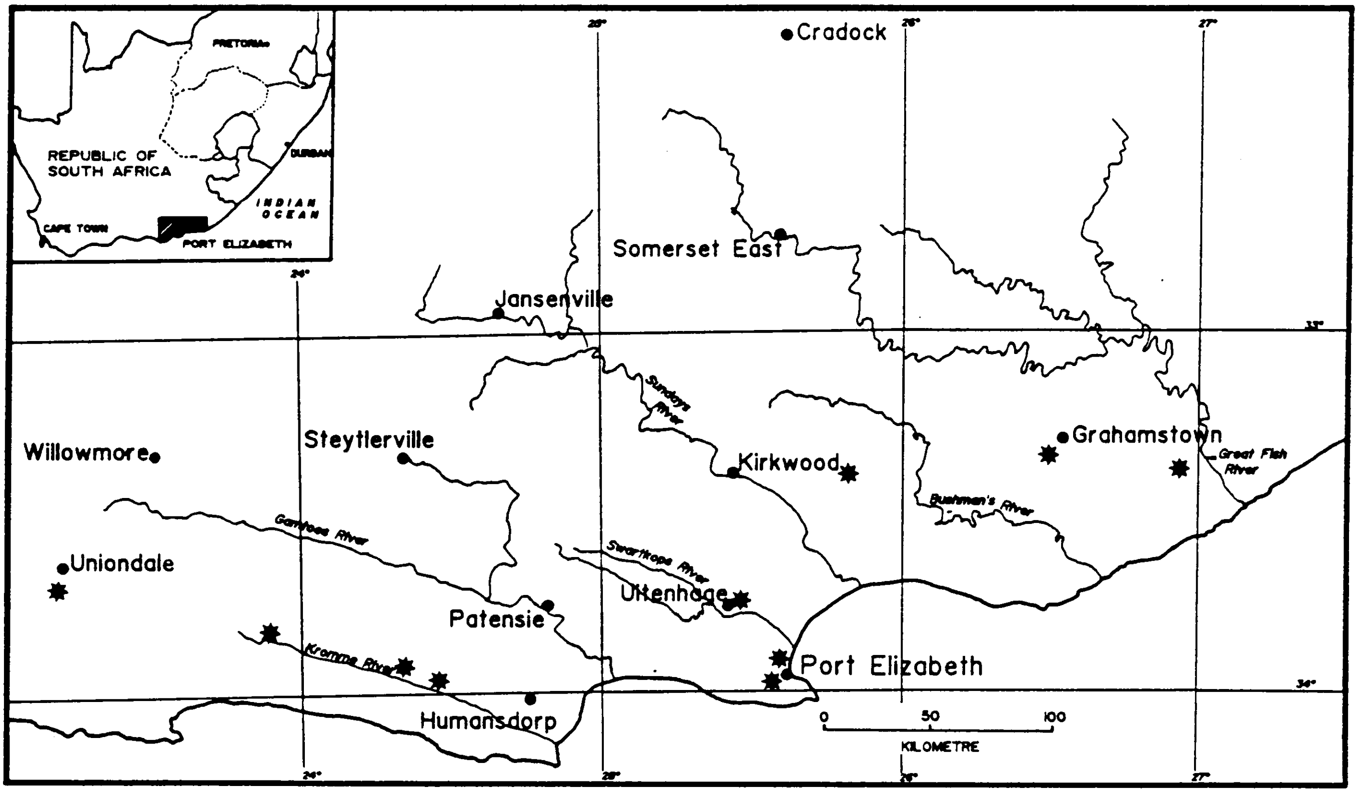

Fig. 3. Geographical distribution range of *Aloe microcantha* Haworth. Localities where *A. microcantha* has been collected are indicated with a star.

It is noteworthy that Madagascar lacks representatives of *Aloe* section *Leptoaloe* even though this island has a diverse *Aloe* flora. This indicates a post-drift origin for the leptoaloes. This section therefore arose some time after the complete sea invasion of the Mozambique Channel in the mid-Cretaceous (100 million years before present) (Flores 1970; McElhinny *et al.* 1976).

Aloe microcantha has a fairly wide geographical distribution range (*ca.* 500 km between the extremes) and does not appear on recent lists of threatened plant taxa (Hall *et al.* 1980; Hall and Veldhuis 1985). Although *A. microcantha* is not endangered across its entire range of distribution, the populations of this species in the Port Elizabeth metropolitan area are on the verge of extinction. Great pressure is being placed on the natural resources of southern Africa, the eastern Cape being no exception (Baird *et al.* 1988; Macdonald and Crawford 1988). As could be expected the major threat to *A. microcantha* populations in this region is urban expansion. However, this account does not constitute an unrealistic plea to halt urban development in the Port Elizabeth area (or any metropolitan area for that matter). It is rather suggested that closer attention should be paid to threatened and vulnerable species which occur in areas which fall under the jurisdiction of local government (city and town councils and municipalities). Whereas professional botanists occasionally have difficulties in obtaining permits from relevant authorities for collecting specimens for research purposes, private landowners often eradicate large numbers of protected species without anyone taking notice.

The only recent annotated systematic checklist of Spermatophyta from the Port Elizabeth area which mentions *A. microcantha,* is that of Olivier (1977). In this paper she states that *A. microcantha* is rare in fynbos of the Baakens River Valley. The latter river is approximately 15 km long and winds its way through a number of suburbs of Port Elizabeth, reaching the sea in the harbour area. "Fynbos" is a vernacular term literally meaning "fine-leaved bush". This term has recently gained acceptance by the international scientific community and is more suitable than "macchia" in South Africa. The Fynbos biome of southern Africa is characterized by the presence in large numbers of, amongst others, representatives of the families Proteaceae, Restionaceae and Ericaceae. It approximates the Cape Floristic Kingdom which despite its miniscule size has been recognized as one of the world's six Floristic Kingdoms. (Takhtajan 1969; Rutherford and Westfall 1986).

In the Port Elizabeth area pockets of pristine fynbos are becoming increasingly rare. Furthermore, along the entire length of the Baakens River, the vegetation is inundated with aliens. According to Olivier (1977) 23 exotic, naturalized species occur in this valley. These introduced species can ultimately modify the natural habitat of *A. microcantha* and add to its disappearance from once pristine fynbos. Recently Glen and Hardy (1986) has, for example, discussed the detrimental impact of soil acidification by fallen pine needles on populations of *A. albida* in the Barberton district (Fig. 4).

Fig. 4. Natural habitat of *Aloe microcantha* Haworth (Rowallan Park, Port Elizabeth). Note avenue of exotic *Eucalyptus* species in the background.

Conclusion

As should be the case with any plant species in need of protection, nature conservation should have a policy to conserve not only limited populations, but should include the entire range of such species. Instead of simply eradicating populations of *A. microcantha* which are threatened by urban development, such specimens should be re-established in, for example, the Settler's Park Nature Reserve. This 54 ha reserve is close to the central business district of Port Elizabeth (Duggan 1983) and is a natural habitat of *A. microcantha*. This practice would therefore also be ecologically sound and the long-term survival of the Port Elizabeth strain of *A. microcantha* would be assured.

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Populations of *Haworthia fasciata* (Willd.) Haw. (Asphodelaceae: Alooideae) are dwindling in urban Port Elizabeth, eastern Cape, South Africa

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Introduction

Since the recognition of *Haworthia* Duval (1809) as a genus separate from *Aloe* L., it has been burdened by a profusion of species names and infraspecific combinations, most of which do not warrant recognition at any rank in a hierarchical classification system. *H. fasciata* (Willd.) Haw. is no exception to this generalization. The specific epithet was originally published by Willdenow (1811) but he used the name *Apicra* Willdenow (1811) *non* Haworth (1819) for the genus now known as *Haworthia*. Ten years after the name *Apicra fasciata* appeared in print, Haworth (1821) transferred it to *Haworthia*. However, Salm-Dyck (cf. Stearn 1938), Schultes & Schultes (1829) and some later authors, such as Kunth (1843), reverted to using the name *Aloe* in the broad Linnean sense and for many years during the 19th century the species was known as *Aloe fasciata* (Willd.) Salm-Dyck. Baker (1880) eventually took the logical step and transferred the species back to *Haworthia*. During the nineteenth century a single infraspecific taxon was recognized in *H. fasciata*, viz. *H. fasciata* var. *major* (Salm-Dyck) Baker, irrational name proliferation in the species only reaching a peak during the Von Poellnitz era of *Haworthia* classification (1930's – 1940's) (Von Poellnitz 1938; Haworthia Study Group 1975). The plethora of infraspecific epithets that has been published for clones of *H. fasciata* bears witness to some morphological variation between individuals from different populations. However, within individual populations variation is quite small. With the possible exception of the aberrant *H. fasciata* fa. *browniana* (V. Poelln.) Bayer (1976), none of these infraspecific taxa warrant recognition in a taxonomic classification system (cf. also Brandham 1973).

The specific epithet *fasciata* is derived from the Latin "fasciatus" which describes a surface marked transversely with parallel stripes of colour. The prominent white tubercles in more or less continuous bands across the abaxial leaf surfaces of *H. fasciata* (for which this species was aptly named) has lead to it sometimes being confused with certain forms of *H. attenuata* (Haw.) Haw. (Anonymous 1970; Lamb & Lamb 1972; Oosthuizen 1972; Pilbeam 1977, 1983; Harland & Harland 1982; Subik & Kaplicka 1985). However, in contrast to *H. attenuata* and *H. radula* (Jacq.) Haw., both of which also occur in the eastern Cape, the adaxial leaf surfaces of *H. fasciata* are smooth. Furthermore, the leaves of *H. fasciata* are more deltoid in shape than those of *H. attenuata* and *H. radula* which both have lanceolate leaves. The leaves of *H. fasciata* are also less prone to die back from the tips than in the other two species. For additional taxonomic information on *H. fasciata* the standard works of Bayer (1982) and Scott (1985) should be consulted.

In habitat specimens of *H. fasciata* are particularly striking when the rays of a setting sun turn the rosettes into almost translucent fiery orange-green balls. In cultivation plants of *H. fasciata* often take on a drab green colour and loose much of their enchantment. The muted, pinkish, bilabiate flowers and oblong-obtuse capsules of the species are typical of *H.* subg. *Hexangulares sensu* Bayer (1982) (Fig. 1).

Distribution and conservation status

Haworthia fasciata is endemic to the eastern Cape, an area which receives its precipitation at all seasons, usually with peaks in autumn and spring. Rainfall varies considerably in amount and a large part of the eastern Cape is semi-arid. In this region *H. fasciata* occurs from the Gamtoos River Valley in the west to Port Elizabeth in the east (cf. Rowe 1989). It is usually associated with acidic soils which support sclerophyllous (fynbos) vegetation. Although *H. fasciata* is less proliferous than its apparent relatives, it can, in habitat, form mats of up to 0,5 m in diameter. *H. fasciata* flowers in summer (southern hemisphere) and although occurring in a region which can receive rainfall throughout the year, it generally responds to a winter growth cycle.

Although *H. fasciata* is not endangered across its entire range of distribution, populations of this species are becoming increasingly rare in the Port Elizabeth metropolitan area. In this, the eastern extreme of its geographical distribution, scattered colonies are restricted to currently undeveloped stands. The major threats to these remaining populations of the species are urban expansion and injudicious collecting by succulent plant enthusiasts. In the latter instance a number of piles of abandoned plants in varying stages of decomposition were recently come across in habitat. The plants were obviously carefully lifted and the soil removed from their roots. Inexplicably these plants were not removed from the site of collection and simply left to decay.

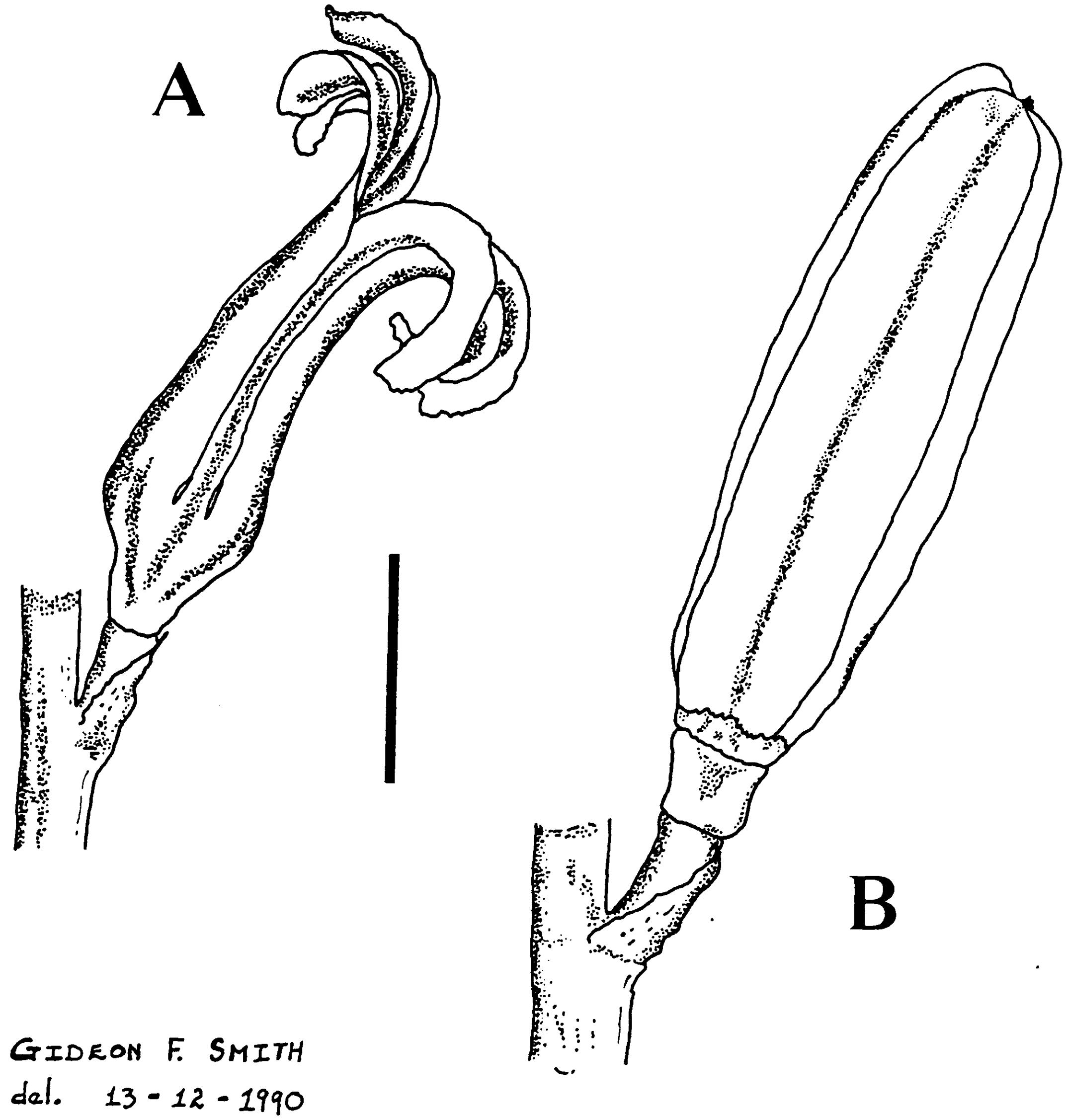

Fig. 1: *Haworthia fasciata* (Willd.) Haw. A, single flower in lateral view, showing the position of the peduncle and bract. B. Fruit, trilocular capsule. Scale line = 5 mm.

During recent prolonged droughts and even in times of moderate water deficiency (which occur frequently in southern Africa), succulent plants came to the fore as extremely well adapted for amenity horticulture (Fourie 1984). Most perennial species live very long and they are compatible with local insect and bird life. Furthermore, evolved characteristics that are coded in the genes and inherited by subsequent generations include factors such as drought resistance. Thus collectors (and even non-hobbyists) are creating a demand for succulent plants in general. As is the case elsewhere (cf. Lyons 1972, 1976) nature conservation authorities simply do not have the staff or equipment to apprehend those who seek to destroy (wittingly or unwittingly) part of the southern African floral heritage. Over the last few decades the conservation of succulent plants and their habitats have received attention at international level (Hunt 1982; Rowley 1973, 1981). However, it should be clear that much remains to be done in terms of the conservation education of the general public and private land owners (Lloyd 1972).

Nature conservation should have a policy to conserve not only limited populations of species in need of protection, but should include the entire range of such species. Instead of simply eradicating populations of *H. fasciata* threatened by urban expansion, such specimens should be re-established in local nature reserves, such as Settler's Park which is only minutes away from the centre of Port Elizabeth (Gardiner 1988).

Conclusion

Habitats of succulent plants are often very sensitive areas and even trampling by humans can damage or kill the plants. These usually inhospitable habitats have always fascinated man for various reasons and are becoming increasingly accessible due to technological development (Castle 1990). In many cases distribution patterns of succulent plants are only now starting to take shape, indicating sequences of past connections [cf. Van der Walt & Vorster 1983 and Hartman 1987 on *Pelargonium* (Geraniaceae) and the subtribe Leipoldtiinae (Mesembryanthemaceae), respectively]. These fragments of information could well be of key importance in reconstructing the biohistory of the southern African subcontinent. Complete eradication of species such as *Haworthia fasciata* from, amongst others, densely populated areas, for example Port Elizabeth, will hamper future phytogeographical analyses of the genus and will certainly give a distorted picture of species frequency and distribution. As Mr. M. Bruce Bayer (1985), well-known authority on *Haworthia*, so aptly remarked: "Why don't plant lovers, like their counterparts, the bird-watchers, use glass (magnifying or binoculors) and camera, to record and conserve for posterity?"

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7.5 ECOLOGY AND CONSERVATION STATUS OF *CHORTOLIRION* AND *POELLNITZIA*

7.5.1 Background

Before discussing the ecology and conservation status of *Chortolirion angolense* and *Poellnitzia rubriflora*, it is important to note the differences amongst the concepts of the biome (Figure 7.1), floral kingdom (Figure 7.2), phytochorion (Figure 7.3) and veld type (Figure 7.4). These terms are used throughout this text and detailed definitions will prevent confusion. Firstly, a biome is (Rutherford & Westfall 1986):

a) the largest land community unit recognized at a continental or subcontinental scale. The use of such an enormous land surface area makes the biome (biocoenoses) an absolute entity and not subject to relative repositioning in a hierarchical classification system, for example those used by phytosociologists.
b) a unit mappable at a scale of no smaller than about 1:10 million. A biome can therefore not be restricted to a small localized area.
c) distinguished from other biomes primarily on the basis of dominant plant and animal life forms in climax sytems. This definition therefore necessitates the inclusion of the animal component in biome delimitation. Since life forms form the basis for biome classification it should be obvious that there is no place here for floristic classification.
d) distinguished from other biomes secondarily on the basis of those major climatic features that most affect the biota.
e) not an unnatural or major anthropogenic system and hence large areas of urbanization, cultivation and plantations are not taken into account in biome delimitation.

The biome concept should not be confused with the ecosystem approach to, amongst others, biogeographical studies (see for example Kormondy 1976, Tivy 1982, Meadows 1985 and Bredenkamp 1987). This approach also links the biological and physical environments, but includes man and views him as an integral part of the ecosystem. Broadly defined an ecosystem is a functioning, interacting system composed of one or more living organisms and their effective environment.

Secondly, certain major floristic kingdoms (or divisions) — usually six — can be distinguished in the world flora. Each have certain predominant floristic elements and often have characteristic endemics. Most floristic kingdoms have more or less natural physiographic boundaries and can be subdivided into smaller units (regions, subregions) (Good 1947; Von Denffer 1976; Takhtajan 1986).

Two of the world's six floristic kingdoms are found in South Africa: the summer rainfall flora in the central and northern parts (Palaeotropical Kingdom) and the more or less winter rainfall flora of the southern and south-western Cape Province (Capensis Kingdom) (Takhtajan 1969, 1986; Bond & Goldblatt 1984). The boundaries of the latter kingdom closely approximates those of the Fynbos Biome.

Thirdly, the classification of the vegetation of Africa into phytochoria (floristic regions) is based solely on the plants themselves, sometimes supplemented by features of the environment which can be seen, such as bodies of standing water or outcrops of rock. Thus, the phytochoria of White (1983) are based almost entirely on the physiognomy [external appearance (morphology) of the vegetation of a plant community; sometimes used to refer to the overall composition of a community, for example forest, grassland, desert, etc.] and floristic composition of the vegetation and not on climate. By definition the richness (or lack thereof) of their endemic floras at the species level also play an important role in the delimitation of phytochoria. For Africa White (1983) recognized 18 major phytochoria and for Madagascar two.

Finally, the concept of veld type was developed in South Africa by Acocks (1953, 1988) and is still used extensively in ecological studies. Acocks (1953, 1988) broadly classified (mapped at a scale of 1:1 500 000) the southern African vegetation into 70 main veld types and a further 75 variations. A veld type has been defined as a unit of vegetation "... whose range of variation is small enough to permit the whole of it to have the same farming potentialities." This definition was thus partly arrived at after considering both the floristic composition and the agronomical potential of the veld.

7.5.2 *Chortolirion angolense*

Chortolirion occurs in the Palaeotropical Kingdom and is a floristic component of FIVE of the seven biomes of southern Africa [compare the distribution range of *Chortolirion* (Figure 7.5) with the boundaries of the biomes (Figure 7.1); the scale of the figures are identical]. The biomes in which the genus occurs are: 1, Desert; 2, Grassland; 3, Succulent Karoo; 4, Nama-Karoo and 5, Savanna. It is absent only from the Forest and Fynbos Biomes. Furthermore, it occurs in more than 35 veld types (Acocks 1988). However, the main geographical distribution range of *Chortolirion* corresponds closely with the boundaries of the Kalahari — Highveld Regional Transition Zone (White 1983). This phytochorion separates the Zambezian and Karoo-Namib Regional Centres of Endemism. It runs diagonally across southern Africa from 13°S in southern Angola to 33°S in the north-eastern Cape. The phytochorion has very few endemic species and the greater part of the interior has a very poor flora. *Chortolirion* also occurs in the Tongaland-Pondoland

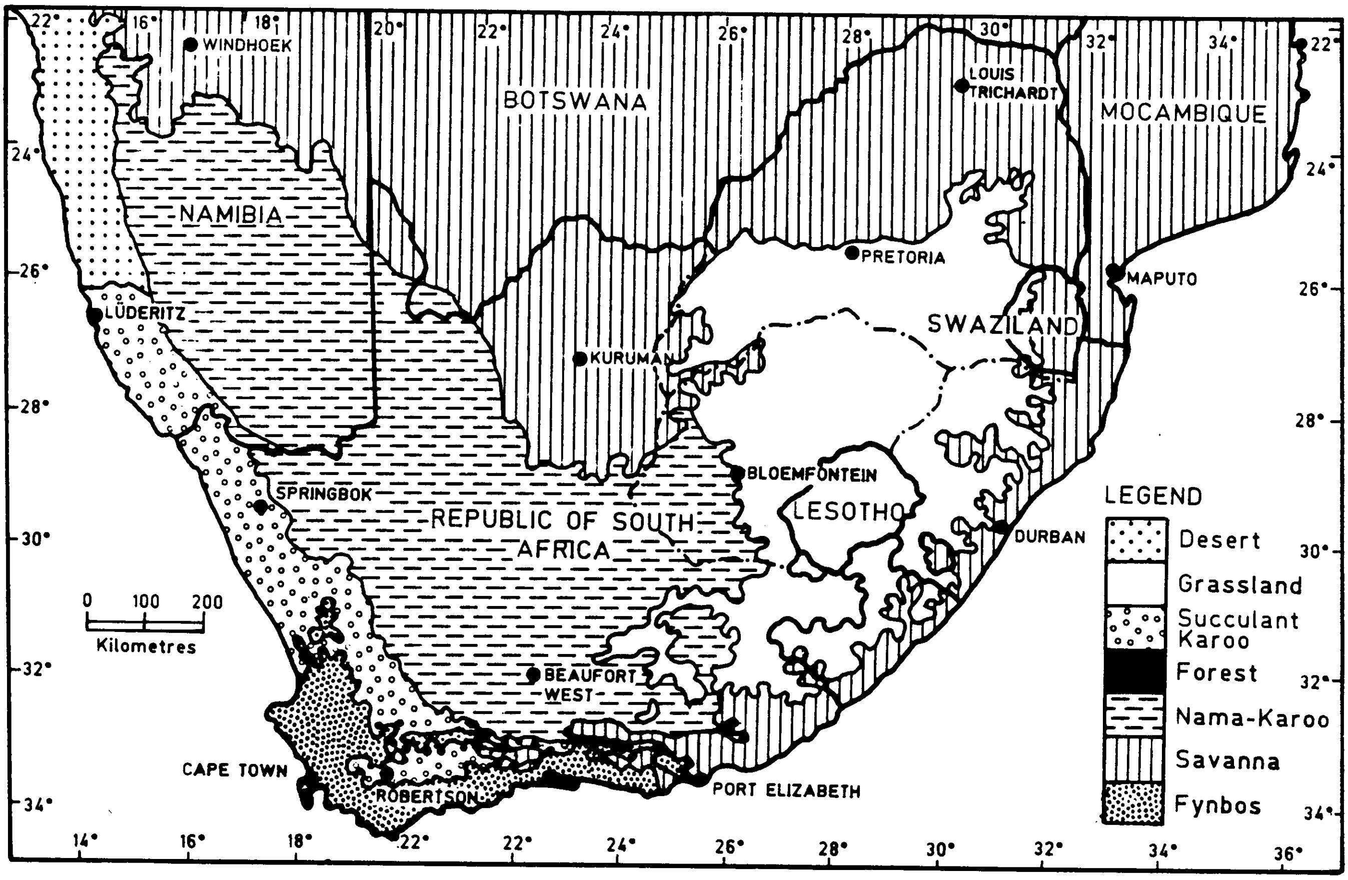

Figure 7.1 The biomes of southern Africa at 1:10 000 000 scale (after Rutherford & Westfall 1986).

Regional Mosaic, the Zambezian Regional Centre of Endemism and the Karoo-Namib Regional Centre of Endemism. However, some of the specimens of *C. angolense* which have been collected in the latter phytochorion (Lüderitz area) are aberrant, at least in terms of leaf morphology and requires further investigation. In this instance the SAM specimen (kept at NBG, Kirstenbosch) *E. Jansen s.n.* sub Herbarium Musei Austro-Africana 60 910 from Lüderitz Bay, South West Africa (now Republic of Namibia) is a case in point. The leaves of this specimen are entire and more flaccid than those of *Chortolirion* in general. This is undoubtedly the only species of the subfamily Alooideae which displays such a divergent range of ecological conditions. It is unusual for an intraspecifically undifferentiated species so distinctive and relatively constant in terms of both vegetative and reproductive morphology to be so extraordinarily successful in terms of the ecological niches which it can occupy. This makes a detailed discussion of its habitat and ecology virtually impossible, in contrast to *Poellnitzia* which has a very restricted geographical distribution range (see 7.5.2). The following is therefore a brief and general discussion of the ecology and habitat of *Chortolirion*.

Chortolirion is found from near sea level (Lüderitz) up to altitudes of more than 2 000 m (foot hills and mountains of Lesotho). The general habitat of the genus is the climatically severe southern African inland above the Great Escarpment. Bar the Lüderitz district (Desert Biome), *Chortolirion* is absent from the coastal arid, semi-arid and summer-dry regions of southern Africa. In habitat the sepecies is subject to extreme temperature fluctuations (up to -10°C in winter and +40°C in summer), severe frost is common in winter and heavy snow falls occur frequently in the mountainous areas of its distribution range. Mean annual rainfall of between 20 (western extreme of its distribution: Diaz Point Lighthouse near Lüderitz) and 750 mm (eastern Transvaal: Nooitgedacht Agricultural Station at Ermelo) has been recorded in habitat (Weather Bureau 1984). The active growing season of *Chortolirion* coincides with the summer rainfall. The genus does, however, enter the winter rainfall region in southern Namibia. Robust specimens of *Chortolirion* bearing inflorescences of up to 1 m in length have been recorded from Marandellas (altitude 1 500 m) in the Harare district of Zimbabwe (Court 1981). The climate here is temperate with average daily temperatures in mid-winter of between 20 and 23°C. In the interior of South Africa individuals of *Chortolirion* generally do not exceed 0,4 m in height, including inflorescences.

Chortolirion is adapted to sparse or dense grasslands in which a wide variety of graminoids and forbs dominate (Burt-Davy & Pott-Leendertz 1912; Louw 1951; Rattray 1960; Van der Meulen 1979). These grass-

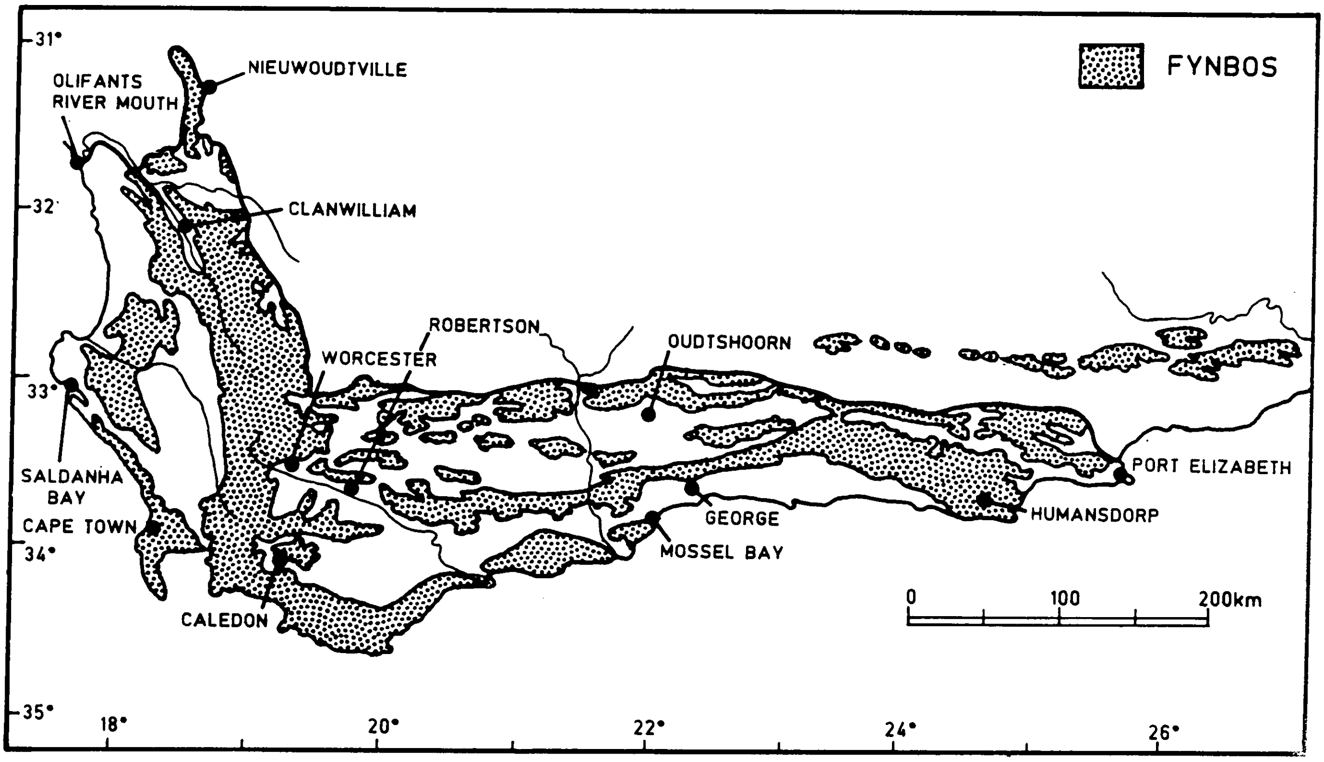

Figure 7.2 The Cape Floral Kingdom (after Bond & Goldblatt 1984). The rest of southern Africa is included in the Palaeotropical Kingdom (cf. Takhtajan 1969).

lands are usually subject to natural or deliberate seasonal burning. The genus is unique amongst haworthioid species in that it is the only grassland taxon of which the leaves are deciduous and die back to ground level after fires or frost. Survival under these circumstances is due to the presence of a perennial bulb and succulent, fusiform roots, the species having reverted to a less succulent leaf consistency. This habit is shared by a rich and diverse southern African geophytic flora (Van Wyk & Malan 1988; Jeppe & Duncan 1989; Du Plessis *et al.* 1989).

No signs of insect predation of vegetative parts have been observed in habitat. However, in cultivation the genus is extremely prone to infestations of red spider mite *(Tetranychus cinnabarinus)* and mealy-bug (woolly aphids; *Planococcus citri*). Both insect pests are lethal and specimens of *Chortolirion* generally do not survive for long in collections of succulent plants.

In general species of *Haworthia* do not immediately recolonize a habitat once it has been disturbed (Craib 1990), and the same appears to apply to *Chortolirion* (Hargreaves 1989). However, the species has a very effective defense mechanism (camouflage) in that, in its natural grassland habitat, casual succulent plant collectors are likely to mistake its linear leaves with those of a grass species. The inflorescence and flowers of *Chortolirion* are also very inconspicuous. In pristine and well-managed pastures grazing pressure is also minimal since the abundance of palatable grass species associated with it will certainly be utilized preferentially. Once severe habitat modificiation has taken place, populations will undoubtedly dwindle and eventually disappear. However, at least at present, *Chortolirion* can be included in the "Not threatened" conservation category (see 7.1 for a definition of the category). Where possible populations should be monitored for decline or expansion, especially since *Chortolirion* occurs in some of the most densely populated areas of South Africa (Pretoria, Johannesburg-Soweto, Vaal Triangle) and even the rural and more remote areas of its distribution are not entirely uninhabited, and particularly in the Grassland Biome subjected to extensive agricultural activity.

7.5.3 *Poellnitzia rubriflora*

Although *Poellnitzia* is a floristic component of the Cape Floral Kingdom (Capensis), the Robertson Karoo (districts of Robertson, Bonnievale and McGregor) where the genus is endemic, is one of the drier winter rainfall areas bordering the Fynbos Biome (Anonymous 1983; Gie 1987). A detailed geographical distribution map of the genus is given in Chapter 9 (9.5). The distribution of the genus in relation to the biomes of southern Africa and the Cape Floral Kingdom is shown in Figures 7.1, 7.2 and 7.5. The vegetation in the habitat of *Poellnitzia* can be broadly classified as

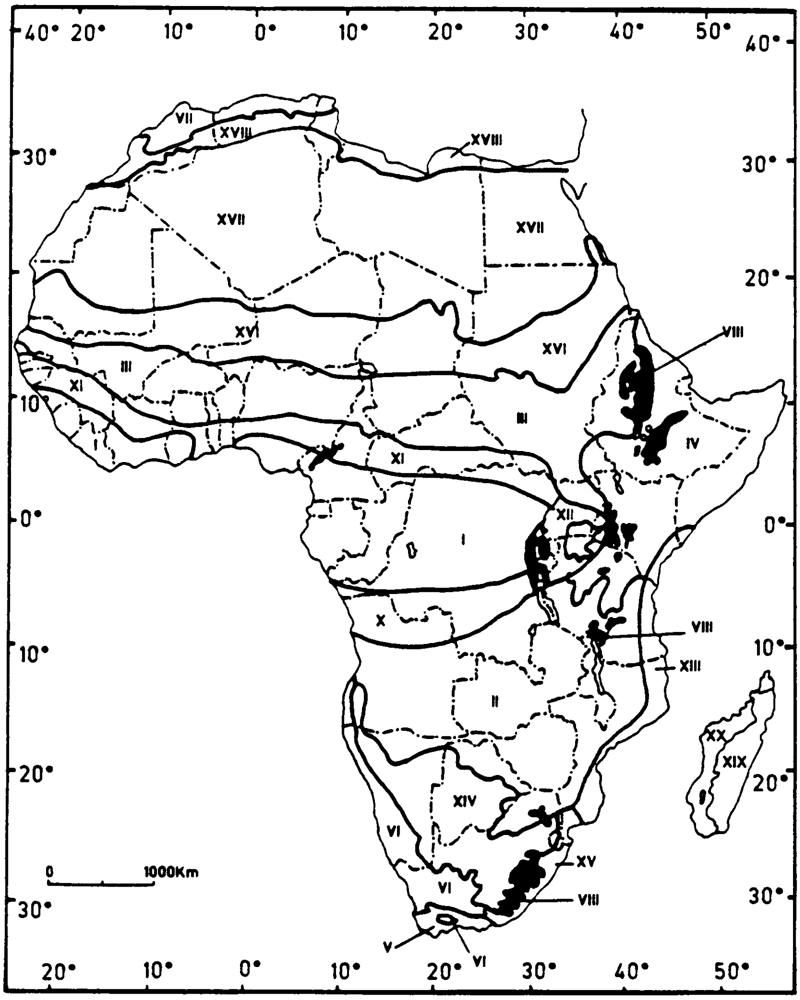

Figure 7.3 Main phytochoria of Africa and Madagascar. I. Guineo-Congolian regional centre of endemism. II. Zambezian regional centre of endemism. III. Sudanian regional centre of endemism. IV. Somalia-Masai regional centre of endemism. V. Cape regional centre of endemism. VI. Karoo-Namib regional centre of endemism. VII. Mediterranean regional centre of endemism. VIII. Afromontane archipelago-like regional centre of endemism, including IX, Afroalpine archipelago-like region of extreme floristic impoverishment (not shown separately). X. Guinea-Congolia/Zambezia regional transition zone. XI. Guinea-Congolia/Sudania regional transition zone. XII. Lake Victoria regional mosaic. XIII. Zanzibar-Inhambane regional mosaic. XIV. Kalahari-Highveld regional transition zone. XV. Tongaland-Pondoland regional mosaic. XVI. Sahel regional transition zone. XVII. Sahara regional transition zone. XVIII. Mediterranean/Sahara regional transition zone. XIX. East Malagasy regional centre of endemism. XX. West Malagasy regional centre of endemism. [Taken from White (1983)].

Karroid Shrublands (Moll *et al.* 1984) and the entire range of distribution of the genus falls within the Succulent Karoo Biome (Rutherford & Westfall 1986). Acocks (1988) included the Robertson Karoo in variation b: Little Karoo of his veld type 26, Karroid Broken Veld, while White (1983) included the region in his Karoo-Namib Regional Centre of Endemism.

Poellnitzia is found between altitudes of approximately 150 and 250 m above sea level. Summer temperatures occasionally exceed 40°C, but nights are cool throughout the year. Mean annual rainfall is about 280 mm (Robertson Agricultural Station) (Weather Bureau 1984). *Poellnitzia* grows in humic, well-drained, sandy loam soils with a pH (KCl) of 8,4. The habitat typically consists of arid, rocky hillocks which are tenuously covered with succulent (predominant) or mesophytic (less frequent), perennial herbs interspersed with taller shrubs. *Poellnitzia* is usually encountered in bush clumps or next to rocks. This ensures sufficient shading and a constant supply of nutrients. Very rarely stunted plants are found in the open.

Although the vegetation is sparse, species diversity is high for an arid region. The area is especially rich in succulents belonging mainly to the Mesembryanthemaceae (dwarf shrubs) and the Crassulaceae, but also to many other plant families. Furthermore, many of the species are endemics. It is noteworthy that the high succulent plant species diversity of the Succulent Karoo Biome is unparalleled elsewhere in the world (Rutherford & Westfall 1986). Succulents and mesophytic shrubs associated with *Poellnitzia rubriflora* include (herbarium vouchers in brackets — these are kept in the herbarium of the department of Plant Sciences (PUC), Potchefstroom University for Christian Higher Education): *Adromischus maculatus* (Salm-Dyck) Lem., Crassulaceae *(G.F. Smith 190)*; *Aloe microstigma* Salm-Dyck, Liliaceae/Asphodelaceae; *Crassula pseudohemisphaerica* Friedr., Crassulaceae *(G.F. Smith 188)*; *Drosanthemum speciosum* (Haw.) Schwant., Mesembryanthemaceae *(G.F. Smith 184)*; *Euphorbia nesemanii* R.A. Dyer, Euphorbiaceae *(G.F. Smith 192)*; *Psilocaulon utile* L. Bol., Mesembryanthemaceae *(G.F. Smith 191)*; *Pteronia incana* (Burm.) DC., Asteraceae *(G.F. Smith 187)*; *Rhus glauca* Thunb.,

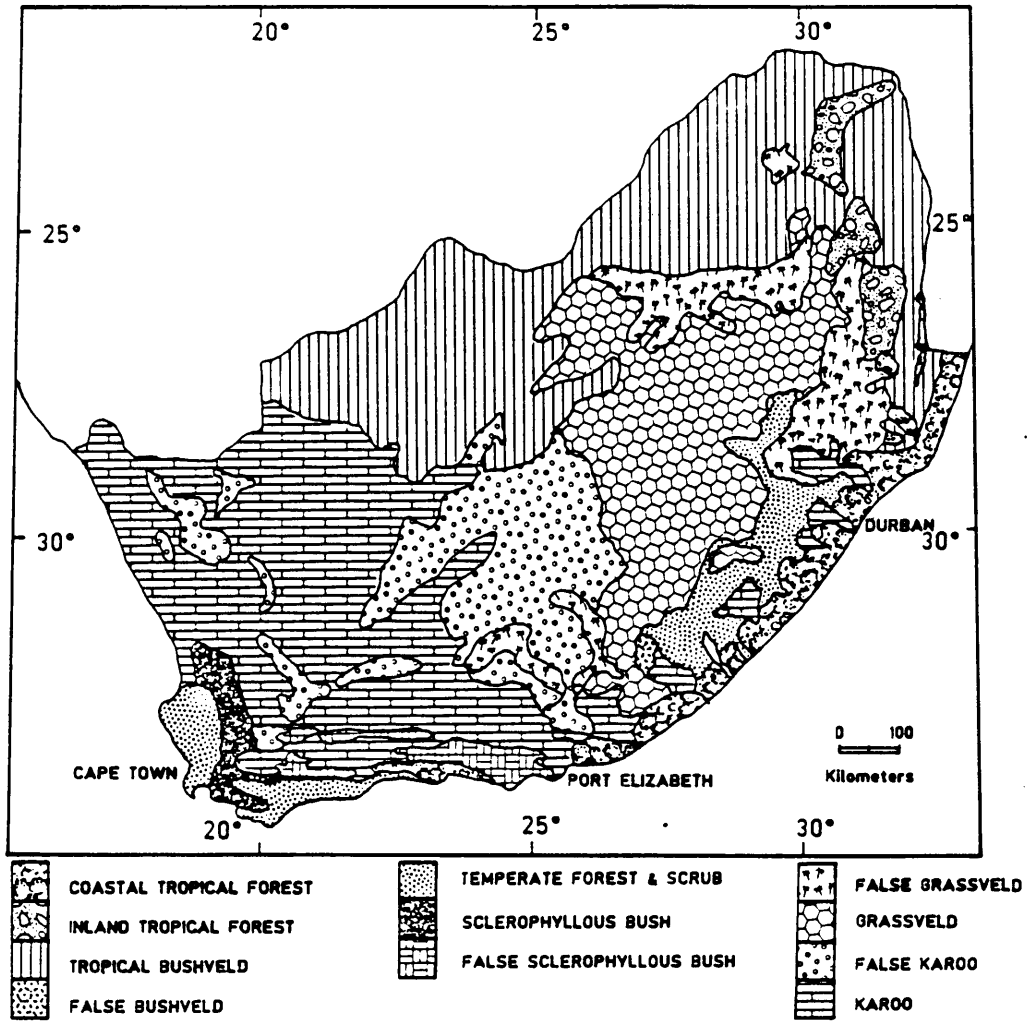

Figure 7.4 Simplified map of the veld types of South Africa of Acocks (1953). [Taken from Moll (1986)].

Anacardiaceae *(G.F. Smith 186)* and *Tylecodon paniculatus* (L.f.) Toelken, Crassulaceae.

Adaptation to aridity through drought tolerance (*sensu* Larcher 1983) by storage of water is clearly displayed by the succulents of the Robertson District (and other arid regions, for that matter). *Poellnitzia* stores water mainly in its succulent leaves. In times of drought the leaves become deeply channeled but recover rapidly after rain. The shallow, spreading root system enables individuals of the species to utilize even very light precipitation as well as nutrients available in the rich upper soil layer. In contrast to *Gasteria* (Van Jaarsveld 1989), plants of *Poellnitzia* are not subject to browsing by herbivores and no signs of insect predation of vegetative parts have been observed in habitat. The pungent-acuminate leaf tips and fairly sharp leaf margins apparently serves as effective mechanical defense mechanisms against herbivory (Rodgers 1979; Keen 1982) and the asperulous epidermis appears to deter phytophagous insects. Although most species of *Gasteria* and *Haworthia* are known to regenerate from single leaves or pieces of leaves (Swan 1976; Pilbeam 1981; Van Jaarsveld 1989), this phenomenon has not been observed in *Poellnitzia*, either in habitat or in cultivation.

At present urbanization does not pose a threat to populations of *Poellnitzia rubriflora*. In the entire Succulent Karoo Biome only two medium-sized towns (Worcester and Oudtshoorn) and various smaller centres, for example Robertson and Bonnievale, occur. Cultivation of especially wine grapes is limited to fairly narrow strips alongside water courses, such as the Breë River (Anonymous 1975; Wood 1991). The colonies of *P. rubriflora* are mostly confined to rocky hillocks and appear to be in no immediate danger of agricultural activities. However, due to its small world population and its confinement to a restricted geographical area, *Poellnitzia* should be removed from the "Indeterminate" category designated to it by Hall *et al.* (1980) (under the name *Haworthia rubriflora*) and Hall & Veldhuis (1985) and be reclassified as "Critically Rare" (see 7.1 for definitions of the respective conservation categories).

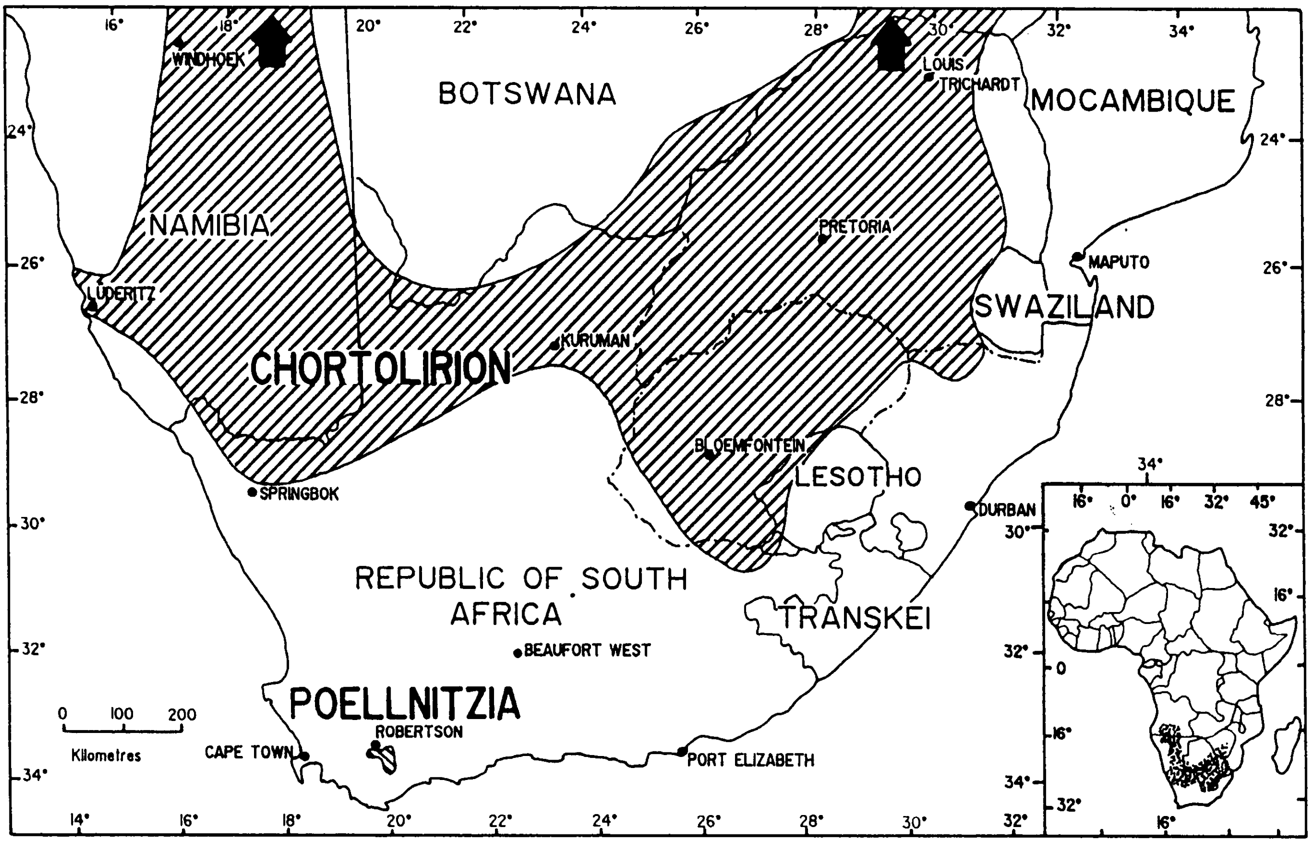

Figure 7.5 Approximate geographical distribution of the genera *Chortolirion* Berger and *Poellnitzia* Uitewaal. [Information for both genera from Smith (1985)].

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CHAPTER 8

GENERAL DISCUSSION, WITH A KEY TO THE GENERA OF ALOOIDEAE

"The cladistic programme is impressive: to reclassify the biota of the planet in the light of new methods for objective reconstruction of their phylogenies."

H.P. Linder: 1988

"Despite criticism [of cladistic methodology] ......, there appears to be no alternative method for reconstructing phylogenies in an empirical way."

A.L. Schutte & B-E. van Wyk: 1990

CONTENTS

CHAPTER 8

GENERAL DISCUSSION, WITH A KEY TO THE GENERA OF ALOOIDEAE

8.1 INTRODUCTION

8.1.1 Background

No subject can rival cladistics for the degree of controversy and argument that it has brought to taxonomy (Cronquist 1987; Hall 1988; Stace 1989). Yet, most biologists consider evolution to be the unifying concept of biology (Funk & Brooks 1990). [For a critique of cladism *versus* transformed cladism (theory of evolution kept out of classification), Ridley (1986) should be consulted.] However, understanding evolutionary relationships between groups of organisms remains one of the aims of systematics. For this reason methods have been developed that enable systematists to analyze patterns of character variation in accordance with stated criteria (e.g. outgroup comparison of cladistics) in order to arrive at plausible hypotheses about the evolutionary history of groups of organisms [see *e.g.* Duncan (1980) on the *Ranunculus hispidus* complex].

Cladistics (classification by means of shared, derived characters) can be applied to all organisms and at all levels of the hierarchy [Linder 1988; see also Dahlgren & Bremer (1985) on Angiosperms; Dahlgren & Rasmussen (1983) on Monocotyledons; Johnson & Briggs (1984) on Myrtales and Myrtaceae and Taylor & Zappi (1989) on Cereeae (Cactaceae), to name but a few]. The method uses characters that organisms possess to sort them into characterizable groups --- each group is defined by characters shared by all its members. One of the attractions of cladistics is that all the steps in the reasoning are explicit, i.e. the evidence used to construct the chosen cladogram is clearly shown (Jones & Gray 1983).

A prerequisite for cladistic analysis is a thorough knowledge of the group to be analyzed. Clearly, the group (in this case the genera of Alooideae) should be properly circumscribed and the characters sufficiently understood for homologies to be demonstrated. If this is not the case character transformation (polarization of characters) might be incorrectly assigned.

All characters of a taxon potentially are valuable for inferring evolutionary trends. However, only some of them are strong enough indicators of evolutionary directionality to be useful for cladistic analysis. For the present study only those characters were used for which primitive and advanced states could be assigned satisfactorily. Seventeen qualitative characters, each representing a basis for comparison, were utilized. With reference to the group being studied my concept of primitiveness is the following: the primitive state of a character is that which is found or I infer was present in the most recent common ancestor of the group (subfamily Alooideae) whose phylogeny is to estimated. An outgroup is ideally the sister group of the group being analysed. They are therefore believed to share a common ancestor. The plesiomorphic character states have occurred in the common ancestor of the study group and its sister group (outgroup). I have chosen *Kniphofia* as outgroup in this analysis of the genera of Alooideae. Based on the data used in this investigation it is one of the genera of Asphodeloideae in which most character states are plesiomorphies.

The information presented in the contributions included in this dissertation by no means represent all results obtained up to now. Gross morphological characters, e.g., have only briefly been alluded to in most chapters, while other observations have not yet been published. These observations are discussed below (8.2) and in Chapter 9 and will receive more attention in forthcoming publications. In this chapter the discussion of relationships amongst genera of the Alooideae is based on a cladistic analysis. Thus, it presents, for the first time, a hypothesis of phylogenetic relationships within the subfamily. Alooideae genera recognized in this investigation, data employed, polarization of character states and cladistic method used are discussed in detail in 8.2 (Smith & Van Wyk in press).

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GENERIC RELATIONSHIPS IN THE ALOOIDEAE (ASPHODELACEAE)

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Summary

Within the Asphodelaceae the subfamily Alooideae is a natural (monophyletic) group. All the genera in this subfamily are therefore considered to have evolved from a common ancestor, based on the possession of character states which distinguish this complex from all other genera of the Asphodelaceae. However, no comprehensive interpretation of phylogenetic relationships within the entire subfamily based on comparative morphological data and phytogeographical considerations has yet been accomplished. The present paper investigates phylogenetic relationships of the genera *Aloe* L., *Astroloba* Uitewaal, *Chortolirion* Berger, *Gasteria* Duv., *Haworthia* Duv., *Lomatophyllum* Willd. and *Poellnitzia* Uitewaal using cladistic methodology. The most obvious similarities amongst these genera are the succulent leaf consistency, crescentiform or cymbiform leaf outline in cross-section and the markedly bimodal karyotype of 2n = 14 chromosomes. For the cladistic analysis 16 characters were used and the genus *Kniphofia* was selected as outgroup. The characters are discussed in detail, polarized into plesiomorphic and apomorphic states and then employed in the generation of a phylogenetic hypothesis using the 'Hennig86' software package. It is suggested that the concept of the Alooideae be broadened to include *Kniphofia*, based on the synapomorphies of tubular flowers and fusion of perianth segments.

Introduction

The subfamily Alooideae (Asphodelaceae) includes about 7 genera and approximately 450 species (Table 1). It is fundamentally an Old World group with most genera occurring in sub-Saharan Africa. The genus *Aloe* L. is also found on the Arabian Peninsula, Madagascar and Socotra, while *Lomatophyllum* Willd. has been reported from the Aldabra Islands, Madagascar and Mauritius. The greatest concentration of genera and of species is in southern Africa, that is, roughly, the region south of the Kunene, Okavango and Limpopo Rivers. In this region the Liliaceae, in which the aloeoid taxa has previously been included, form a major part of the petaloid monocotyledons and contribute substantially to the size of the flora (Goldblatt, 1978; Gibbs Russell, 1985).

[INSERT TABLE 1 NEAR HERE]

Most research workers recognize the Alooideae as a taxonomically difficult subfamily. The morphology of these leaf succulents often varies considerably depending on environmental conditions [cf. Schelpe (1958) and Bayer (1980) on *Gasteria* Duval] and in some instances taxa seem to intergrade [cf. Bayer (1975) and

Glen and Hardy (1987) on *Aloe* series *Saponariae* Berger and Bayer (1973a) and Scott (1981) on the *Haworthia reinwardtii* Haw. - *H. coarctata* Haw. complex]. Recent studies, notably in the principal genera, namely *Aloe*, *Gasteria* and *Haworthia* Duval, have been primarily taxonomic in nature and have involved the study of variation in morphology (Reynolds, 1966, 1982; Van Jaarsveld, 1989; Bayer, 1982; Scott, 1985), leaf exudate chemistry [reviewed by Reynolds (1985a, b); (cf. Reynolds (1990)], leaf surface sculpturing (cf. Riley and Majumdar, 1979) and cytogenetics (cf. Riley and Majumdar, 1979). Furthermore, apart from recent contributions by Smith (1988, 1990), the smaller Alooideae genera (Table 1) have been omitted from most previous taxonomic and biosystematic investigations of this group (see also Beaumont et al., 1985). Since the initial work in the larger genera was concerned with the basic problem of patterns of variation and how the variation could best be recognized taxonomically, little attention was given to possible phyletic relationships.

The genera of Alooideae recently have been analised phenetically in numerical-taxonomic studies (Rowley, 1967a, 1969). Due to the uncertain taxonomic status of some of the genera recognized, the results of these studies are inconclusive (Bayer, 1972; Rowley, 1976a). Furthermore, existing generic boundaries were accepted and no real attempt was made to derive generic limits from the results (Ivimey-Cook, 1971). A few previous studies on the phylogeny of some genera of the Alooideae have been presented (Kok, 1973; Holland, 1978). However, these are often highly speculative and open to conjecture (Newton, 1973).

The present cladistic analysis has been conducted to obtain a better understanding of the relationships of the members of the Alooideae and to present for the first time a hypothesis of phylogenetic relationships within the subfamily.

Materials and Methods

Alooideae genera recognized in this study. - The subfamily Alooideae of the Asphodelaceae, with which this article is primarily concerned, has traditionally been treated as one of 28 tribes, namely Aloineae, of the Liliaceae (Hutchinson, 1959). More recently two extensively revised classification systems were published (Cronquist, 1981; Dahlgren et al., 1985) which not only differ from the system of Hutchinson (1959), but also from each other. Cronquist (1981) included the aloeoid genera, along with *Kniphofia* Moench in the Aloeaceae. *Bulbine* Wolf was, however, retained in the Liliaceae. Dahlgren et al. (1985) classified the aloeoid genera in the subfamily Alooideae of the Asphodelaceae while both *Kniphofia* and *Bulbine* were included in the type subfamily. Within the Alooideae 27 genus names are available for the approximately 450 species included therein. Only seven of these names currently enjoy general recognition. For the purposes of this article the following generic synonymy is accepted: [For additional nomenclatural information on the synonyms Rowley (1976a, b) should be consulted. For every genus upheld a reference to a recent treatment is given.]

1. *Aloe* Linnaeus: 319 (1753). [cf. Reynolds (1966, 1982)]. *Catevala* Medikus: 67 (1786) pro parte; *Kumara* Medikus: 69 (1786); *Rhipidodendrum* Willdenow: 164 (1811); *Pachidendron* Haworth: 35 (1821); *Bowiea* Haworth: 299 (1824) non J.D. Hooker: t. 5619 (1867); *Agriodendron* Endlicher: 144 (1836); *Papilista* Rafinesque: 137 (1840); *Succosaria* Rafinesque: 137 (1840); *Busipho* Salisbury: 76 (1866); *Ptyas* Salisbury: 76 (1866); *Chamaealoe* Berger: 43 (1905); *Leptaloe* Stapf: t. 9300 (1933); *Aloinella* Lemée: 27 (1939) non Cardot: 76 (1909); *Guillauminia* Bertrand: 41 (1956).

2. *Gasteria* Duval: 6 (1809). [cf. Van Jaarsveld (1989)]. *Atevala* Rafinesque: 136 (1840).

3. *Haworthia* Duval: 7 (1809) nom. cons. [cf. Bayer (1982)]. *Catevala* Medikus: 67 (1786) pro parte; *Apicra* Willdenow: 167 (1811) non Haworth: 61 (1819); *Kumaria* Rafinesque: 137 (1840); *Tulista* Rafinesque: 137 (1840).

4. *Lomatophyllum* Willdenow: 166 (1811). [cf. Jacobsen (1986)]. *Phylloma* Ker: t. 1585 (1813).

5. *Chortolirion* Berger: 72 (1908). [cf. Smith (1985)].

6. *Poellnitzia* Uitewaal: 61 (1940). [cf. Smith (1985)].

7. *Astroloba* Uitewaal: 53 (1947a). [cf. Roberts Reinecke (1965)]. *Apicra* Haworth: 61 (1819) non Willdenow: 167 (1811).

The seven genera were considered as units of study [EU's, Evolutionary Units, fide Estabrook (1977)].

Data employed. - The sources of the data used in the cladistic analysis are listed in Table 1. Additional information was obtained from Coetzee and Van der Schijff (1969), Baijnath (1980) and Van der Riet (1977). Nectar sugar composition was analysed by one of us (B-E. van Wyk). The chromosomal data come principally from De Wet (1960), Sharma and Mallick (1966), Jones and Smith (1967), Brandham (1971) and Riley and Majumdar (1979). Sources of distributional information are given in the legends of Figs 3-7.

All characters of a taxon are potentially valuable for inferring evolutionary trends. However, only some of them are strong enough indicators of evolutionary directionality to be useful for cladistic analysis. For the present study the 16 characters listed in Table 2 were used, i.e., all those for which we could confidently assign primitive and advanced states. The basic data matrix is shown in Table 3.

[INSERT TABLE 2 NEAR HERE]

Polarization of character states. - The selection of operational criteria by which to assign primitive (plesiomorphic) and advanced (apomorphic) conditions to character states is one of the most difficult, but critical steps in inferring a phylogeny (cf. Cronquist, 1987). Due to the absence of fossils in the Alooideae and the relatively uniform, bimodal karyotype of its members [x = 7; one long submetacentric, three long acrocentrics and three short acrocentrics; cf. Brandham and Johnson (1977) and Brandham (1983)], the branching patterns of evolution in this group was inferred by evaluating character states in extant taxa for their evolutionary significance. Character state polarization was achieved by reference to a chosen outgroup taxon (in this case the genus *Kniphofia*). Monophyly of *Kniphofia* and the genera of the Alooideae is assumed based on two synapomorphies, namely the tubular perianth (character 7; Table 2) and the fusion of the perianth (character 8; Table 2).

[INSERT TABLE 3 NEAR HERE]

Cladistic method used. - The basic methodology we have followed is that of cladistic or phylogenetic analysis as described by Humphries and Funk (1984) and Linder (1988). The above data matrix (Table 3) was analysed using the 'Hennig86' software package, which is a method for inferring phylogenies under the principle of maximum parsimony.

Results and Discussion

The 16 characters and their states (Table 2) used in the basic data matrix (Table 3) are listed and discussed below.

1. **Habit.** - Subfamily Alooideae includes taxa displaying a wide range of habit, from geophytes (*Chortolirion*), small, highly specialized, rosulate leaf succulents (for example *Aloe* sect. *Aloe* subsect. *Humiles* Berger, *Astroloba*, *Haworthia*), shrubs (for example Complex XI of *Aloe*, viz. shrubby Madagascan species, such as *Aloe acutissima* Perr.) and climbers (*Aloe* sect. *Aloe* subsect. *Prolongatae* Berger series *Macrifoliae* Haw.) to small to large trees (for example *Aloe* sect. *Dracoaloe* Berger). On the basis of Reynolds' (1950a, 1966) keys to *Aloe*, Holland (1978) assumed that the arborescent forms of this genus (comprising ca. 13% of the species) are more advanced than the herbaceous forms. It is noteworthy that Reynolds did not support

this point of view as he interpreted *A. suzannae* R. Decary, the tallest of the Malagasy aloes with a stem length of 3-4 m as the most primitive (Reynolds, 1966). Holland's (1978) assumption is also not borne out by cytogenetic data presented by Brandham (1983), who proposes that the species of *Aloe* with a scandent habit (and usually relatively mesophytic leaves, such as *A. tenuior* Haw.) represents the primitive state. We in large part support the point of view of Brandham (1983) and propose that in the Alooideae as a whole, both small, highly succulent taxa and arborescent forms were derived from a mesophytic, comparatively acaulescent taxon.

Kamstra (1975) also argues that the ancestor of *Aloe* was a small plant, probably some 150 mm high. This assumption is firstly based on the fact that other genera of the subfamily Alooideae contain species of relatively small stature, for example, *Astroloba*, *Chortolirion* and *Haworthia*. Secondly, this is also the case for members of the closely related subfamily Asphodeloideae of the Asphodelaceae [tribe Asphodeleae sensu Hutchinson (1959)] which have achieved a relatively wide Gondwana distribution, for example *Bulbine* which also occurs in Australia (Watson, 1987) and *Bulbinella* with an African-New Zealand distribution (Watson, 1986a,b; Perry, 1987, 1990).

In *Kniphofia* one or two species, such as *K. northiae* Bak., could develop an aerial stem of rarely more than 0,5 m long (Roux, 1985). However, by far the majority of *Kniphofia* species are acaulescent (Codd, 1968). By reference to *Kniphofia* (the outgroup), *Chortolirion*, which has a short vertical axis bearing slightly fleshy leaf bases, are scored as primitive (a reversal). The variable *Aloe* also has a few bulbous species, for example *A. buetnerri* (Jankowitz, 1975) and *A. kniphofioides* Baker (Dyer, 1951). However, more than 90% of species of *Aloe* develop a stem, even if very short [for example *A. juvenna* Brandham & Carter (1979)]. In all other Alooideae taxa, notably *Astroloba*, *Haworthia* subgenus *Hexangulares* Uitewaal ex Bayer, *Lomatophyllum* and *Poellnitzia*, caulescent species occur. *Gasteria* has few caulescent species, *G. rawlinsonii* Oberm. and *G. bicolor* Haw. being exceptions. These species form long, leafy stems instead of basal (rosulate or distichous) rosettes (Obermeyer, 1976). It is noteworthy that the tree or shrub habit has also evolved independently in other monocotyledonous taxa, such as *Yucca* (Agavaceae) (Dahlgren and Clifford, 1982).

While it might be expected that secondary thickening will be linked to plant habit, these are not perfectly correlated in the subfamily Alooideae. Thus, Coetzee and Van der Schijff (1969) have shown that geophytic asphodelaceous taxa, such as *Chortolirion stenophyllum* (Bak.) Berger, *Bulbine coetzeei* Oberm. and *Trachyandra saltii* (Bak.) Oberm. all exhibit secondary thickening. In these taxa its development is, however, much less pronounced than in the well-known arborescent taxa, for example *Aloe* (Cutter, 1975; Esau, 1977). Secondary thickening growth also occurs in *Kniphofia* (Dahlgren et al., 1985). As in the case of the development of the arborescent habit, secondary thickening growth probably evolved independently a number of times in several distinct monocotyledonous families, such as Asphodelaceae (Dahlgren and Rasmussen, 1983), Iridaceae (Manning et al., 1990) and Dracaenaceae (Dahlgren et al., 1985.). Its distribution in the Alooideae is insufficiently known to allow this character to be used as a generic synopomorphy.

2. **Leaf arrangement.** - In general the dorsiventral leaves of most taxa of Alooideae are strongly tufted in terminal (arborescent species) or basal rosettes. The non-succulent leaves of *Kniphofia* are usually densely congested in basal rosettes and arranged in distinct ranks. Furthermore, with the exception of *Aloe* and *Lomatophyllum*, the leaves of most Alooideae taxa are closely compressed, whether arranged on a leafy stem or in a basal rosette. Both *Aloe* and *Lomatophyllum* have species in which the leaves are comparatively widely spaced.

Leaves with a broad lamina would have the disadvantage of shading each other, if concentrated in a tightly packed rosette. However, as discussed by Schönland (1910a), mutual shading can protect plant parts from excessive solar radiation. Thus, the small to miniature, congested, rosulate habit of some Alooideae species would represent an adaptation to successful establishment and survival under harsh environmental conditions (Smith and Correia, 1988). This is substantiated by the fact that leaf shape and size of rosulate species of the New World *Agave*, which are similar in vegetative morphology to most species of Alooideae, are often correlated with the environmental regimes of their native habitats (Nobel and Smith, 1983).

Parallel to this evolutionary line, some species of *Aloe* and *Lomatophyllum* have adapted to microhabitats where lower levels of light could be a limiting factor to plant development. Thus, their leaves are more loosely arranged on a central axis (less shading of leaves). This is illustrated by the occurrence in dry forest in southwestern Madagascar of tree-like species, such as *A. vaombe* Decorse et Poiss. and *A. divaricata* Berger (Rauh, 1977a, 1983) and the general lack of arborescent *Aloe* species from parts of the semi-arid Karoo region of southern Africa (Palmer, 1989). In general desert climates do not favour gigantic growth, some massive cacti and tree aloes (*A. dichotoma* Masson and *A. pillansii* L. Guthrie) being notable exceptions [cf. Jankowitz (1985) and Rebelo et al. (1989)]. With regard to tree aloes it is likely that they developed in a bush zone bordering arid belts (Kamstra, 1975). From such a zone they probably evolved into drought loving species (cf. Baines, 1866) and higher rainfall loving species (cf. Thiselton Dyer, 1874; Reynolds, 1950b). Especially in the juvenile condition the leaves of drought loving tree aloes are shorter and more closely packed (more mutual shading) than those of the tree aloes with a temperate preference (for example *A. bainesii* Th. Dyer).

A further extreme in leaf morphological adaptation in the Alooideae is the occurrence of so-called window-leaved species (Rauh, 1974). Within the Alooideae window-leaved taxa are unique to *Haworthia*. This phenomenon does, however, occur in other families which have species with succulent leaves, such as Mesembryanthemaceae: *Frithia pulchra* N.E. Br. and Piperaceae: *Peperomia columella* Rauh et Hutch. (Krulik, 1980; Simpson and Moore, 1984). Amongst the window-leaved species of *Haworthia*, Hutchison (1951) and Cutler (1985) have distinguished a phylogenetic series of groups with those which have most of the leaf below soil level (leaf tip/window only exposed) being most advanced. It is clear that subterranean succulent plants [including some cacti which utilize inorganic windows (Weisser et al., 1975)], represent a derived line, since they have evolved complex adaptations which allow them to photosynthesize underground.

Two further topics are relevant to this discussion of leaf arrangement in the Alooideae. Firstly, in *Gasteria* a number of species remain distichous throughout their lifecycles. This represents an extension of early developmental phases into maturity (neoteny), a process uncommon in the Alooideae. However, distichous juveniles occur frequently in the Alooideae, a well-known example being *Aloe suprafoliata* Pole Evans. Apart from *Gasteria*, distichous adults are found only in four species of *Aloe* (*A. calcairophylla* Reynolds, *A. compressa* H. Perr., *A. haemanthifolia* Berger et Marloth and *A. plicatilis* (L.) Mill.) and *Haworthia* (*H. truncata* Schonland, a window-leaved species). The significance of neoteny in the evolution of flowering plants in general has been discussed by Takhtajan (1976). He suggested that neotenous forms arise under some kind of environmental stress. This is confirmed by the fact that at least some of the distichous *Gasteria* species [*G. baylissiana* Rauh (1977b) and *G. armstrongii* Schonland (Court, 1981)] are endemic to the eastern Cape Province, which represents a major climatic, topographical and geological transition zone (Smith and Marx, 1990). The compact distichous leaf phyllotaxy encountered in *Gasteria* appears to be a derived condition.

Secondly, an associated variable of phyllotaxy is the angle of divergence of the leaves of an individual specimen (180° in the case of distichy). In the Alooideae the leaves are produced consecutively at the growing point of the plant and are arranged in a continuous spiral about the stem. This spiralisation is easily observed in a number of species, such as *Aloe polyphylla* Schonland ex Pillans (Bolus and Pillans, 1934; Reynolds, 1934), *Haworthia reinwardtii* Haw. and *H. coarctata* Haw. (Bayer, 1973b), *H. limifolia* Marloth (Anonymous, 1975) and in the genera *Astroloba* and *Poellnitzia* (Bayer, 1973b). Although Obermeyer (1967) suggested that phyllotaxy could be taxonomically useful to distinguish between *H. limifolia* and *H. koelmaniorum* Oberm. et Hardy, Bayer (1973b) showed conclusively that the angle of divergence of the leaves from one individual of a species to another is not necessarily constant. This character cannot be used as definitive for species circumscription and it appears to be phylogenetically insignificant.

3. **Leaf consistency.** - The Alooideae is wholly composed of leaf succulents. The succulent leaves of Alooideae taxa represent a character specialization hypothesized to have evolved in response to aridity in combination with fire and other environmental variables such as high levels of irradiance.

Eller et al. (1983) measured the optical properties of a variety of mesophytic and succulent plants from the arid Richtersveld, including *Aloe ramosissima* Pillans. Since succulent leaves function as water stores, the associated presence of large quantities of water storage parenchyma gives rise to low leaf transmittances. Eller et al. (1983) also showed that absorptance in the photosynthetically active spectral band (400-750 nm) by *A. ramosissima* (and other leaf succulents) was lower than that of mesophytic leaves. They propose that these adaptations serve to reduce the radiation load of these plants, since irradiance in the desert would nearly always be high enough to saturate their photosynthetic mechanisms.

Succulent plants often inhabit inhospitable environments where response to high levels of thermal energy could be critical to their survival (Pearson, 1914). The relatively large heat capacity and small area available for heat dissipation can cause the fleshy organs of succulent plants in general to exceed air temperature by between 10 and 30°C (Lewis and Nobel, 1977; Larcher, 1983). Two highly succulent species of Alooideae, namely *Haworthia retusa* (L.) Duv. and *H. turgida* Haw. were shown to have such extreme temperature tolerances (to 1h at -16 and 68°C) (Nobel, 1989). Thus, although these two species of *Haworthia* are usually partially buried, thereby suggesting avoidance of, amongst others, freezing and predation of their water stores (Cutler, 1985), they have evolved mechanisms to ensure survival in habitats subject to high levels of insolation.

Since many species of Alooideae grow in warm, dry habitats and grasslands where the plants are surrounded by fuel (Gibbs Russell, 1987), these species are subject to regular fires. Weisser and Deall (1989) have, however, shown that the succulent-leaved *Aloe petricola* Pole Evans is well adapted to survive moderate fires. In some cases [*A. peglerae* Schonland (Scholes, 1988)] flowering improves in the season following fire, while other species will only flower if subjected to a fire [*A. chortolirioides* Berger (Laubscher, 1973a; Thomas and Goodson, 1986)]. Further adaptations by species of Alooideae to cope with fire are the evolution of a continuous cover of persistent, dead leaves in many arborescent species [*A. ferox* Miller (Bond, 1983)] and a thick corky bark consisting of overlapping, irregular layers [*A. plicatilis* (L.) Miller (Van Jaarsveld, 1987)].

Some taxa of Alooideae which occur in (often high rainfall) grasslands, notably *Aloe* sect. *Graminialoe* Reynolds and *Aloe* sect. *Leptoaloe* Berger (Laubscher, 1973b) and *Chortolirion* have reverted to a less succulent leaf consistency. Most of these species have contractile roots and tend to be geophytic. Unfavourable environmental conditions, such as fires, therefore do not pose a threat to the survival of populations of these species.

4. **Leaf tuberculation.** - The presence of distinctive, white or concolorous tubercles on the leaves of some species of *Astroloba*, *Gasteria* and *Haworthia* is hypothesized to be a derived condition. The rare occurrence of this character in *Aloe* (for example *Aloe aristata* Haw.) is here considered to be a parallel development. The development of this character serves a threefold function. Firstly, it probably evolved in response to herbivore pressure. Especially *Gasteria* leaves are sought after by herbivores (Van Jaarsveld, 1989), since they lack the bitter constituent found in leaves of species of *Aloe* (Watt and Breyer Brandwijk, 1962). The presence of conspicuous, rigid tubercles, often confluent in bands, probably make leaves less palatable and form an effective mechanical defence mechanism. In species of *Gasteria* the leaf tubercles are most prominent in the juvenile condition, the leaves of mature specimens often being smooth, for example *Gasteria acinacifolia* (Jacq.) Haw. In such cases the leaves of mature specimens are usually copiously spotted, thereby effectively camouflaging the plants against herbivores.

Secondly, similar to the reflective function of a surface layer of wax particles or hairs which can increase reflectance from leaves of the leaf succulent *Cotyledon orbiculata* L. by 22% (visible spectrum) and 12% (infrared spectrum) (Sinclair and Thomas, 1970), tubercles are an important adaptation to prevent irradiation and heat damage to underlying tissues in leaves of species of Alooideae. Since the temperature of the tubercles is likely to be lower than the temperature of the rest of the leaf, due to their usually whitish colour and improved convective cooling, they could also serve as foci for dew deposition. Although Schönland (1910b) showed that the succulents *Mesembrianthemum barbatum* L., *Anacampseros filamentosa* Sims and *Crassula cymosa* L. cannot absorb any appreciable quantity of water through their aerial organs, it is here suggested that the tubercles of leaves of species of Alooideae function, amongst others, to improve canalization of water to the root systems of such species.

Thirdly, the tubercles (scattered or confluent) of especially the smaller species of Alooideae (for example *Haworthia attenuata* (Haw.) Haw. in the eastern Cape Province) make them resemble their surroundings (camouflage) and difficult to locate by herbivores.

Leaf tubercles are absent in *Chortolirion*. This monotypic genus occurs mainly in the grassland biome of southern Africa where it grows socially with an abundance of palatable grass species. The lack of herbivore pressure presumably resulted in a loss of leaf tubercles, and it thus appears to be a reversal, back to its ancestral condition. It is noteworthy that leaf tuberculation is a dominant character, as evidenced by first fillial crosses between the smooth-leaved *Haworthia cymbiformis* (Haw.) Duv. and a species with prominent leaf tubercles (*H. attenuata*).

5. **Outline of leaf cross-section.** - In transverse section the non-succulent leaves of species of *Kniphofia* are distinctly keeled (V-shaped), with the exception of some clones of *K. northiae* and *K. stricta* Codd (Codd, 1968; Baijnath, 1980). In contrast, leaves of most species of Alooideae are crescentiform or cymbiform. The latter leaf outline is considered to be a consequence of the development of leaves with a succulent consistency (see 3. above). The crescentiform/cymbiform leaf outline is an obvious adaptation to aridity and represents a synapomorphy for all taxa of Alooideae.

Many species of Alooideae display abaxially on the leaves a usually incomplete, oblique marginiform keel (sensu Van Jaarsveld, 1989), also called a "marginate apex" by Roberts Reinecke (1965). This character is common in *Astroloba*, *Gasteria* and *Poellnitzia*, less frequent in *Haworthia*, rarely encountered in *Aloe* (*A. variegata* L. being a notable exception) and absent in *Chortolirion*. This process is not considered to be homologous with the V-shaped keel in *Kniphofia*. As in the case of leaf tuberculation the often very sharp keel is considered to have evolved in response to herbivory.

6. **Inflorescence compaction.** - In species of Alooideae and *Kniphofia* the inflorescence is a many-flowered spike or a simple or branched raceme. In the Alooideae the inflorescence appears to be axillary but is actually apically (Berger, 1908). Consequently, the stems are monopodial until an inflorescence is formed, after which it becomes sympodial (Obermeyer, 1976). Thus, the rosette bearing an inflorescence does not die after flowering, as it does in *Agave*. In most species of Alooideae and *Kniphofia* flowering progresses from the base of the inflorescences upwards (acropetal). In the case of a few central African species of *Kniphofia* (Reynolds, 1966; Codd, 1968) and *Aloe capitata* Bak., however, flowering proceeds basipetally (Verdoorn, 1970; Glen and Hardy, 1988).

The inflorescences of the majority of species of *Kniphofia*, *Aloe* and *Lomatophyllum* are densely flowered. This contrasts sharply with the other genera of Alooideae where the inflorescences are invariably lax racemes. Densely flowered racemes are hypothesized to be plesiomorphic in the Alooideae and probably evolved in response to a generalist pollination syndrome. Hoffman (1988), for example, showed conclusively that by offering different rewards to different pollinators, *A. ferox* exploits divergent pollinator groups. From a long distance off in their natural habitats the racemes of *Aloe* and *Kniphofia* appear as brightly coloured patches, thereby making them stand out prominently against the often drab background of the semi-arid southern African landscape. The racemes of these genera will therefore lure a variety of potential pollinators.

Although the flowers of both *Gasteria* and *Poellnitzia* are also brightly coloured, the racemes of these taxa are not nearly as dense as those of most species of *Aloe* and *Kniphofia*. The flowers of species of *Astroloba*, *Chortolirion* and *Haworthia* are usually laxly dispersed in a wiry raceme. The flowers of these taxa are fairly inconspicuous and more difficult to locate in their native habitats than those of, for example, *Aloe*. This probably represents an adaptation to a specialized pollination syndrome. The laxly flowered racemes are hypothesized to be the apomorphous condition.

7. **Flower shape.** - Variations in flower structure of the various Alooideae genera are shown in Fig. 1. Even though a few distinct trends in floral structure are evident in the Alooideae (for example towards zygomorphy in *Chortolirion*, *Gasteria* and *Haworthia*), the flowers of all taxa of Alooideae and *Kniphofia* are tubular. The tubular perianth is an excellent reservoir for the copious amounts of nectar that the flowers of most species produce. Furthermore, the dessicating perianth tube serves to guide nectar from the ovary towards the apex where it accumulates in a glistening droplet. This usually coincides with the ripening of the stigma of the protandric flowers and serves as an additional attractant to potential anemophilous pollinators (Mottram, 1977; Van Jaarsveld, 1987).

The perianth (or more correctly perigone) is comprised of six members arranged in two whorls of three each. These six lobes are united into a short or prominent tube, the union being more marked in some genera, such as *Gasteria*. However, with the exception of the monotypes *Chortolirion* and *Poellnitzia* there is considerable intrageneric variation in the size and shape of the tubular flowers. This variation has been used as the basis of the infrageneric classification of *Haworthia* (Uitewaal, 1947b; Bayer, 1971) and *Gasteria* (Van Jaarsveld, 1989). However, in contrast to the variation in floral morphology, Vaikos et al. (1978) have shown that in *Aloe*, *Gasteria* and *Haworthia* the vascular supply to the members of the perianth is remarkably uniform. The tubular flowers of genera of the Alooideae and *Kniphofia* is a strong synapomorphy for these taxa and suggests a close phylogenetic affinity amongst them.

[INSERT FIGURE 1 NEAR HERE]

8. **Fusion of perianth** segments. - The fusion of the petaline tepals is the second character shared by *Kniphofia* and the Alooideae which suggests monophyly. However, this character varies considerably, even within a single genus. In some species of *Aloe*, for example *A. pictifolia* Hardy (1976), the perigone segments are free to the base whereas in other taxa fusion extends almost to the tips of the flowers (*Aloe* sect. *Eualoe* subsect. *Prolongatae* ser. *Macrifoliae*). Yet other species of *Aloe* (for example *A. albiflora* Guill. from Madagascar) are characterised by the absence of a distinct perianth-tube (Mathew, 1974). Although the basic morphology

of the flowers of species of Alooideae is very simple and fairly constant, the occurrence of a number of aberrant floral morphologies have previously lead to the splitting off of monotypic genera from especially *Aloe* (*Aloinella* Lemèe non Cardot; *Guillauminia* Bertr.; *Chamaealoe* Berger). However, all these generic names are currently included in the synonymy of *Aloe*.

9. Flower colour. - Of the Alooideae genera *Aloe*, *Gasteria*, *Lomatophyllum* and *Poellnitzia* all have species with brightly coloured flowers. In these genera and *Kniphofia* the dominating flower colours are red, yellow and orange. Species with bicoloured or even trichromatic flowers are also quite common [*Aloe excelsa* Berger: red and yellow (Leach, 1977); *A. marlothii* Berger: scarlet and greenish cream (Reynolds, 1935); *A. mutabilis* Pillans: red and greenish yellow (Reynolds, 1950a); *Gasteria acinacifolia* (Jacq.) Haw.: pink and whitish green; *G. nitida* (Salm-Dyck) Haw.: reddish pink and yellow (Van Jaarsveld, 1989); *Kniphofia sarmentosa* (Andr.) Kunth: coral and salmon (Codd, 1968)]. As proposed for *Gasteria* (Van Jaarsveld, 1989), those species in the Alooideae as a whole with monochromatic flowers are hypothesized to represent the derived condition. In the Alooideae flower colour appears to be taxonomically insignificant. Within some species of *Aloe* flower colour varies considerably, yellow, orange, pink and red flowering forms of *A. chabaudii* Schonl. having been recorded (Leach, 1977).

In comparison to species of the abovementioned genera, flowers of representatives of *Astroloba*, *Chortolirion* and *Haworthia* are relatively dull-coloured. For these genera the dominant flower colour is white, usually with tinges of green, brown or grey. In contrast, taxa of *Aloe* and *Kniphofia* with green or white flowers are rare, species such as *A. albida* (Stapf) Reynolds, *A. albiflora* Guill. (Verdoorn, 1966), *A. calcairophylla* (Reynolds, 1961), *A. chlorantha* Lavranos (1973), *A. compressa* (Hardy, 1985) and *A. prinslooi* Verdoorn et Hardy (Verdoorn, 1965) being exceptions. It is noteworthy that these species are usually of relatively small stature, as is the case for *Astroloba*, *Chortolirion* and *Haworthia* and the flowers of at least *Aloe albida*, *A. compressa* and *A. prinslooi* bear a superficial similarity to the bilabiate flowers of *Chortolirion* and *Haworthia*. Species of *Haworthia* with brightly coloured flowers are extremely rare, some clones of *H. nortieri* G.G. Smith having golden yellow inner perianth segments (Anonynous, 1974) and some specimens of *H. herbacea* (Mill.) Stearn sensu Bayer (1982) displaying pinkish beige flowers. Homology with the pinks and yellows of the flowers of some species of *Aloe* has not yet been established.

With reference to the outgroup, *Kniphofia*, the general presence in *Astroloba*, *Chortolirion* and *Haworthia* of muted white flowers is hypothesized to be the derived condition.

10. Flower disposition. - At anthesis representatives of the three genera with predominantly whitish flowers, *Astroloba*, *Chortolirion* and *Haworthia*, bear their flowers ascending on vertical peduncles [cf. generic character of *Haworthia* fide Duval (1809) "Calyx petaloideus, rectus, ... "]. For these genera the angle between the pedicel and peduncle is always less than 90° (Fig. 1). At no stage of the development of the flowers or capsules of these taxa are they pendulous. This is hypothesized to be the derived condition which developed in response to a specialised, predominantly entomophilous pollination syndrome.

The floral buds, wilted flowers and capsules of some species of *Aloe*, notably series *Saponariae*, are often borne vertically, but at anthesis the flowers are distinctly pendulous or spreading. The erect capsules which, in the case of most species of Alooideae, are borne on relatively tall inflorescences, suggest an adaptation to wind dispersal of seed (anemochory). This is supported by the fact that the flattish, triangular-elliptical seeds of most species have short (for example *Haworthia* spp.) or prominent (for example *Aloe variegata* L.) papery wings. However, at least at species level in *Aloe* seed morphology appears to be taxonomically insignificant (Kamstra, 1968).

The erect (or pendulous) disposition of flowers at anthesis should not be confused with the secund arrangement of the flowers of, for example *Aloe marlothii*, *A. secundiflora* Engler and *Poellnitzia*. The latter taxa have their flowers vertically disposed on more or less horizontal inflorescence axes. This is a distinct adaptation to bird pollination, the usually robust, horizontal peduncles acting as perches for avian visitors. Since the flowers are borne upright these visitors gain easy access to the nectar reward. In contrast, the secund flowers of some species of *Gasteria* [for example *G. acinacifolia* (Jacq.) Haw. which has a flat-topped panicle] are always borne pendulously. Non-hovering avian visitors therefore either have to lift the flowers with their culmens or have to bend down to reach the nectar.

11. Perianth symmetry. - In general zygomorphy is rare in the Asphodelaceae, floral symmetry in *Kniphofia* and most genera of the Alooideae being more or less regular (Rowley, 1967b; but see Bayer, 1972.). The zygomorphic flowers of *Chortolirion*, *Gasteria* and *Haworthia* were derived from this basic type. However, only *Chortolirion* and *Haworthia* have representatives with bilabiate flowers. This is a strong synapomorphy for these genera. They are distinguished florally from the other genera of Alooideae in that the tips of the perianth segments are obliquely flared to strongly recurved. It is noteworthy that the flowers of subgenus *Robustipedunculares* Uitewaal ex Bayer, the basal group within *Haworthia*, are only weakly zygomorphic.

The flowers of representatives of *Gasteria* (and to a lesser extent those of *Poellnitzia*) show distinct trends towards zygomorphy. The three most noticeable features of the flowers of *Gasteria* are the swollen base of the perianth, the curvature of the terminal portion of the tube and the constriction below the globose gasteriform portion. However, gasterioid flowers are never bilabiate (Fig. 1).

In the majority of species of *Aloe*, *Kniphofia* and *Lomatophyllum* the perianth tube is cylindrical, campanulate or funnel-shaped. *Aloe*, however, has a number of species with ventricose (weakly zygomorphic) flowers [cf. Smith (1990) on *A. bowiea* Schult. et J.H. Schult.]. Very few species of *Aloe* have distinctly zygomorphic flowers, notable exceptions being *A. albida* (Stapf) Reynolds and *A. myriacantha* (Haw.) Schult. et J.H. Schult., both of *Aloe* sect. *Graminialoe* Reynolds. However, the mouths of the flowers of these species are upturned, a character absent from *Haworthia*. Although the background of zygomorphy is not entirely clear, it represents an advanced state derived from the plesiomorphic regular pattern (Dahlgren and Rasmussen, 1983). It is strongly adaptive, being associated with greater selectivity in the type of pollinating agent.

12. Floral fragrance. - The great majority of species of the Alooideae have scentless flowers. In the subfamily floral fragrance is restricted to a small number of species of *Aloe* and *Kniphofia*. The fragrant species of *Kniphofia* all have short, yellow or brownish flowers and form a closely related group (Codd, 1968). The species are *K. brachystachya* (A. Zahlbr.) Codd, *K. parviflora* Kunth, *K. typhoides* Codd and *K. umbrina* Codd.

In contrast to *Kniphofia*, the fragrant species of *Aloe* do not form a coherent group and fragrance is absent in many taxa where one expects it to be present [cf. *A. inconspicua* Plowes (1986)]. With the exception of the southern African *A. modesta* Reynolds, fragrant aloes are restricted to Madagascar (Bornman and Hardy, 1971; Van der Riet, 1977). This lends support to the point of view of Holland (1978) who claims that the ancestral aloes originated in the highlands of south-east Africa some time before the complete sea invasion of the Mocambique Channel in the mid-Cretaceous (100 million years B.P.)[Flores, 1970; McElhinny et al., 1976; but see Croizat (1968) on Madagascan species of *Euphorbia*]. This assumption is borne out by the fact that the species of *Aloe* occurring in Madagascar have no counterparts on the African mainland and vice versa (Reynolds, 1955/1956, 1965), and testifies to an ancient divergence into separate evolutionary paths. Madagascan species of *Aloe* which have fragrant flowers are *A. compressa* (Hardy, 1985), *A. conifera* H. Perr. (Hardy, 1989), *A. cryptoflora* Reynolds, *A. haworthioides* Baker (Hardy, 1988) and *A. suzannae* R. Decary (Popiel and Ellert, 1982). In these species fragrance is very strong during the evening, suggesting nocturnal entomophilous pollination [Hardy (1985, 1989); but see Glass and Foster (1983)]. With reference to the outgroup, *Kniphofia*, the absence of floral fragrance in the Alooideae is scored as derived.

13. Anther position. - Most taxa of Alooideae have bright orange or yellow, dorsifixed, oblong to linear-oblong anthers with introrse dehiscence. At anthesis the anthers of the flowers of the majority of the species of *Kniphofia*, *Aloe* and *Lomatophyllum* are much exserted. In contrast, representatives of *Astroloba*, *Chortolirion*, *Gasteria*, *Haworthia* and *Poellnitzia* have their anthers included in the perianth tube. This distinction is fairly sharp and certainly represents a significant discontinuity between *Kniphofia*, *Aloe* and *Lomatophyllum* and the other genera of Alooideae. It is hypothesized that flowers with included anthers can only be effectively pollinated once a potential pollinator has actively forced its feeding organ (culmen; proboscis) into a fairly narrow perianth tube to reach the nectar reward. In the Alooideae the ultimate in anther inclusion is found in *Poellnitzia* where the flowers do not open except for three narrow slits formed by the connivent perianth tips. This character is an autapomorphy for the genus. In the case of flowers with exserted anthers pollination is possible by casual anemophilous visits or via floral visitors that collect pollen only. With reference to the outgroup anther inclusion is scored as apomorphic and probably represents an adaptation to a specialised pollination syndrome.

14 and 15. Nectar sugars. - Individual flowers of most taxa of *Kniphofia* and Alooideae are nectariferous and last from one to several days. In the subfamily nectar secretion occurs by means of septal nectaries (Schnepf and Pross, 1976). Flower size is correlated with nectar volume, the large-flowered species of *Aloe* producing nectar in much larger quantities than representatives of, for example, *Chortolirion* and *Haworthia* [cf. Beyleveld (1973) on selected species of series *Saponariae* of *Aloe* and Mottram (1977) and Hoffman (1988) on *A. ferox* Mill.]. The nectar of *A. ferox* apparently contains a narcotic compound, as children who suck nectar excessively suffer from persistent weakness of the joints (Watt and Breyer-Brandwijk, 1962; Fox and Norwood Young, 1988).

The sugar composition (glucose, fructose, sucrose) of the nectar of representative samples of *Kniphofia* and all the genera of Alooideae was recently determined. This investigation revealed that sugar composition is remarkably constant within a genus and that three distinct nectar types can be recognised. These are: 1, aloeoid type [present in *Aloe* (including *Chamaealoe*), *Kniphofia*, *Lomatophyllum* and *Poellnitzia* (sucrose virtually absent; fructose and glucose present in more or less equal quantities)], 2, gasterioid type [present in *Gasteria* only (sucrose dominant; fructose and glucose present in more or less equal quantities)] and 3, haworthioid type [present in *Astroloba*, *Chortolirion* and *Haworthia* (sucrose dominant; glucose present in much larger quantities than fructose)]. With reference to the outgroup, sucrose dominance (character 14) and the asymmetrical proportion of fructose and glucose (character 15) are regarded as apomorphous.

16. Base chromosome number. - The majority of species of Alooideae has been investigated cytologically. These studies were initiated early in the 20th century (cf.

Taylor, 1925) and have resulted in an extensive bibliography on the cytology of this group [for reviews see Muller (1941); Riley (1959a, b, c); Brandham (1971, 1983); Riley and Majumdar (1979)]. The Alooideae is one of the most uniform and distinctive groups as regards chromosome number and the markedly bimodal karyotype. All species have the same basic chromosome number (x = 7) which comprise four long and three short chromosomes. In the entire subfamily the basic diploid karyotype (2n = 14) is only very rarely altered (Brandham, 1969). This character represents a synapomorphy for all the taxa of Alooideae. A large number of intra- and intergeneric hybrids have been produced in the Alooideae (Rowley, 1982). This clearly testifies to the close cytogenetical relationship which exists amongst species of the subfamily (Rollins, 1953).

Based on overall genome size and increased bimodality, Brandham (1983) has shown that, at least in *Aloe*, there is a gradation from smaller chromosomes in species which have retained a number of plesiomorphic characters (*A. tenuior* Haw.: actinomorphic flowers; weak scandent stems; mesophytic) to larger ones in species with morphological apomorphies (*A. peckii* Bally et Verdoorn: stemless; extreme xerophyte). This interpretation is largely borne out by the results of Holland's (1978) biogeographical analysis of *Aloe* (but see 1. Habit, above). He proposed that the ancestral aloes originated in the highlands of south-east Africa (see **13. Floral fragrance**, above) and also suggested the existence of eleven secondary centres of speciation for the genus. One of these, the eastern Cape Province, South Africa, is home to the presumably primitive, scandent species of *Aloe*, such as *A. tenuior* and *A. ciliaris* Haw. The latter is the only known autohexaploid in the genus. Although this region is far away from the proposed centre of origin for *Aloe*, *A. ciliaris* has also been discovered in the Turkana desert of northen Kenya, some 3 300 km north of the coastal bush of the eastern Cape (Reynolds, 1950a). Since these plants were discovered far from any settlement, it is unlikely that they escaped from cultivation (Hunt, 1978). If this is the case, the current disjunct distribution of *A. ciliaris* would be indicative of palaeoendemism, the species previously having enjoyed a wider, continuous distribution.

In contrast to the Alooideae, *Kniphofia* has a basic set of six chromosomes (2n = 12). This represents a sharp discontinuity between the two taxa and suggests a distinct barrier to gene interchange (De Wet, 1960). With reference to the outgroup, *Kniphofia*, the haploid chromosome set of n = 7 is scored as apomorphic.

Phylogenetic implications. - To the best of our knowledge no attempt at cladistic analyses of the Alooideae has previously been made and the results of phenetic analyses are inconclusive (see **Introduction** for references). However, it is safe to assume that the subfamily Alooideae as a whole is monophyletic. It is unlikely that the combination of such a distinctive karyotype and the characteristic leaf morphology have arisen more than once. In this regard *Bulbine* (type subfamily of Asphodelaceae) appear to be problematical, since some of its species have karyotypes and morphologies similar to that of certain taxa of Alooideae [cf. Spies and Hardy (1983) on *B. latifolia* (L.f.) Schult. et J.H. Schult. and Rowley (1954) on *Bulbine* in general]. However, *Bulbine* can be clearly distinguished from genera of the Alooideae on the basis of its open, yellow (only very rarely white or orange) flowers (Perry, 1987; Trager, 1984), free perianth segments, bearded filaments, lack of nectar production and the annual nature of some of its species (for example *B. alata* Baijnath). Furthermore, *Bulbine* has an African-Australian distribution whereas the Alooideae is absent from Australia. Mainly for these reasons *Bulbine* was not considered as an outgroup for the Alooideae.

In the present analysis of relationships amongst the genera of Alooideae, an attempt is made to combine all available information amenable to phylogenetic interpretation. These data are expressed as a cladogragm (Fig. 2). Using the "ie" option of 'Hennig86' the data leads to a single, robust cladogram with a consistency index value of 88 and a length of 18 character state changes.

[INSERT FIGURE 2 NEAR HERE]

The genera of Alooideae differ from other Asphodelaceae in their conspicuous succulent leaf consistency, crescentiform or cymbiform leaf outline in cross-section and the markedly bimodal karyotype consisting of 2n = 14 chromosomes. In contrast, leaf succulence is absent in *Kniphofia*, the leaf outline (cross-section) is V-shaped and it has a chromosome base number of 6. However, synapomorphous characters suggesting monophyly and therefore the transferral of *Kniphofia* from the Asphodeloideae to the Alooideae are the tubular flowers and fusion of the perianth segments. We regard these characters as sufficient evidence to justify the choice of *Kniphofia* as outgroup for the Alooideae. Previously *Kniphofia* has been separated from the Alooideae on the basis of, amongst others, differences in the anatomical construction of their leaves (Baijnath, 1980; Dahlgren et al., 1985). Typically the vascular bundles of taxa of Alooideae sensu Dahlgren et al. (1985) have a well-developed cap of thin-walled parenchyma cells at the phloem pole. These are often referred to as aloin cells. In contrast, *Kniphofia* has well-defined fibres present in a cap at both the xylem and phloem poles (Beaumont et al., 1985). The presence of aloin cells varies considerably within and amongst taxa (and sometimes even within a leaf of a single provenance) of the Alooideae and this character is not readily amenable for phylogenetic interpretation. However, the conclusion of Beaumont et al. (1985) that the parenchymatous condition (presence of thin-walled cells rather than schlerenchyma) is derived corroborates our choice of *Kniphofia* as outgroup for (and therefore monophyletic with) the Alooideae.

In the cladogram *Aloe* and *Lomatophyllum* are shown as basal to the rest of the subfamily. In contrast, *Astroloba*, *Chortolirion* and *Haworthia* are the most derived genera, with *Gasteria* and *Poellnitzia* in an intermediate position. The Alooideae line is defined by four apomorphies, one of which (caulescent habit) has a reversal higher up (*Chortolirion*). The controversy that has surrounded generic delimitation in the Alooideae is reflected by the lack of autapomophies for some of the genera upheld in this study. Only *Gasteria* (three distinct apomorphies), *Chortolirion*, *Lomatophyllum* and *Poellnitzia* (one distinct apomorphy each) are reasonably well defined. However, it is noteworthy that three of these genera, *Chortolirion*, *Lomatophyllum* and *Poellnitzia* are notorious for taxonomic confusion. In the past they have been variously combined with and separated from *Aloe*, *Astroloba* and *Haworthia*. Reverting to a Duvalian concept of aloeoid classification in which only three "supergenera", *Aloe*, *Gasteria* and *Haworthia*, are recognized would be inconsistent with our result. Although inclusion of *Astroloba* and *Chortolirion* in *Haworthia* would furnish the genus with at least two apomorphies (characters 11 and 15), such a treatment would not be in accordance with traditional usage within the Alooideae (cf. Smith, 1991) and cognizance would first have to be taken of the infrageneric classification of *Haworthia*.

Geographical considerations. - The approximate geographical distributions of the genera *Aloe*, *Astroloba*, *Chortolirion*, *Gasteria*, *Haworthia*, *Lomatophyllum* and *Poellnitzia* are shown in Figs 3-7. *Aloe* occurs over much of sub-Saharan Africa, ranging from the southern tip of Africa to the Arabian Peninsula. It is also found on Madagascar and Socotra. The distribution of *Kniphofia* is also mainly palaeotropical [Sudano-Angolan and Namib-Karroo Regions of the African Subkingdom, Palaeotropical Kingdom sensu Takhtajan (1969)] and largely overlaps with that of *Aloe*, but the genus is absent from Socotra, Namibia and Botswana (Codd, 1968). The species of *Kniphofia* seem to favour moist habitats and are found mainly along the mountain ranges. In contrast *Aloe* is ecologically heterogeneous within its range of distribution and has diversified into almost every possible habitat, ranging from deserts, grassland and savanna to comparatively high rainfall coastal forest types. In terms of number of species both *Aloe* and *Kniphofia* are presently concentrated in southern Africa. The fleshy-fruited *Lomatophyllum* is restricted to a few of the Mascarene Islands off the south-east coast of Africa.

[INSERT FIGURES 3-7 NEAR HERE]

The distribution patterns of *Astroloba*, *Gasteria* and *Haworthia* are fairly similar. These three genera are endemic to southern Africa and are more of less restricted to the summer-dry semi-arid coastal regions below the inland escarpment of the subcontinent. *Gasteria* and *Haworthia* have outliers in the arid river valleys of Natal, Swaziland and the eastern Transvaal, with a single species of *Haworthia* [*H. venosa* (Lam.) Haw. subsp. *tessellata* (Haw.) Bayer] occurring in the climatically severe central-southern Africa. The distribution of *Astroloba* is more restricted than those of *Gasteria* and *Haworthia* and it is usually found in slightly more arid environments of the Fynbos and Succulent Karoo Biomes of southern Africa. These three genera and *Aloe* have relatively large numbers of species indigenous and endemic to the arid subtropical transitional thickets of the eastern Cape where they show signs of active speciation.

Of the genera of Alooideae, the monotypic *Poellnitzia* has the most restricted distribution. This genus is found only in the Robertson and Bonnievale districts of the south-western Cape Province. In contrast, the other monotype, *Chortolirion*, is widely distributed in the summer rainfall grasslands of southern Africa. The genus does, however, enter the winter rainfall region in southern Namibia.

Conclusion

Available evidence suggests only one obvious generic phylogeny for the Alooideae. It is clear from our result that the inclusion of *Lomatophyllum* in *Aloe* and the inclusion of *Chortolirion* and *Astroloba* in *Haworthia* can be justified, but there can be little doubt about the generic status of *Poellnitzia*. We suggest, however, that the generic concepts as proposed in this study be retained. Pending detailed taxonomic revisions of, particularly *Aloe*, *Haworthia* and *Lomatophyllum*, any reclassification of "groups of species" (fide Funk, 1985) would be premature. As has been shown in the past, such a practice is also not in the best interest of nomenclatural stability.

Infrafamilial phylogeny in the Asphodelaceae is becoming clearer and, as seen here, the inclusion of *Kniphofia* in the type subfamily is decidedly inconsistent with cladistic interpretation; it results in the Asphodeloideae being paraphyletic. We therefore recommend that *Kniphofia* be placed in an enlarged Alooideae. This broadened concept is supported by at least two unique character states not known from other genera of the Asphodeloideae. The transfer of *Kniphofia* to the Alooideae would therefore result in a more natural and consequently more predictive classification.

In support of the slight modifications to the limits of the subfamily Alooideae that have resulted from the present study, we present the following key:

1. Leaves herbaceous, soft, non-succulent, immaculate, lacking distinct spines, in basal rosettes (apically in *Kniphofia northiae*) .... *Kniphofia*
1. Leaves thick, rigid, succulent, maculate, often margined with prickly teeth, in basal or apical rosettes or cauline:
   2. Fruit a berry .... *Lomatophyllum*
   2. Fruit a capsule:

3. Capsule apically acuminate, underground parts bulbous .... *Chortolirion*
3. Capsule apically rounded or obtuse, underground parts rhizomatous (if rarely bulbous then flowers > 10 mm long, regular):
    4. Perianth segments apically connivent .... *Poellnitzia*
    4. Perianth segments apically spreading or recurved:
        5. Flowers pendulous at anthesis, bulbous-based, perianth tube curved upwards .... *Gasteria*
        5. Flowers erect, suberect or spreading at anthesis, perianth tube straight or curved downwards:
            6. Perianth bilabiate .... *Haworthia*
            6. Perianth regular (if rarely bilabiate then flowers > 10 mm long, mouth upturned):
                7. Flowers usually brightly coloured, smooth, fleshy, stamens as long as or longer than the perianth .... *Aloe*
                7. Flowers dull coloured, occasionally with inflated tissue, flimsy, stamens included ...... *Astroloba*

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TABLE 1. Genera of the Asphodelaceae sensu Dahlgren et al. (1985).

Genus	Approximate number of species	Geographical distribution	Data source
		Subfamily Asphodeloideae	
Asphodeline Reichb.	14	Mediterranean, West Asiatic	Tuzlaci (1987)
Asphodelus L.	12	Mediterranean, West Asiatic	Dahlgren et al. (1985)
Bulbine Wolf	60	Southern Africa, Australia	Watson (1986a)
Bulbinella Kunth	16	Southern Africa, New Zealand	Perry (1987)
Bulbinopsis Borzi	–	Congeneric with *Bulbine*	Watson (1986a)
Eremurus Bieb.	35	Central Asia	Dahlgren et al. (1985)
Jodrellia Baijnath	3	Tropical Africa	Baijnath (1978)
Kniphofia Moench	70	Southern and eastern Africa, Madagascar, southern Arabia	Codd (1968); Marais (1973)
Simethis Kunth	1	Western Europe and western Mediterranean	Dahlgren et al. (1985)
Trachyandra Kunth	50	Southern Africa	Obermeyer (1962)
Verinea Pomel	–	Congeneric with *Asphodelus*	Jackson (1895)
		Subfamily Alooideae	
Aloe L.	333	Southern and eastern Africa, Madagascar, southern Arabia	Reynolds (1966, 1982)
Astroloba Uitewaal	7	Southern Africa (Fynbos & Succulent Karoo biomes)	Roberts Reinecke (1965)
Chortolirion Berger	1	Southern Africa (mainly Grassland biome)	Smith (1988)
Gasteria Duval	14	Southern Africa (mainly Fynbos biome)	Van Jaarsveld (1989)
Haworthia Duval	68	Southern Africa (mainly Fynbos biome)	Bayer (1982)
Lomatophyllum Willd.	12	Madagascar, Mauritius	Jacobsen (1986)
Poellnitzia Uitewaal	1	Southern Africa (Succulent Karoo biome)	Smith (1985)

TABLE 2. Postulated transformation series of 16 characters used in constructing the cladogram in Fig. 2.

Number	Character	States recognised
1	Habit	Acaulescent = 0; caulescent = 1
2	Leaf arrangement	Congested = 0; widely spaced = 1
3	Leaf consistency	Mesophytic = 0; succulent = 1
4	Leaf tuberculation	Absent = 0; present = 1
5	Outline of leaf cross-section	V-shaped = 0; crescentiform/cymbiform = 1
6	Inflorescence compaction	Dense = 0; lax = 1
7	Flower shape	Not tubular = 0; tubular = 1
8	Fusion of perianth segments	Free = 0; fused = 1
9	Flower colour	Yellow-red = 0; green-white = 1
10	Flower disposition	Not slanted upwards = 0; slanted upwards = 1
11	Perianth symmetry	Not bilabiate = 0; bilabiate = 1
12	Floral fragrance	Present = 0; absent = 1
13	Anther position	Exserted = 0; included = 1
14	Nectar sugars	Sucrose ± absent = 0; sucrose dominant = 1
15	Nectar sugars	Glucose and fructose ± equal = 0; glucose ≫ fructose = 1
16	Base chromosome number (n)	6 = 0; 7 = 1

TABLE 3. Phylogenetic character states of the genera *Kniphofia* (KNIP), *Aloe* (ALOE), *Astroloba* (ASTR), *Chortolirion* (CHOR), *Gasteria* (GAST), *Haworthia* (HAWO), *Lomatophyllum* (LOMA) and *Poellnitzia* (POEL). Character states are numbered as in Table 2. HYPO = hypothetical ancestor. Character states: 0 = plesiomorphic; 1 = apomorphic; ? = state uncertain, data not available.

	CHARACTER NUMBER															
TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
HYPO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KNIP	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
ALOE	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1
ASTR	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1
CHOR	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
GAST	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1
HAWO	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
LOMA	1	1	1	0	1	0	1	1	0	0	0	?	0	0	0	1
POEL	1	0	1	0	1	1	1	1	0	0	0	1	1	0	0	1

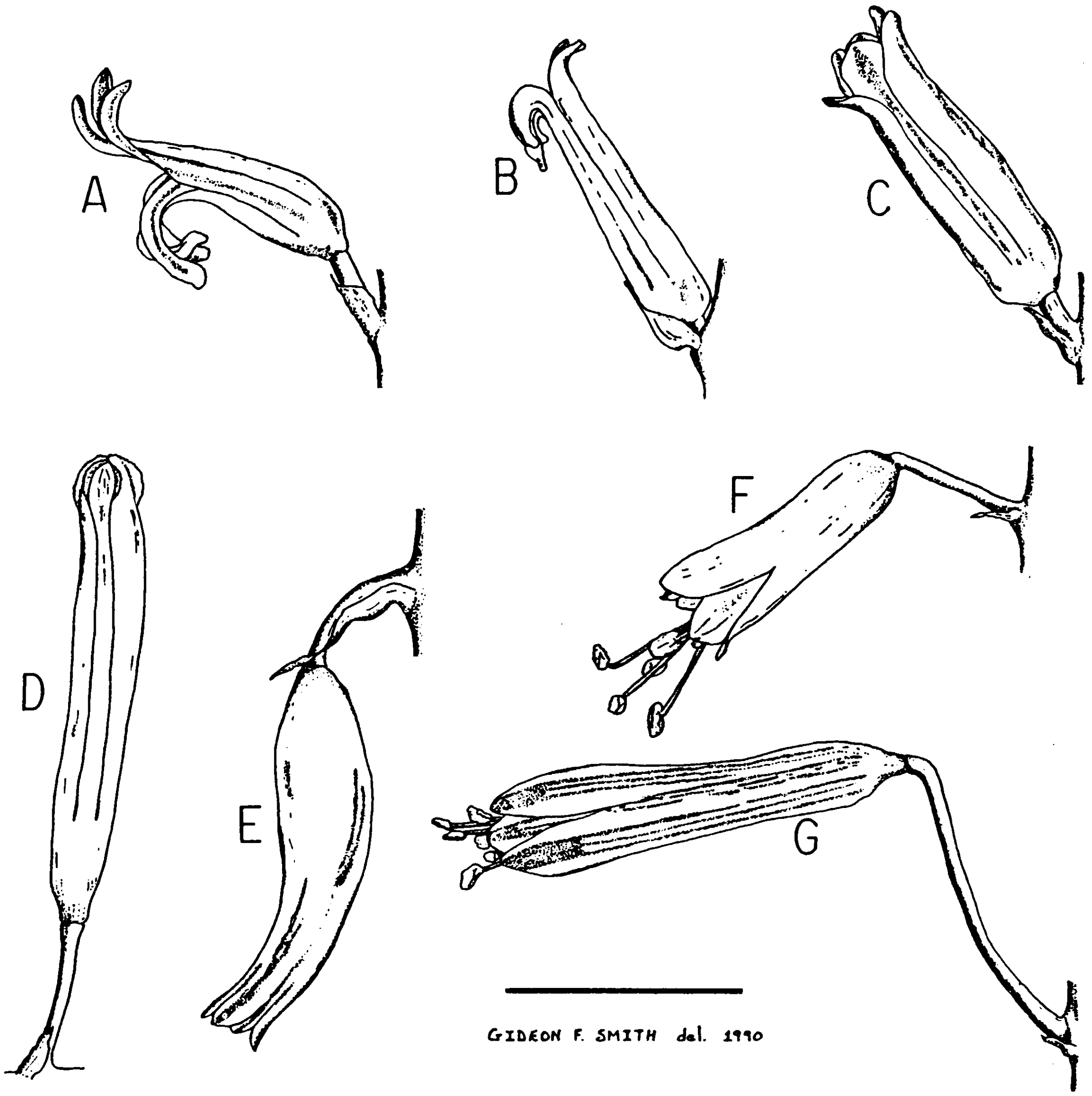

Fig. 1. Flowers from one representative of each of the genera *Aloe* L., *Astroloba* Uitewaal, *Chortolirion* Berger, *Gasteria* Duval, *Haworthia* Duval, *Lomatophyllum* Willd. and *Poellnitzia* Uitewaal as seen in lateral view. With the exception of *Chortolirion* and *Poellnitzia* there are considerable intrageneric variation in the size, shape and disposition of individual flowers. Some of these variations have in the past been split off as monotypes [cf. generic synonymy of *Aloe*, for example, *Chamaealoe*, *Guillauminia*]. The basic perigone structure in the respective genera is, however, fairly constant and is of taxonomic value at generic level. A. *Haworthia gracilis* Von Poellnitz; B. *Chortolirion angolense* (Bak.) Berger; C. *Astroloba foliolosa* (Haworth) Uitewaal; D. *Poellnitzia rubriflora* (L. Bol.) Uitewaal; E. *Gasteria pulchra* (Haworth) Haworth; F. *Aloe tenuior* Haworth var. *rubriflora* Reynolds; G. *Lomatophyllum* cf. *purpureum* (Lam.) Th. Dur. All drawings were made from live material. Scale bar = 5 mm.

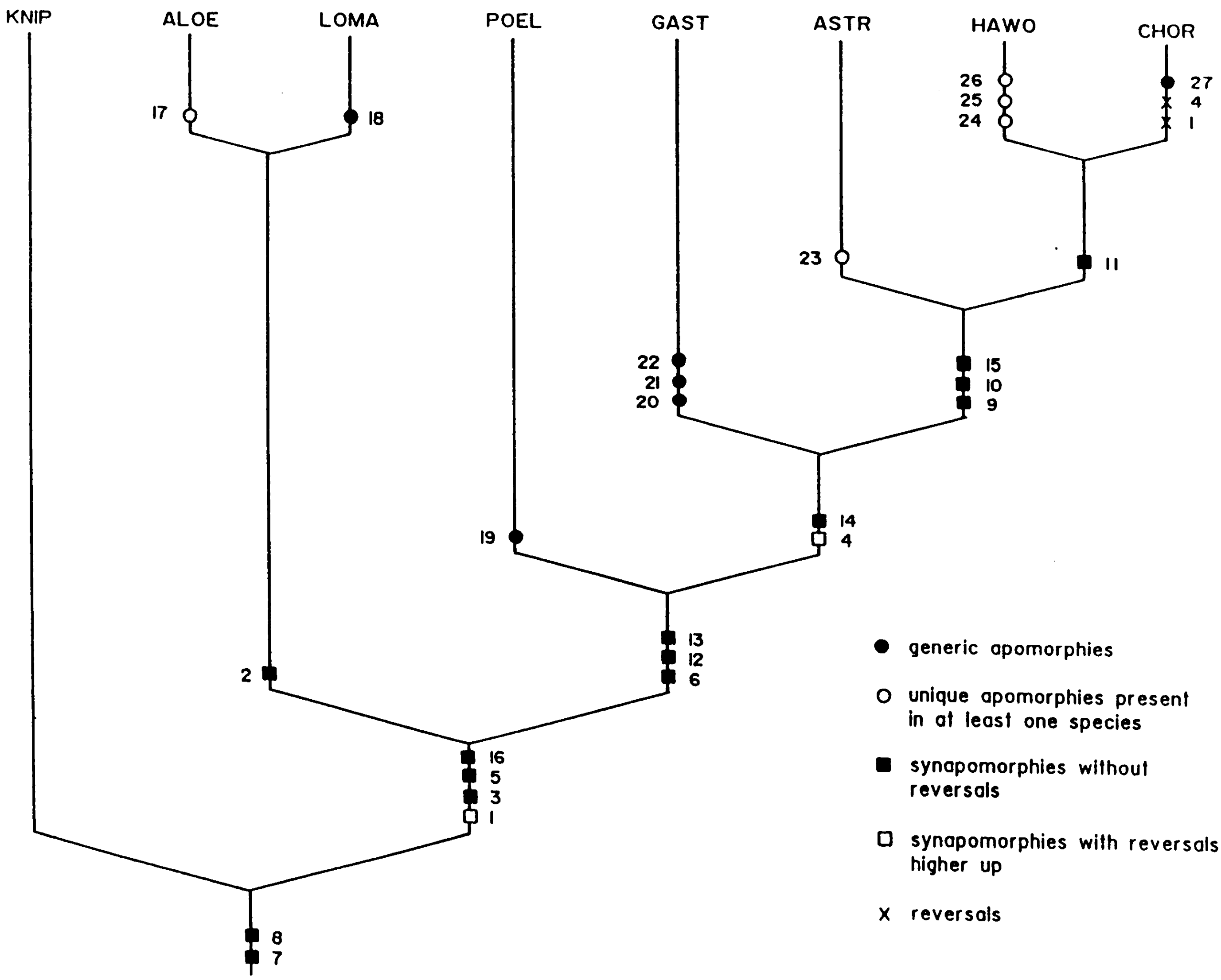

Fig. 2. Cladogram of hypothetical phylogenetic relationships among the genera *Aloe*, *Astroloba*, *Chortolirion*, *Gasteria*, *Haworthia*, *Kniphofia*, *Lomatophyllum* and *Poellnitzia*. Numbers 1-16 refer to characters given in Table 2. Character states and character polarization for the genera are listed in Table 3. Genera are labeled with the first four letters of their names (see Table 3). Generic apomorphies and unique apomorphies present in at least one species of a genus are: 17, flowers tomentose; 18, fruit baccate; 19, tips of perianth segments connivent; 20, pedicels pendulous at anthesis; 21, perianth curved upwards; 22, perianth basally gasteriform; 23, perianth with inflated tissue; 24, leaf tips retuse; 25, leaves with windows; 26, perianth curved downwards; 27, capsule acuminate.

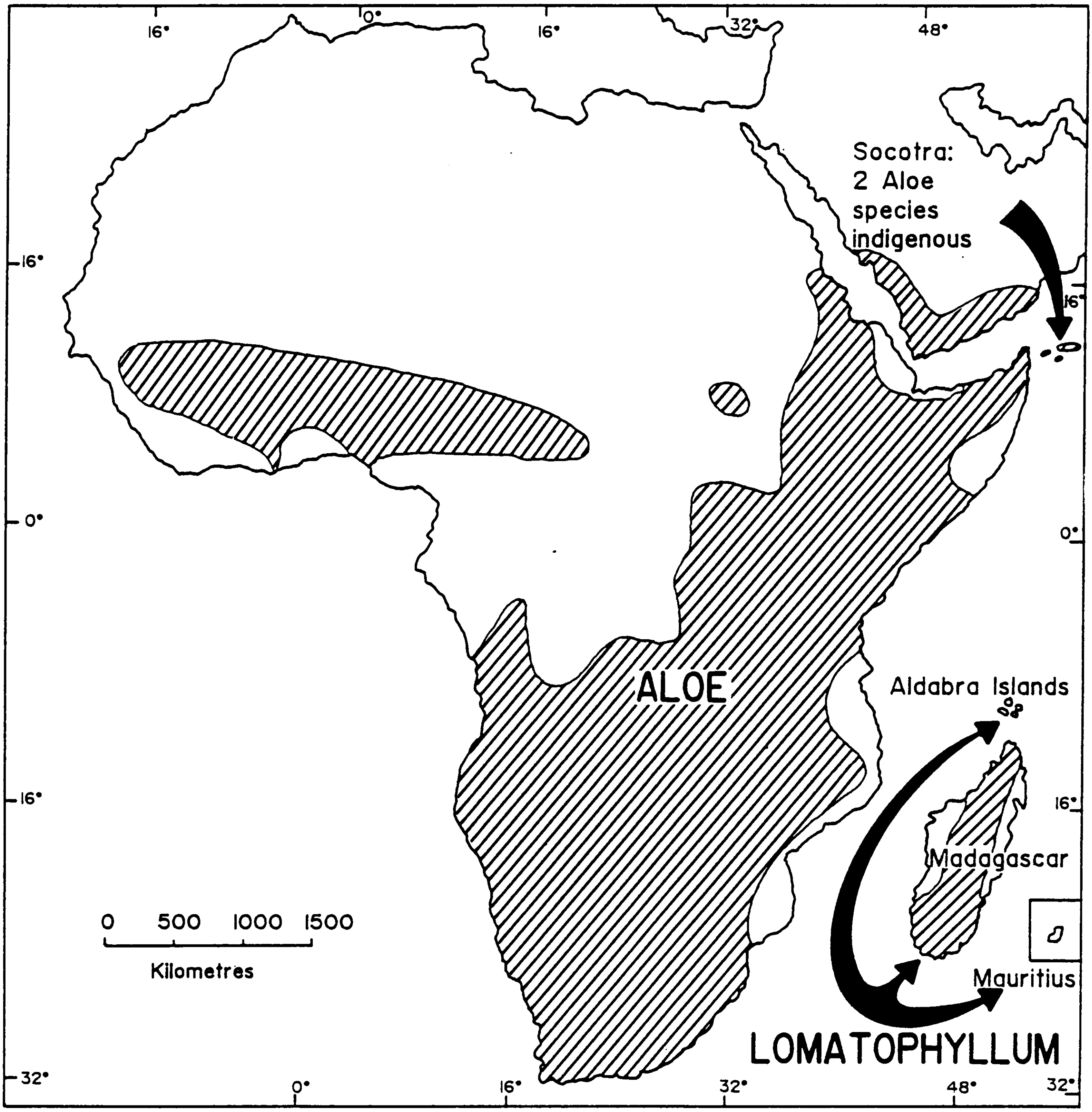

Fig. 3. Approximate geographical distribution of the genera *Aloe* L. and *Lomatophyllum* Willd. [Information for *Aloe* from Reynolds (1950a, 1966), Lavranos (1969) and Wood (1983) and for *Lomatophyllum* from Jacobsen (1986)].

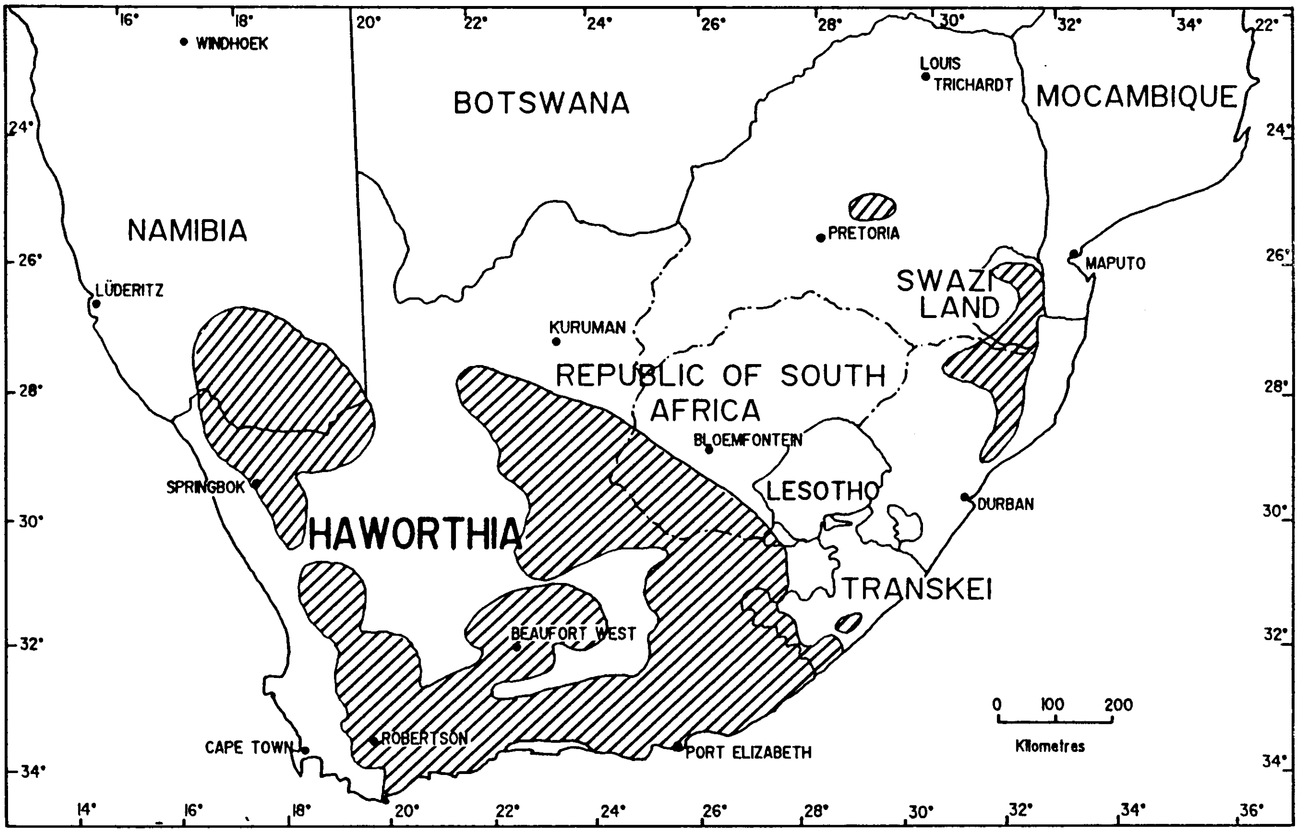

Fig. 4. Approximate geographical distribution of the genus *Haworthia* Duval. [Information from Pilbeam (1983), but see Bayer (1986)].

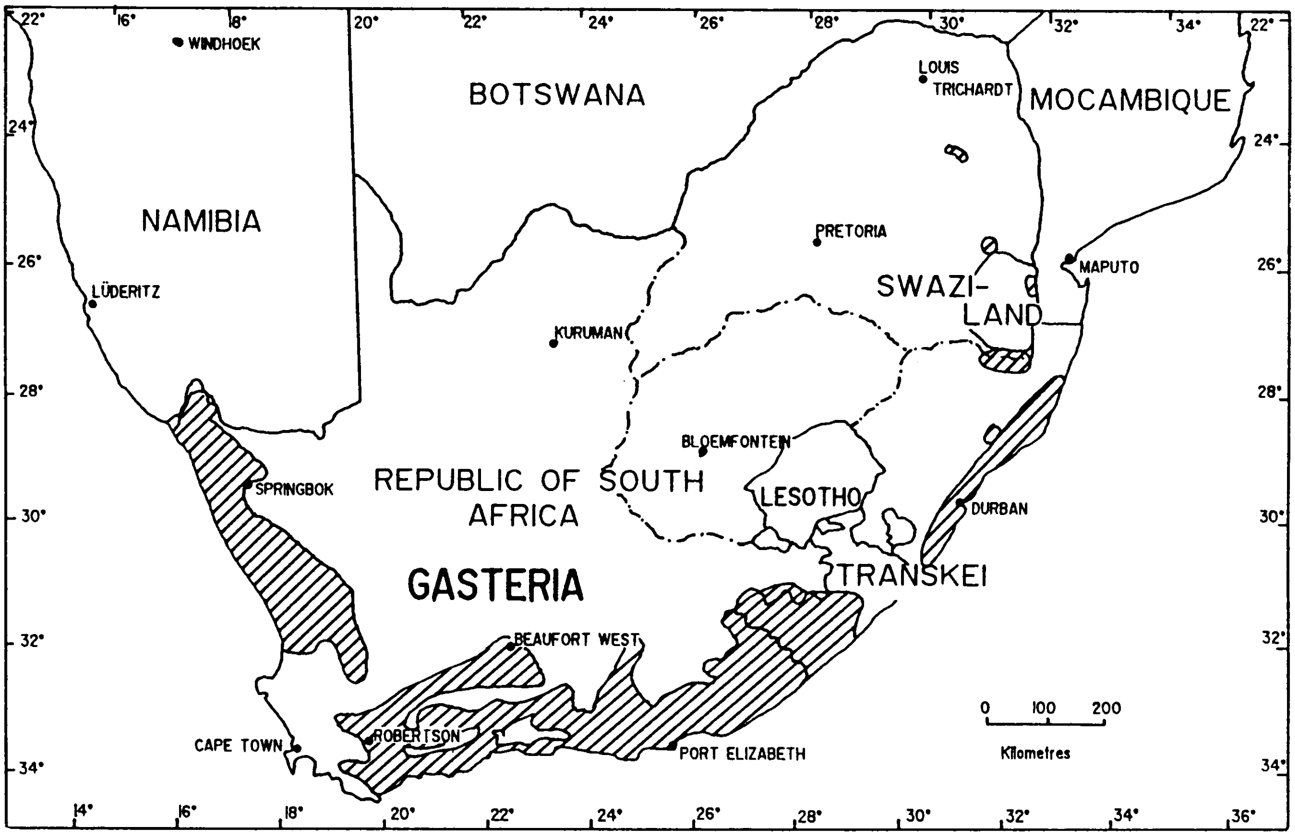

Fig. 5. Approximate geographical distribution of the genus *Gasteria* Duval. [Information from Van Jaarsveld (1989)].

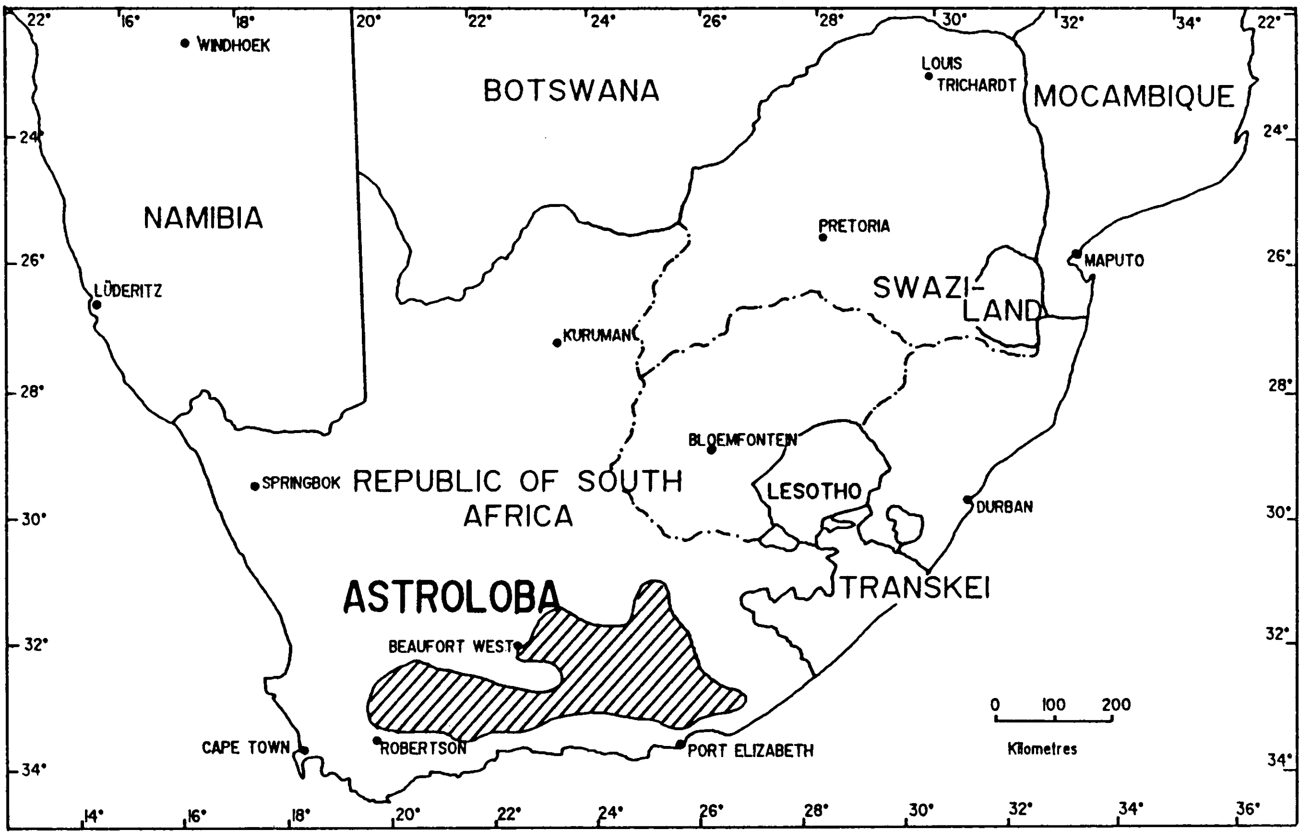

Fig. 6. Approximate geographical distribution of the genus *Astroloba* Uitewaal. [Information from Roberts Reinecke (1965)].

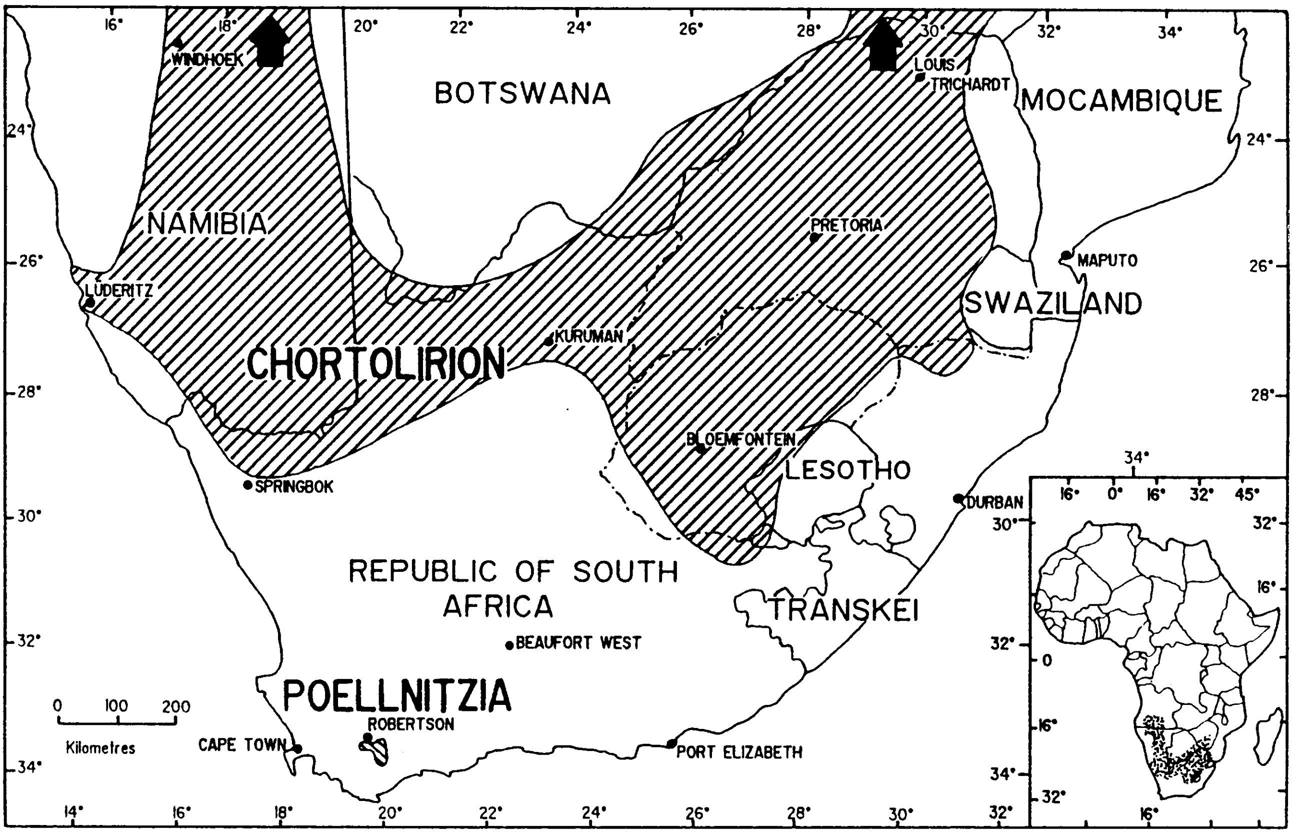

Fig. 7. Approximate geographical distribution of the genera *Chortolirion* Berger and *Poellnitzia* Uitewaal. [Information for both genera from Smith (1985)]. It is not unlikely that *Chortolirion* occurs further north in Botswana and further south in Natal. When not in flower its likeness to a small tuft grass is remarkable and it could easily go undetected in habitat.

CHAPTER 9

AN ENUMERATION OF THE TAXA INCLUDED IN *ALOE BOWIEA* (= *CHAMAEALOE AFRICANA*), *CHORTOLIRION* AND *POELLNITZIA* IN SOUTHERN AFRICA, WITH NOTES ON DIAGNOSTIC CHARACTERS, TYPIFICATION AND SYNONYMY

"Botanical nomenclature, with all its faults, is still the only means of communication between scientists about the identity of plants."

G.E. Gibbs Russell, R.P. Ellis & B. De Winter: 1982

CONTENTS

CHAPTER 9

AN ENUMERATION OF THE TAXA INCLUDED IN *ALOE BOWIEA (= CHAMAEALOE AFRICANA)*, *CHORTOLIRION* AND *POELLNITZIA* IN SOUTHERN AFRICA, WITH NOTES ON DIAGNOSTIC CHARACTERS, TYPIFICATION AND SYNONYMY

9.1 INTRODUCTION

9.1.1 Background

This chapter supplements the outline of the genus concept in the Alooideae as proposed in Chapter 8, especially with regard to *Aloe bowiea* (=*Bowiea africana*, *Chamaealoe africana*), *Chortolirion* and *Poellnitzia*. Its aim is to serve as an introduction to these taxa in anticipation of the generic synopses of *Chortolirion* and *Poellnitzia* which is now in preparation. The taxonomic treatment of *A. bowiea* has been covered in full in Smith (1990d) and Smith & Van Wyk (submitted). To assist in conveying my concept of the taxa, detailed descriptions emphasizing diagnostic features are provided (9.2.5, 9.4.3, 9.5.1). Also included are notes on the correct publication date of *Chamaealoe* [9.2.1; Smith (1990a)], the correct author citations of *A. bowiea* and *A. myriacantha* [9.2.2; Smith (1990b)], and the typification of the names *A. bowiea* [9.2.3; Smith (1990c)] and *C. bergerianum* [9.4.1; Smith (1990f)]. Since *A. myriacantha* was initially described as a species of *Bowiea* Haworth *non* W.H. Harvey *ex* J.D. Hooker (along with *A. bowiea*), this name is also typified [9.3; Smith (1990e)]. Type specimens of all the names included in *A. bowiea*, *Chortolirion* and *Poellnitzia* have been investigated. This was necessary since these taxa have been burdened by major nomenclatural problems. Type localities are given as published by the original author.

The sections of this chapter dealing with *Aloe bowiea*, *Chortolirion* and *Poellnitzia* are in each case concluded with their taxonomic treatments for the *Flora of southern Africa (FSA)*. In the latter instance the "Guide for contributors to *Flora of southern Africa (FSA)*" has been followed (Anonymous 1991). The major findings of the taxonomic investigation of *Chortolirion* is summarized in 9.4.2 (Smith 1990g).

In addition to the representative specimens supplied in this chapter, voucher specimens for most species are listed in many of the papers included in this dissertation. The acronyms for herbaria cited below and elsewhere in the dissertation are those recommended by Holmgren *et al.* (1981).

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NOMENCLATURE

THE CORRECT PUBLICATION DATE OF *CHAMAEALOE* BERGER (ASPHODELACEAE: ALOOIDEAE)

Gideon F. Smith[1]

Summary

In the literature, discrepancies exist with regard to the correct publication date of *Chamaealoe* Berger. The confusion concerns two publications of Alwin Berger which appeared in 1905 in *Engl. Bot. Jahrb.* and in 1908 in *Das Pflanzenreich*, respectively. The former publication has unfortunately been overlooked during recent revisions and this has led to an undesirable variance in citations of title and year of publication appended to the name *Chamaealoe*. It is shown below that *Chamaealoe africana* (Haw.) Berger was validly published in *Engl. Bot. Jahrb.* 36: 43 (28 February 1905).

Introduction

James Bowie, who collected plants at the Cape from 1816–1823, sent specimens of a small aloeoid taxon to Kew where it was received in 1822 and eventually described as *Bowiea africana* (Haworth, 1824). Three years later the protologue of *B. africana* was briefly extended and published along with

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Table 1. Comparison of date and place of publication given by a selection of botanical publications for *Chamaealoe* Berger.

Reference	Place, date of publication of *Chamaealoe* Berger
Berger (1908)	Engl. Bot. Jahrb. 36: 43 (1905)
Marloth (1915)	Das Pflanzenreich 4, 38, 3, 2: 121 (1908)
Stapf (1933)	1905 (Publication not mentioned)
Uitewaal (1947)	Engl. Bot. Jahrb. 36: 43 (1905)
Rowley (1967, 1976)	Engl. Bot. Jahrb. 36: 43 (1905)
Obermeyer (1973)	Das Pflanzenreich 4, 38, 3: 120 (1908)
Dyer (1976)	Das Pflanzenreich 4, 28, 3: 130 (1908)
Farr et al. (1979)	Engl. Bot. Jahrb. 36: 43 (1905)
Court (1981)	1908 (Publication not mentioned)
Reynolds (1982)	Das Pflanzenreich 4, 38, 3: 120 (1908)

the description of a second species of *Bowiea*, namely *B. myriacantha* Haworth (1827). However, Schultes and Schultes (1829) regarded the criteria on which Haworth (1824, 1827) based the genus *Bowiea* as insufficient for affording these two species separate generic status. These authors took the logical step and transferred the species of *Bowiea* Haw. to *Aloe*. Since the specific epithet *africana* had previously been validly published for a distinctive species of *Aloe* (Miller, 1768), *B. africana* was renamed *A. bowiea*. It should be noted that *Bowiea* Harv. ex Hook. f. is currently conserved against *Bowiea* Haw. for another genus of small, bulbous plants (Greuter, 1988). However, Berger (1905) decided that the characteristics of *A. bowiea* Schult. & J. H. Schult. warrant separate generic recognition and he erected the monotypic genus *Chamaealoe* for this species. In his benchmark publication on *Aloe*, Reynolds (1950) accepted Berger's interpretation.

In the literature, discrepancies exist with regard to the correct publication date of *Chamaealoe* Berger (Table 1). The aim of this article is to establish the correct date of valid publication of this monotypic genus. For some years *Chamaealoe* has been included in *Aloe* (Smith, 1983) so that the present proposal may seem academic. However, at some later date it may be decided to once again restore this entity to separate generic status. However, as Farr et al. (1979) justifiably state, the name *Chamaealoe* was superfluous when published. Hence, if the generic concept were revived, a new generic name would have to be given to what has been called *Bowiea* Haw. (*nom. rej.*) and *Chamaealoe* Berger (*nom. illeg.*), unless a proposal to conserve *Chamaealoe* Berger was passed. In such an event, it is important that the correct date and place of publication of *Chamaealoe* be used.

Date and Place of Publication of Chamaealoe

The confusion regarding the correct date and place of publication of the combination *Chamaealoe africana* primarily concerns two publications of Engler to which Berger (1905, 1908) contributed treatments of *Aloe* and related genera. For the following reasons Berger (1905) should be accepted as constituting valid publication of the monotypic *Chamaealoe*: 1) The 1905 article of Berger was effectively published in *Engler's Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie,* 2) the name *C. africana* was accompanied by a diagnosis: "Dahingegen sehe ich in der *Bowiea africana* Haworth oder *Aloë Bowiea* Schultes fil. eine Pflanze, die von den typischen *Aloë* in eben dem Grade abweicht, wie dies bei *Apicra* und *Haworthia* der Fall ist. Die kleinen schmalen Blätter in dichten rasenbildenden Rosetten, der schlanke Blütenschaft mit den kurzen deltoiden Brakteen, die kurz gestielten, aufrecht und entfernt stehenden, weisslichen Blüten mit weit hervorragenden Staubfäden sind Eigentümlichkeiten, die für sie eine gleichberechtigte Stellung zur Seite der beiden ebengenannten Gattungen erheischen. Die bis zum Grunde freien Segmente des Perianths bringen sie jedoch den *Aloë* näher als *Haworthia* und *Apicra,*" 3) apart from the diagnosis Berger (1905) also included a perfectly unambiguous, indirect reference to the previously effectively published description by Haworth (1824) by writing "*Bowiea africana* Haworth," 4) Berger (1905) definitely indicated that the specific epithet *africana* should be used in conjunction with *Chamaealoe* by writing "*Chamaealoe africana* (Haw.) A. Berg.," and 5) Berger, as author, explicitly accepted the combination *C. africana.* This is substantiated by the fact that, in his 1908 treatment of *Chamaealoe,* he quoted his 1905 publication as having constituted valid publication of this combination.

A comparison of those publications which claim erroneously that *Chamaealoe* Berger was validly published on 8 May 1908 in *Das Pflanzenreich* also shows that discrepancies exist concerning the citation of the family number given to the Liliaceae in this publication and the page on which *Chamaealoe* was discussed (Marloth, 1915; Obermeyer, 1973; Dyer, 1976; Reynolds, 1982).

Since *Das Pflanzenreich* was issued in parts over a period of years difficulties have clearly arisen for botanists wishing to cite from separate editions of this work. However, Davis (1957) has published an analysis of *Das Pflanzenreich* in which are listed items of information such as, family and Heft numbers, authors and dates of publication. This guide, which should be consulted by anyone citing from *Das Pflanzenreich*, clearly shows that the Liliaceae tribe Aloineae was treated in Heft 33 and allocated the number IV, 38, III, II. Furthermore, *Chamaealoe* was discussed on pp. 120-122 and not p. 130 as stated by Dyer (1976).

Conclusion

From the above discussion it is clear that for the purposes of uniformity, precision and stability the date and place of publication of *Chamaealoe* should be cited as follows: *Chamaealoe africana* (Haw.) Berger, *Engl. Bot. Jahrb.* 36: 43 (28 February 1905).

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Notes on African plants

VARIOUS AUTHORS

LILIACEAE/ASPHODELACEAE

THE CORRECT AUTHOR CITATIONS OF *ALOE BOWIEA* AND *A. MYRIACANTHA* (ALOOIDEAE)

INTRODUCTION

Available botanical indexes and catalogues indicate a discrepancy regarding the authorship of the names *Aloe bowiea* and *A. myriacantha* (Table 2). These two species were originally described by Haworth (1824, 1827), but in Roemer & Schultes, *Systema vegetabilium*, both were transferred to *Aloe* (Schultes & Schultes 1829).

Monotypic generic status was later suggested for *A. bowiea* as *Chamaealoe africana* (Haw.) Berger (1905) whereas Stapf (1933) transferred *A. myriacantha* to *Leptaloe*. Recently Obermeyer (1973) and Smith (1983) suggested that *C. africana* should best be regarded as a synonym of *Aloe bowiea*. Reynolds (1947) sank *Leptaloe* Stapf under *Aloe* and included *A. myriacantha* in the section *Graminialoe*. The aim of this paper is to establish

TABLE 2.—Comparison of author citations given by a selection of botanical publications for *Aloe bowiea* and *A. myriacantha*, respectively

Reference	Author citation	
	A. bowiea	*A. myriacantha*
Salm-Dyck (1834, 1836)	Schultes	
Kunth (1843)	Roemer & Schultes	Roemer & Schultes
Baker (1880, 1896)	Schultes f.	Roemer & Schultes
Bentham & Hooker (1883)	Schultes	Schultes
Jackson (1895)	Schultes f.*	Schultes f.
Berger (1905)	Schultes f.	Roemer & Schultes
Berger (1908)	Roemer & Schultes	(Haw.) Roemer & Schultes
Reynolds (1947, 1950, 1954, 1966)		(Haw.) Roemer & Schultes
Jacobsen (1954, 1977)	Schultes*	(Haw.) Roemer & Schultes
Bornman & Hardy (1971)		(Haw.) Roemer & Schultes
Obermeyer (1973)	Roemer & Schultes f.	(Haw.) Roemer & Schultes f.
Jeppe (1977)	Roemer & Schultes	(Haw.) Roemer & Schultes
Reynolds (1982)	Roemer & Schultes f.	(Haw.) Roemer & Schultes
Bond & Goldblatt (1984)	Roemer & Schultes**	
Gibbs Russell *et al.* (1985)	Roemer & Schultes	(Haw.) Roemer & Schultes

* *Aloe bowiea* incorrectly listed as an orthographic variant, viz. *Aloe bourea*.
** *A. bowiea* incorrectly listed as an orthographic variant, viz. *Aloe bowieae*.

the correct author citations of *Aloe bowiea* and *A. myriacantha*, respectively.

DISCUSSION

After Linnaeus's death in 1778, the botanical part of the editions of the *Systema naturae* was frequently published in amended form as *Systema vegetabilium* (Stafleu & Cowan 1983). The sixteenth edition of *Systema vegetabilium* was published in seven volumes which appeared in print between 1817 and 1830. Volumes 1–4 were authored by Johann Jakob Roemer (1763–1819) and Josef August Schultes (1773–1831); volumes five and six by J.A. Schultes, except for Umbelliferae (6: 315–628) which is by K.P.J. Sprengel, and special entries which are by other authors; and volume seven by J.A. Schultes and Julius Herman Schultes (1804–1840).

Although Roemer died in 1819, Stafleu & Cowan (1983) justifiably suggest that citation of edition 16 (volumes 1–7) of *Systema vegetabilium* should be to 'Roemer and Schultes, *Syst. veg.*' It is, however, clear that Roemer could not have contributed to nomenclatural or taxonomic changes effected in volume seven of *Syst. veg.* since it was published 10 years after his death. Furthermore, on the title page of volume 7,1, the authors are clearly given as Jos. Augusto Schultes and Jul. Herm. Schultes, Roemer not being mentioned. The preface of this part is also attributed to J.A. and J.H. Schultes only.

However, it is insufficient to refer to J.A. Schultes and J.H. Schultes only when citing authority for taxonomic and nomenclatural changes made in volume seven of *Syst. veg.* J.A.Schultes had two sons who had identical christian names, namely Julius Herman (Stafleu & Cowan 1985) and the use of J.H. Schultes or Schultes fil. only as co-author along with J.A. Schultes is therefore ambiguous and incorrect. These two brothers can be distinguished by birth dates, J.H. Schultes I having lived from 1804 to 1840 and J.H. Schultes II from 1820 to 1887. J.A. Schultes, J.H. Schultes (1804–1840) and J.H. Schultes (1820–1887) are abbreviated as Schult., J.H. Schult. and J.H. Schult. II, respectively (Stafleu & Cowan 1985). Since J.H. Schult. II was only nine years old when *Syst. veg.* 7,1 was published, it is clear that Schult. and J.H. Schult. should be held responsible for new combinations and *nomina nova* which were published in volume seven of *Syst. veg.*

Part one of the latter volume included the treatment of Linnaeus's Class VI Hexandria Monogynia with *Aloe* sensu Linnaeus (1753) being monographed on pp. 631–715. The name *Aloe bowiea* was published here. This species was originally described under the name *Bowiea africana* by Haworth (1824, 1827). The specific epithet *africana* had, however, previously been validly published for a tall-stemmed species of *Aloe* (Miller 1768). For this reason, *B. africana* had to be renamed. *B. myriacantha* Haw., the only other species described in *Bowiea* Haw., was also transferred to *Aloe* in *Syst. veg.* 7,1. Since the specific epithet *myriacantha* had not previously been used in *Aloe*, it was correctly retained. *Aloe bowiea* should therefore be ascribed to Schult. & J.H. Schult. only. In the case of *Aloe myriacantha* the author of the basionym, namely Haworth, should be cited in parentheses followed by Schult. & J.H. Schult., the authors who effected the transfer (Greuter *et al.* 1988, Article 49).

From the above discussion, it is clear that in all the publications listed in Table 2 the author citations of *Aloe bowiea* and *A. myriacantha* are listed incorrectly. These two species should be cited as follows: *Aloe bowiea* Schult. & J.H. Schult.; *Aloe myriacantha* (Haw.) Schult. & J.H. Schult.

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Neotypification of *Aloe bowiea* (Asphodelaceae: Alooideae)

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Aloe bowiea Schult. & J.H. Schult. is neotypified by an unpublished Thomas Duncanson drawing which is kept in K.

Aloe bowiea Schult. & J.H. Schult. word geneotipifiseer deur 'n ongepubliseerde Thomas Duncanson-tekening wat in K gehuisves word.

Keywords: *Aloe bowiea*, Asphodelaceae, typification

ıtroduction

Vhile conducting biosystematic investigations toward a ɜvision of the smaller genera of the subfamily ʌlooideae of the Asphodelaceae (Dahlgren *et al.* 1985) ı southern Africa, I became aware that Haworth (1824, 827) did not cite any specimens when he described *ɔowiea africana* and that this name had never been ɣpified satisfactorily. This species was subsequently ɜnamed as *Aloe bowiea* (Schultes & Schultes 1829), ʼhereas Berger (1905) decided that it warranted recog-ıition as a monotypic genus, namely *Chamaealoe*. Both *ɔ. africana* and *C. africana* are currently included in the ɣnonymy of *A. bowiea* (Smith 1983).

Previous monographs and synoptic works including ɜvisions by Kunth (1843), Baker (1880, 1896) and ɔerger (1905, 1908) have avoided precise type designa-on for the name *B. africana*. Obermeyer (1973) claimed ıat *A. bowiea* is typified by a Bowie specimen kept at ːew. However, she has not seen this specimen which she laims is the holotype. G. Ll. Lucas (pers. comm.) ıdicated that Kew does not possess any *A. bowiea* pecimens deposited by either Haworth or Bowie. ʌlthough Hutchinson (1946) stated that Bowie's pecimens are housed at K and BM, personal visits by ıe present author showed that no Haworth or Bowie pecimens of *A. bowiea* are extant in either of these ıstitutions. The fate of Bowie's considerable botanical ollections are unknown and it is likely that they have erished altogether (Harvey 1838). Obermeyer's (1973) ttempt at typifying the name *Aloe bowiea* with a non-xistent specimen is therefore invalid. Apart from this bortive typification attempt, nowhere in the literature ould any reference to the typification of *Aloe bowiea* be ·aced, from which it was concluded that the name had ever been validly typified. In this paper the author resents the results of his search in an attempt to stablish a type of *A. bowiea*.

'he neotypification of *Aloe bowiea*

ʌccording to the ICBN (Greuter *et al.* 1988; Chapter II, ection 2, Articles 7.1 and 7.2) all taxa of the rank of ɜmily or below must have a nomenclatural type. 'urthermore, Article 7.4 of the same section clearly specifies that if no holotype was indicated by the author who described a taxon, or if the type has been lost or destroyed, a lectotype or, if permissible (Articles 7.9 and 7.10) a neotype, must be designated as a substitute for it. A lectotype is a specimen or illustration selected from the original material to serve as a nomenclatural type (Article 7.5). However, the protologue of *B. africana* does not include any citation of specimens or reference to published or unpublished illustrations or descriptions. In addition, Haworth did not supply his description with illustrations nor did he mention any plant material which he used in establishing this taxon. Therefore, since no 'original material' exists, *A. bowiea* (= *B. africana*) is here neotypified. Since a type must be a specimen or illustration, Haworth's (1824, 1827) description of *B. africana* cannot serve as a lectotype (Greuter *et al.* 1988).

During the late 1700's and early 1800's Adrian Hardy Haworth (19 April 1768 – 24 August 1833) was a leading authority on succulent plants in England. He was especially interested in succulent-leaved, petaloid monocotyledons and fig-marigolds and described numerous new species of amongst others, *Aloe sensu* L. and *Mesembryanthemum sensu* L. (Haworth 1965, Stearn 1971). At the time of his death, Haworth had almost 1 000 succulent plants in cultivation in his collection at Chelsea. Rowley (1951) stated that some of the material cultivated by Haworth had survived to the present day. N.E. Brown of Kew and W.W. Saunders of Reigate played a major role in distributing original Haworth clonotypes to amongst others, John Thomas Bates (1884–1966), another English collector of succulent plants (Roan 1948; Rowley 1985). Although the Bates collection is currently scientifically administered (Roberts 1983), it differs considerably from Bates' original collection and these plants cannot be authenticated as having been the material described by Haworth.

Haworth also assembled a herbarium which was sold to Henry Barron Fielding (1805–1851) of Oxford. Fielding used it for study, but unfortunately threw away most of the specimens (Stafleu & Cowan 1979). Although some of Haworth's specimens are still in the Fielding–Druce Herbarium at the University of Oxford

(Holmgren *et al.* 1981), none of *A. bowiea* (= *B. africana*) which could be designated as type of this name has survived (S.K. Marner pers. comm.). It is also likely that Haworth did not always make herbarium material of the novelties he described.

Haworth was a friend of W.T. Aiton (1766–1849) of Kew and many of the new species which he described originated from this institution. Through this friendship he no doubt received many of the novelties sent to Kew from the then Cape of Good Hope by James Bowie. One of these, a small aloeoid specimen collected in the eastern Cape Province (Smith & van Wyk 1989) was described as *Bowiea africana* (Haworth 1824).

In the same year (1822) that specimens of *A. bowiea* (= *B. africana*) were received at Kew, Thomas Duncanson, a young gardener from the Royal Botanic Garden Edinburgh was appointed as the first artist with the objective of drawing the new and unfigured plants then in the garden at Kew (Hunt 1988). Duncanson had a special talent for drawing plants and from 1822 to 1826 he executed more than 700 drawings, 350 of which are of succulent plants. He unfortunately suffered a mental illness in the summer of 1826 (Daniels 1974). Duncanson's drawings were indexed and numbered in systematic order and the catalogue numbers inscribed on the drawings by Richard Cunningham in 1826–1827 (Hunt 1988).

Of Duncanson's drawings of succulent plants, over 70 are of Alooideae species, one of them being of *Bowiea africana* (G. Ll. Lucas pers. comm.) (Figure 1). This drawing of a fertile specimen bears the number 862 in its right upper corner and an illegible number (704?) in the left upper corner, but is uncatalogued. The name 'Bowiea africana Haw.' is written at the bottom of the drawing and, in the same handwriting (possibly that of Duncanson) a note reading 'Received from Mr. Bowie in the year 1822 from the Cape of Good Hope' has been added. Since Haworth usually wrote 'A.H.' and not 'Haw.' after his name on index cards of the *nomina nova* that he published (Haworth 1965), it is unlikely that he added the latter name and inscription to the drawing. This handwriting also differs from that of James Bowie, the discoverer of *A. bowiea*. Good examples of Bowie's handwriting are included in six unpublished volumes which were his personal diaries and sketch and note books. These books are in the possession of the Mary Gunn Library, National Botanical Institute, Pretoria (Smith & van Wyk 1989). After Schultes & Schultes (1829) transferred *B. africana* to *Aloe*, the name 'Aloe bowiea, Schult. fil.' was attached to the drawing. However, there is no indication that this name is in Haworth's hand and it does not compare favourably with his handwriting as reproduced in Clokie (1964). Although J.A. Schultes, one of the authors who effected the transferral of *B. africana* to *Aloe* as *A. bowiea*, knew Haworth and visited him at Chelsea (Stearn 1971), there is therefore no evidence that Haworth supported the latter taxonomic reclassification. The third and final name which appears on the drawing is 'Chamaealoe africana (Haw.) Berger' and is in the handwriting of G.W. Reynolds. This name which, too, is unsigned, reflects the contemporary classification of this taxon i the first half of the twentieth century.

In many cases drawings of the novelties received a Kew were made before their descriptions were publishe (for example: *A. gracilis* Haw.: drawn 1824, describe 1825; *A. pluridens* Haw.: drawn 1823, described 1824; *A striatula* Haw.: drawn 1824, described 1825 and *Hawor thia altilinea* Haw.: drawn July 1824, described Octobe 1824). It is therefore likely that Haworth had see Duncanson's drawing of *B. africana* before th description of this species was published.

Since the protologue of *B. africana* does not contai any cited specimens, descriptions or illustrations, a typ should be chosen with other factual evidence, (in thi case the description only) as basis. After considering th description and associated circumstantial evidence it wa concluded that Duncanson's undated drawing should b chosen to serve as a neotype of *B. africana* for th following reasons:

1. Duncanson's drawing is conspecific with the specie nowadays known as *A. bowiea* (= *B. africana*) an clearly identifiable with field populations of thi species.
2. This drawing is in accordance with the protologue o *B. africana* (Haworth 1824).
3. Through Haworth's friendship with W.T. Aiton o Kew and because drawings of novelties received a Kew were in many cases made before they wer formally described, it is likely that Haworth had see the drawing prior to the name *B. africana* appearing i print.
4. In the case of succulents, a drawing is often mor 'diagnostic' than a dried specimen, hence the selec tion of a drawing rather than a specimen as neotype

Furthermore, the typification of species names in th Alooideae with iconotypes is not uncommon, name such as *Aloe pumila* L. (*cf.* Heath 1989, 1990), *Alo viscosa* L. and *Aloe disticha* L. having been typified b Commelin plates (Wijnands 1983, 1985). By implication the Duncanson drawing of *B. africana* also typifies th combinations *A. bowiea, C. africana* and *Aloe* L. sect *Graminialoe* Reynolds subsect. *Bowieae* (Haw.) G.F Smith (1990).

The type of *Bowiea africana* therefore is:

South Africa: Cape of Good Hope without precis locality, unpublished drawing by Thomas Duncanson neotype (iconotype), here chosen (K!).

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Figure 1 *Bowiea africana* Haw. at present included in the synonymy of *Aloe bowiea* Schult. & J.H. Schult.: Iconotype. (Reduced photograph of an unpublished painting by Thomas Duncanson at Kew, of James Bowie's material. The inscription reads 'Received from Mr. Bowie in the year 1822 from the Cape of Good Hope'). British Crown Copyright. Reproduced with permission of the Controller, Her (Brittanic) Majesty's Stationery Office, and The Trustees, Royal Botanic Gardens, Kew.

respectively, and to Mms E. Potgieter and B.F. Lategan for supplying copies of scarce publications and illustrations. Permission granted by the Director of K to use copyright material in this article is gratefully acknowledged. This study was partly financed by the Potchefstroom University for Christian Higher Education.

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Nomenclatural notes on the subsection *Bowieae* in *Aloe* (Asphodelaceae: Alooideae)

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A revision of *Chamaealoe* Berger revealed that it should best be regarded as a synonym of *Aloe* L. *A. bowiea* Schult. & J.H. Schult., previously known as *C. africana* (Haw.) Berger, is a distinctive species which shows organographic affinities with *Aloe* sect. *Graminialoe* Reynolds. However, it is clearly distinct from its nearest congeners by the combination of its dense, grass-like rosettes, lax, elongated racemes, shortly pedicellate flowers and much exserted anthers and style. By virtue of these characters the genus *Bowiea* Haw. *non* Harv. ex Hook *f. pro parte quoad A. myriacantha* (Haw.) Schult. & J.H. Schult. is here reinstated as a subsection in the section *Graminialoe*, namely, *Bowieae* (Haw.) G.F. Smith, with *A. bowiea* the only species. This taxon is described, typified and its position in the 'Key to sections, subsections and series' in Reynolds' The aloes of South Africa, is also indicated.

'n Hersiening van *Chamaealoe* Berger het aan die lig gebring dat hierdie genus 'n sinoniem van *Aloe* L. is. *A. bowiea* Schult. & J.H. Schult., voorheen bekend as *C. africana* (Haw.) Berger, is 'n eiesoortige spesie wat organografiese verwantskappe met *Aloe* seksie *Graminialoe* Reynolds toon. Hierdie spesie kan egter duidelik van verwante spesies onderskei word op grond van 'n kombinasie van sy digte, grasagtige rosette, yl, verlengde raseme, kort-gesteelde blomme en uitgestote meeldrade en style. Op grond van hierdie kenmerke word die genus *Bowiea* Haw. *non* Harv. ex Hook. *f. pro parte quoad A. myriacantha* (Haw.) Schult. & J.H. Schult. heringestel as 'n subseksie in die seksie *Graminialoe*, naamlik *Bowieae* (Haw.) G.F. Smith, met *A. bowiea* die enigste spesie. Hierdie takson word beskryf, getipeer en sy posisie in die 'Sleutel tot seksies, subseksies en series' in Reynolds se The aloes of South Africa word bespreek.

Keywords: *Aloe, Bowieae*, nomenclature, taxonomy, typification

Introduction

Modern students of *Aloe* L. owe much credit to Dr G.W. Reynolds who made the study of African and Madagascan aloes his life's work (Reynolds 1950, 1966). Reynolds (1950) recognized 132 southern African species in *Aloe* and arranged these in numerous sections, subsections and series. Towards the completion of his monographs on *Aloe* Reynolds apparently developed a much stricter species concept (Lavranos 1973). However, some of the taxa which he did not regard as warranting specific rank or considered to be separate genera, have since been recognized as good species, for example, *A. meyeri* van Jaarsveld and *A. bowiea* Schult. & J.H. Schult.

To stabilize aloeoid taxonomy and to facilitate the identification of these and other newly discovered species, it is important that they are incorporated in Reynolds' infrageneric key to *Aloe*. This has been done by most of the recent authors of *Aloe* species, for example, Leach (1968, 1971a, b) for *A. tauri, A. cannellii, A. trigonantha, A. esculenta* and *A. inamara*; Giess (1973) for *A. dewinteri*; Hardy (1976) for *A. pictifolia* and van Jaarsveld (1981, 1982, 1985) for *A. meyeri, A. dabenorisana* and *A. komaggasensis*.

The genus *Aloe* in southern Africa is currently being revised by H.F. Glen and D.S. Hardy and it is the contention of the present author that the recognition of distinctive, natural categories will contribute toward a better understanding of relationships within the genus. One such a category is *Aloe* section *Graminialoe* subsection *Bowieae*.

The present paper emanates from a detailed taxonomic study of the smaller genera of the subfamily Alooideae, Asphodelaceae *sensu* Dahlgren *et al.* (1985). This study includes *Chamaelaoe* Berger, which was previously upheld as a monotypic genus, and confirmed that it should best be regarded as a species of *Aloe*. However, the infrageneric classification of *A. bowiea* has not yet been clarified. The aim of this article is to correctly place *A. bowiea* in *Aloe* and for this purpose the *Bowieae* is reinstated at subsectional level in the section *Graminialoe*. This taxon is described, typified and its relationships with closely allied taxa are discussed.

Early history of the *Bowieae*

After Medikus' (1786) abortive subdivision of the heterogeneous *Aloe sensu* Linnaeus (1753), Haworth (1804) produced the first real attempt to divide this genus into smaller, more natural units. Although Haworth (1804) still retained *Aloe* for all the genera of the subfamily Alooideae, he erected the infrageneric *Grandiflorae, Parviflorae* and *Curviflorae* for taxa currently classified in *Aloe, Haworthia* Duval and *Gasteria* Duval, respectively. Five years later Duval (1809) separated *Haworthia* and *Gasteria* from *Aloe* at generic level, thereby giving *Aloe* its current definition. The latter generic arrangement was, however, not universally accepted.

Salm-Dyck (1834), one of the authors who reverted to using the name *Aloe* in the broad Linnaean sense, published a catalogue of the plants which he cultivated in his gardens at Schloss Dyck. Salm-Dyck upheld

Haworth's (1804) *Parviflorae* and *Grandiflorae*, the latter being divided into two categories, respectively defined by 'Tubo recto' (*Aloe*) and 'Tubo curvato' (*Gasteria*). Within the *Parviflorae* he recognized 14 sections, unambiguously designated as such by the statement 'Sectionum characteres' on p. 312 of his Hortus Dyckensis (Salm-Dyck 1834). One of these sections, *Bowieae*, was based on *Bowiea* Haworth (1824), the genus in which *A. bowiea* was originally described as *B. africana*. A second species of *Bowiea*, namely *B. myriacantha*, was subsequently described by Haworth (1827), but two years later both these species were transferred to *Aloe* by Schultes & Schultes (1829).

Salm-Dyck (1834) established *Bowieae* on *A. bowiea* only, *A. myriacantha* apparently having been unavailable to him. In his monumental work on rosulate, petaloid leaf succulents and fig-marigolds, Salm-Dyck (1836) upheld the section *Bowieae* and also suggested that *A. myriacantha* should be included in this section which he regarded as transitional between *Haworthia* and *Aloe*. Kunth (1843) supported the latter point of view whilst Endlicher (1836) and Bentham & Hooker (1883) in their synoptic works simply listed *Bowiea* Haw. as a synonym of *Aloe* L. Baker (1880, 1896) accepted Duval's (1809) subdivision of *Aloe sensu* L. (1753) and replaced the sections proposed by Salm-Dyck (1834, 1836) with subgenera. Baker included both *A. bowiea* and *A. myriacantha* in group 1 *Acaules* of the subgenus *Eualoe*.

Although obviously related and belonging in the same genus, *A. bowiea* and *A. myriacantha* are quite distinct from each other and it is inexplicable why Haworth (1824, 1827) regarded these two species as warranting separate generic recognition in *Bowiea*. This is further illustrated by the fact that generic status was later suggested for both *A. bowiea* and *A. myriacantha* as *Chamaealoe africana* (Haw.) Berger (1905, 1908) and *Leptaloe myriacantha* (Haw.) Stapf (1933), respectively. The genus *Leptaloe* was short-lived, Reynolds (1947) including it in the synonymy of *Aloe*. However, Marloth (1915), Groenewald (1941) and Reynolds (1950, pp. 57–58, 94) upheld the monotypic *Chamaealoe*. Recently Obermeyer (1973) and Smith (1983) again suggested that *C. africana* should best be regarded as a synonym of *A. bowiea* Schult. & J.H. Schult.

Infrageneric affinities and systematic position of subsection *Bowieae*

Although *A. bowiea* shows superficial floral morphological affinities with the section *Anguialoe* Reynolds (Obermeyer 1973; Court 1981), all members of this infrageneric category, with the exception of *Aloe vryheidensis* Groenewald (1936) attain tree-like dimensions (Reynolds 1940; Dyer 1941; von Breitenbach 1986). *A. bowiea* on the other hand is an acaulescent, miniature aloe and does not exceed 130 mm (Figure 1).

In terms of stature and gross morphology, *A. bowiea* is more closely related to the section *Graminialoe*, Reynolds. As in the case of most members of the *Graminialoe, A. bowiea* also possesses relatively short,

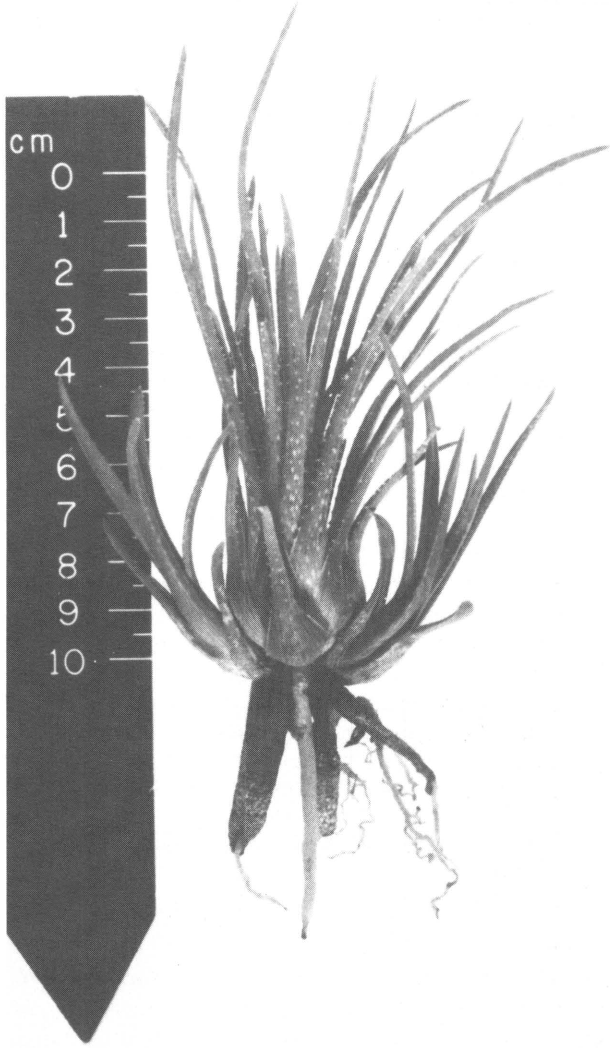

Figure 1 Growth form of *Aloe bowiea* showing dense, grass-like rosettes of narrowly linear leaves and fusiform roots. (Specimen from Coega, eastern Cape Province).

narrowly linear, erect leaves. The leaves of *A. bowiea* are, however, borne in a dense, grass-like rosette (never distichous) and are distinctly succulent. Like all the representatives of the *Graminialoe, A. bowiea* also has fleshy, fusiform roots. However, amongst the grass aloes the floral morphology of *A. bowiea* is unique in that the small, shortly pedicellate, spreading, greenish-white flowers are laxly dispersed in a slender raceme (Figure 2). Furthermore, in all the other species of the section *Graminialoe* the anthers and style are included or very shortly exserted whilst, in contrast, those of *A. bowiea* are always much exserted. Since this species does not fit into existing infrageneric aloeoid categories and to emphasize its aberrant nature, *A. bowiea* is here considered to be best treated as the only species of a monotypic subsection. For this purpose the genus *Bowiea* Haw. is reinstated as *Aloe* sect. *Graminialoe* subsect. *Bowieae* (Haw.) G.F Smith. Outstanding organographic differences between the subsections *Graminialoe* and *Bowieae* are summarized in Table 1.

Table 1 Summary of main organographic distinctions between subsections *Graminialoe* and *Bowieae* (Haw.) G.F. Smith of the section *Graminialoe* Reynolds

	Section Graminialoe	
Character	Subsection *Graminialoe*	Subsection *Bowieae*
Leaves		
number	14–16	18–25
arrangement	distichous or rosulate-multifarious	rosulate-multifarious
Racemes	capitate or conic-capitate; rarely cylindrical	lax, elongate
Flowers		
pedicel length (mm)	lowest > 10; rarely absent	1–2 throughout
anthers and stigma	included or very shortly exserted	much exserted

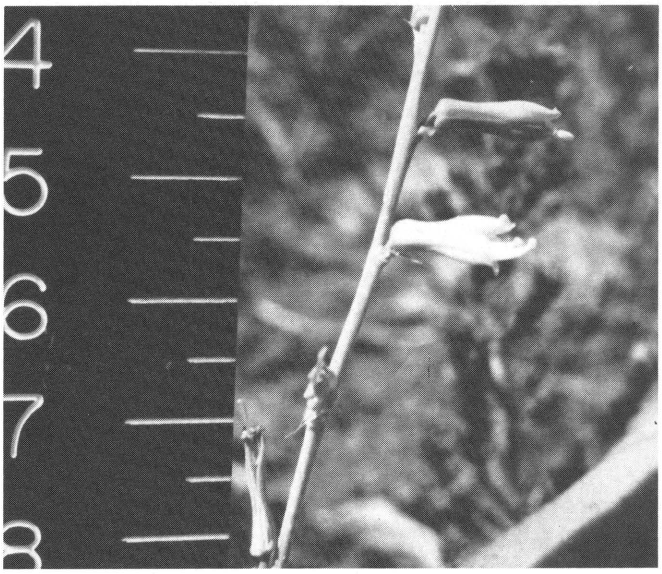

Figure 2 Part of inflorescence of *Aloe bowiea*. Note lax raceme and small, ventricose flowers with anthers and style much exserted. (Specimen from Coega, eastern Cape Province).

Discussion

After the publication of Reynolds' (1950) key to the sections, subsections and series of *Aloe*, two species apparently related to members of the section *Graminialoe*, namely *A. modesta* Reynolds (1956) and *A. inconspicua* Plowes (1986), were described. Both these species appear to be transitional between the sections *Graminialoe* Reynolds (1947) and *Leptoaloe* Berger (1908). *A. bowiea* is, however, clearly distinguished from *A. modesta* and *A. inconspicua* by its lax, elongated racemes and the lack of an underground, ovoid bulb-like swelling. *A. modesta* has densely congested, subcapitate racemes and pedicels shorter than that of *A. bowiea*. *A. inconspicua* has dense, cylindrical racemes and sessile flowers. The underground bulb-like swelling present in *A. modesta* and *A. inconspicua* is more reminiscent of *A. kniphofioides* Bak. of the section *Leptoaloe* Berger.

Although obviously related and monophyletic, these two sections can be readily separated on gross morphology (Bornman 1970; Laubscher 1973a; Jeppe 1977). However, in the case of taxa which have such wide geographical distributions as the *Graminialoe* and *Leptoaloe* (Bornman & Hardy 1971; Laubscher 1973b) the existence of apparent transitional species between and within these sections are to be expected. This clearly points to some of the difficulties surrounding infrageneric aloeoid classification. Furthermore, as Glen & Hardy (1987) justifiably remark, certain of the series which Reynolds (1950) recognized in the section *Eualoe* might well also warrant sectional recognition. These problems of classification in *Aloe* are not restricted to southern African taxa, but also apply to the tropical aloes at all levels of the hierarchy (Lavranos & Newton 1976). *Aloe* is taxonomically complex and the description of new species or infrageneric categories in this genus [or any other Alooideae genus for that matter, *cf.* Bayer (1970, 1972) on *Haworthia*] should be done with great caution.

Nomenclatural notes and description of subsections of *Graminialoe*

Aloe *L.* in Species Plantarum 1: 319 (1753) *pro parte fide* Duval (1809). For generic description and synonymy see Reynolds (1950), Dyer (1976), Webb (1980) and Forster & Clifford (1986).

Aloe section **Graminialoe** *Reynolds* in J. S. Afr. Bot. 13: 104 (1947); Reynolds: 110 (1950); Reynolds: 6 (1966); Jacobsen: 65 (1977). Type species: *A. myriacantha* (Haw.) Schult. & J.H. Schult., designated by Reynolds: 104 (1947).

Genus *Leptaloe* Stapf: t. 9300 (1933).

Description

Plants small, acaulescent. *Roots* fusiform. *Leaves* 4–25, narrowly linear, mostly rosulate-multifarious, sometimes distichous. *Inflorescence* simple. *Peduncle* slender, sterile bracteate in upper two-thirds. *Racemes* capitate, conic-capitate or lax. *Flowers* pedicellate. *Pedicels* 1–2 mm long (subsection *Bowieae*), 10–20 mm long (subsection *Graminialoe*) or rarely absent. *Perianth* 8–20 mm long, basally substipitate, ventricose, the mouth trigonous upturned or bilabiate. *Segments* free. *Anthers* and *style* included, very shortly exserted or much exserted (subsection *Bowieae*).

In southern Africa species of the section *Graminialoe* occur widespread in grassland in the eastern Transvaal, Natal and the eastern Cape Province. The type species, *A. myriacantha* has the second widest geographic distribution of known *Aloe* species, ranging from Grahamstown in the eastern Cape northwards to Kenya and Uganda (a distance of about 5 000 km between the extremes). Other taxa included are: *A. albida* (Stapf)

Reynolds; *A. minima* Bak. var. *minima; A. minima* var. *blyderivierensis* (Groenewald) Reynolds; *A. parviflora* Bak. [probably a synonym of *A. minima; cf.* Addendum I in Reynolds (1982)] and *A. saundersiae* (Reynolds) Reynolds — all confined to southern Africa.

Key to subsections of *Graminialoe*

1a Raceme dense, capitate to conic-capitate (rarely cylindrical); pedicels over 10 mm long (rarely absent); anthers and style included; leaves 4–16 .... **subsection *Graminaloe***

1b Raceme lax, elongate; pedicels 1–2 mm long; anthers and style much exserted; leaves 18–25 .... **subsection *Bowieae***

Section **Graminialoe** *Reynolds* subsection **Graminialoe**

Nomenclature and type as for the section.

Description

Plants small, acaulescent. *Roots* fusiform. *Leaves* 4–16, narrowly linear, mostly rosulate-multifarious, sometimes distichous. *Inflorescence* simple. *Peduncle* slender, sterile bracteate in upper half. *Racemes* capitate or conic-capitate. *Flowers* pedicellate. *Pedicels* 10–20 mm long (rarely absent). *Perianth* 10–20 mm long, basally substipitate, the mouth trigonous upturned or bilabiate. *Segments* free. *Anthers* and *style* included or very shortly exserted.

Section **Graminialoe** *Reynolds* subsection **Bowieae** *(Haw.) G.F. Smith,* comb. et stat. nov.

Type species: *A. bowiea* Schult. & J.H. Schult., here designated.

Genus *Bowiea* Haw.: 299 (1824), 122 (1827) *pro parte quoad A. myriacantha, non* Harv. ex Hook. f. in Hooker: t. 5619 (1867).

Genus *Aloe* section *Bowieae* (Haw.) Salm-Dyck: 313 (1834); Salm-Dyck: Sect. 14, t.1 (1836) *pro parte quoad A. myriacantha*; Kunth: 515 (1843) *pro parte.*

Genus *Chamaealoe* Berger: 43 (1905); Berger: 120 (1908); Jacobsen: 144 (1977).

Description

Plants small, acaulescent. *Roots* fusiform. *Leaves* 18–25, narrowly linear, rosulate-multifarious. *Inflorescence* simple. *Penduncle* slender, sterile bracteate in upper two-thirds. *Racemes* elongate, lax. *Flowers* pedicellate. *Pedicels* 1–2 mm long. *Perianth* 8–15 mm long, basally substipitate, ventricose, the mouth trigonous upturned. *Segments* free. *Anthers* and *style* much exserted (Figures 1–2).

The monotypic subsection *Bowieae* is based on *A. bowiea*, a species previously considered by many authors to be somewhat aberrant within the genus *Aloe*. This rare and endangered plant is endemic to the eastern Cape Province. It is known only from two populations, one in the vicinity of Coega (Figure 3) and the other near Kariega. It recently became extinct at a locality in the neighbourhood of Uitenhage.

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Notes on the pollen morphology and taxonomy of *Aloe bowiea* (Asphodelaceae: Alooideae)

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ABBREVIATED RUNNING TITLE

POLLEN MORPHOLOGY AND TAXONOMY OF *ALOE BOWIEA*

ABSTRACT

The comparative macromorphology and palynology of the monotypic genus Chamaealoe Berger was studied as part of an on-going investigation of generic relationships in the subfamily Alooideae, Asphodelaceae. Pollen morphology was examined using scanning electron microscopy. Pollen grains are free, monosulcate, bilaterally symmetrical, medium in size and have a perforated tectum. Pollen of Chamaealoe is typically aloeoid and the lack of differences in pollen morphology offers additional evidence for the inclusion of the genus in Aloe. Furthermore, no single macromorphological character or combination of characters could be found to be diagnostic at the generic level. Neither vegetative nor reproductive morphology supports the recognition of Chamaealoe as a genus, thereby confirming that C. africana (Haworth) Berger should best be included in the synonymy of Aloe bowiea Schult. & J.H. Schult. An amplified description and the full nomenclatural treatment of A. bowiea are given.

INTRODUCTION

The history of taxonomic work on Aloe L. commenced shortly after Linnaeus (1753) established the genus in his Species Plantarum (see for example Miller 1768). The taxonomy of the taxon started off conservatively as a single genus with nine species and a number of varieties. By 1804 Haworth had recognized the infrageneric heterogeneity of Aloe sensu L. and shortly afterwards Duval (1809) proposed the splitting of the genus into more coherent, natural genera. This process continued for about one-and-a-half century, with the latest additions, Poellnitzia Uitewaal, Astroloba Uitewaal and Guillauminia Bertrand having been described in the 1940's and 1950's (Uitewaal 1940, 1947; Bertrand 1956). This resulted in the unsatisfactory situation where today 27 generic names are available for some 450 species which can easily be accommodated in seven genera.

In recent years taxonomic and biosystematic interest in the subfamily Alooideae, family Asphodelaceae, (Dahlgren et al. 1985), where Aloe and allied genera are classified, have been renewed. Working on cytogenetics and leaf anatomy, respectively, Drs P.E. Brandham and D.F. Cutler, both of the Royal Botanic Gardens, Kew, have, amongst others, played an important part in elucidating patterns of variation within the subfamily. Currently a multidisciplinary project on the systematics of the smaller aloeoid genera is in progress at the Potchefstroom University for Christian Higher Education.

The Alooideae is a fairly large, generally easily recognizable and apparently natural subfamily. Unifying subfamilial characters include the widespread occurrence of secondary thickening growth, leaf succulence, usually tubular petaline flowers, fusion of the perianth segments and a basic diploid karyotype (2n = 14) of four pairs of chromosomes long, and three pairs much shorter. Generic delimitation and species concepts have, however, been the subject of much discussion. This might be due to the fact that, although being a genetically simple group, the Alooideae displays unusual patterns of variation among populations and inconsistent intergradations among species, Haworthia Duval being especially notorious (Bayer 1970, 1971, 1972, 1974, 1982). Furthermore, in most cases the range of variation in individual phenetic traits overlaps.

Among the uncertainties regarding characters of potential diagnostic value, several stand out as warranting additional research. Among these are studies relating to palynology and reproductive biology (Smith 1988, 1991). In the present contribution the scanning electron microscope was used to obtain quantitative and qualitative data on the pollen of Aloe bowiea Schult. & J.H. Schult - a species sometimes treated as a monotypic genus, Chamaealoe Berger (Smith 1990a, b). The principle aim of the study was to examine the taxonomic significance of pollen morphology in a taxonomically controversial unit of the subfamily. Although Smith (1988, 1991) suggested that it is unlikely for palynology to solve classificatory problems in the subfamily, it is unwise to infer this for a taxon, unless a detailed study has been made.

A comparative macromorphological study of Aloe bowiea was conducted in parallel to complement the pollen morphological evidence. The former supplements an earlier contribution on the infrageneric affinities of A. bowiea (Smith 1990a) and was carried out to gain a clearer understanding of its intraspecific variation. Conclusive evidence are presented, showing that those characters previously used for the recognition of Chamaealoe can all be accommodated in the circumscription of Aloe sensu Duval (1809).

Aloe bowiea is endemic to arid parts of the eastern Cape Province (Figure 1). It has a very restricted distribution, and is known from only two localities at present, one in the vicinity of Coega and the other near Kariega. Extensive field work has shown that the species is now extinct at the type locality near Uitenhage. Plants from the latter locality probably survive in cultivation only. Aloe bowiea is ecologically specialized in that it only grows in open areas due to natural breaks in the fairly closed canopy layer of Valley Bushveld vegetation sensu Acocks (1988).

[INSERT FIGURE 1 NEAR HERE]

MATERIALS AND METHODS

Owing to its restricted geographical distribution, small and inconspicuous stature and general scarcity in habitat, only a small number of herbarium accessions are known for Aloe bowiea.

Hence measurements of vegetative and reproductive structures based on herbarium specimens were supplemented by measurements taken from plants in habitat, as well as cultivated plants of known origin grown under uniform conditions in the greenhouse of the Botanical Garden of the Potchefstroom University for Christian Higher Education. The sample sites were selected to reflect the entire geographical distribution range of A. bowiea. These sites were visited regularly over a period of eight years (1983-1990) and measurements were taken from a large number of individuals.

The morphology of the pollen of A. bowiea was investigated using scanning electron microscopy (SEM). Anthers were taken from post-anthesis flowers of material collected in natural habitat and prepared for SEM using the filter technique of Bredenkamp & Hamilton-Attwell (1988) (for details of pollen grain surface) and the osmium tetroxide technique of Smith & Tiedt (1991) (for dimensions, shape, symmetry and aperture features of pollen). Prepared pollen samples were attached to electron microscope stubs using two-sided sticky tape and were subsequently carbon flash evaporated and sputter-coated in an argon atmosphere with gold/palladium (60:40) to a thickness of 3 nm. The samples were studied with a Cambridge Stereoscan 250 S scanning electron microscope operating at about 10 kV, the voltage being adjusted to each preparation. Pollen dimensions were measured from scaled SE micrographs. The descriptive terminology used follows mainly Erdtman (1966, 1969) and the attempts at standardization offered by Reitsma (1970) and Nilsson & Muller (1978). The Smith collections, listed in detail under SPECIMENS EXAMINED, serve as voucher specimens for material included in the palynological investigation.

RESULTS

General

The decision of Berger (1905, 1908) to afford Aloe bowiea separate generic status as Chamaealoe relied heavily upon certain vegetative and reproductive morphological characters which he regarded as irreconcilable with Aloe sensu Duval (1809). The present study has shown that Aloe is polymorphic with respect to the features used by Berger to distinguish A. bowiea as a monotypic genus. These characters are listed in Table 1 and it is shown that none of them is unique to the species, thereby refuting its elevation to generic rank by Berger (1905). To be consistent, many more Aloe segretates would have to be upheld as genera, should Berger´s point of view on the classificaiton of A. bowiea be accepted. This would lead to a large inflation in the number of genera included in the Alooideae and would not be in the best interest of aloeoid taxonomy.

[INSERT TABLE 1 NEAR HERE]

Morphological characters of the leaves (number, arrangement), racemes (shape, density) and flowers (pedicel length, exsertion of anthers and stigma) of Aloe bowiea are useful at the infrageneric level and can be used to discriminate between the species and other members of Aloe sect. Graminialoe Reynolds

(Figures 2 and 3). This investigation therefore confirms Smith's (1990a) earlier reinstatement of Bowieae at subsectional level in Aloe sect. Graminialoe.

[INSERT FIGURES 2 & 3 NEAR HERE]

Pollen morphology

The morphology of pollen grains of Aloe bowiea is basically the same throughout the specimens examined (Figures 4-7). Furthermore, the grains are in most respects morphologically similar to the pollen of other genera of the Alooideae, viz. Chortolirion Berger, Haworthia and Poellnitzia. The following description of A. bowiea pollen includes the entire range of variation for the investigated samples.

Pollen shed as monads. Grains bilaterally symmetrical. Amb elliptical (occasionally pyriform). Grains heteropolar with an inaperturate proximal wall (Figures 4, 6) and a distal, monosulcate aperture (Figure 5). Sulcus well-defined and equal to the dominant equatorial axis. Grain size (dominant axis) varying within fairly narrow limits (35 (41,4) 46 µm) within and between samples. Pollen grain surface perforated by numerous minute micropores (Figures 5-7). Sexine discontinuous and subtectate. Lumina in general circular and less than 0,1 µm in diameter. Muri ca. 0,3 µm wide, smooth. The proximal surface of some grains prepared for SEM by means of the filtering technique displayed a degree of sculpturing superimposed on the perforated sexine (Figure 6).

[INSERT FIGURES 4 - 7 NEAR HERE]

Discussion

The foregoing and contributions by Smith (1990a, b) have illustrated clearly that there is no concensus among previous authors on the generic status of Chamaealoe. This has led to the publication of a number of synonyms for this entity, which provides a misleading reflection of its comparatively uniform, typically aloeoid macromorphology. All its synonyms were created by overseas botanists whom, it appears, often had only a single plant or herbarium specimen at their disposal. In the Alooideae in general scant regard was paid to natural variation and genera were often based on characters which later proved to be insufficient for segregating taxa at any level in a hierarchical classification system. An evaluation of a wide range of morphological characters was carried out with reference to Aloe bowiea (= Chamaealoe). The investigation revealed that none of the characters used by Berger (1905, 1908) as diagnostic for Chamaealoe is unique to the genus. It is therefore concluded that Aloe bowiea does not warrant recognition as a monotypic genus, viz. Chamaealoe.

The pollen of Aloe bowiea specimens examined agrees in general with that described for other genera of the Alooideae. Pollen grains of the species are free, medium in size (dominant equatorial axis), bilaterally symmetrical and heteropolar (monosulcate) with a perforated tectum. No narrow, unsculptured zone bordering the sulcus was observed. The existence of such a zone had previously been reported for pollen of Haworthia (Yuhl & Majumdar 1981). The proximal surface of most pollen grains prepared for SEM using the filtering technique displayed some degree of sculpturing (Figure 6). Due to its inconsistent occurrence this feature does not have any taxonomic significance. The micropores which occur in the pollen grain surface of Aloe bowiea are in general smaller than those of pollen grains of related genera (Smith 1988, 1991). This feature, too, is taxonomically insignificant since pollen of especially Chortolirion often displays extremely small perforations in the pollen grain surface. The mean pollen grain size of A. bowiea is slightly greater than that of related genera. However, the range of grain size of A. bowiea overlaps with that of pollen of Haworthia and Poellnitzia (Erdtman 1966). It is therefore clear that no single pollen morphological character or combination of characters are diagnostic at the specific or generic level.

NOMENCLATURE AND AMPLIFIED DESCRIPTION OF ALOE BOWIEA

Aloe bowiea Schult. & J.H. Schult. in Systema Vegetabilium 7,1: 704 (1829); Salm-Dyck: 14, 313 (1834); Endlicher: 143 (1836); Salm-Dyck: Fasc. 1, t. 24 [Sect. 14, t. 1] (1836); Kunth: 515 (1843); Baker: 158 (1880); Bentham & Hooker: 776 (1883); Baker: 309 (1896); Obermeyer: 119 (1973); Jeppe: 134 (1977); Hardy: 518 (1982); Smith: 10 (1983). Type: SOUTH AFRICA (Cape of Good Hope), without precise locality [probably vicinity of Uitenhage and Algoa Bay (Port Elixabeth), cf. Smith and Van Wyk (1989)], 30 December 1821--26 Febuary 1822, typotype collected by

James Bowie s.n., no material preserved; unpublished drawing by Thomas Duncanson, neotype [iconotype] (K!).

Bowiea africana Haw.: 299 (1824); Haworth: 123 (1827), nom. rej. Type: as for A. bowiea.

Chamaealoe africana (Haw.) Berger: 43 (1905); Berger: 120 (1908); Jacobsen: 348 (1954); Ginns: 57 (1974); Jacobsen: 270 (1974); Rauh: 129 (1979); Court: 174 (1981); Jacobsen: 259 (1986); Innes: 93 (1988), nom illeg. Type: as for A. bowiea.

Aloe bourea Schult. & J.H. Schult. Orthographic variant. Berger: 120 (1908); Jacobsen: 348 (1954); Jacobsen: 270 (1974); Jacobsen: 144 (1977); Jacobsen: 259 (1986).

Aloe bowieae Schult. & J.H. Schult. Orthographic variant. Bond & Goldblatt: 28 (1984).

Icones: Salm-Dyck: Fasc. 1, t. 24 [Sect. 14, t. 1] (1836); Berger: t. 41 (1908); Jacobsen: t. 230, 231 (1954); Lamb: 42 (1960); Jacobsen: t. 257, 258 (1974); Jacobsen: t. 34 (1 & 2)(1977); Jeppe: back of p. 135 (1977); Lamb & Lamb: 802 (1977); Barkhuizen: t. 164 (1978); Rauh: t. 65 (4) (1979); Smith: t. 4 (1983); Jacobsen: t. 257, 258 (1986).

Species excluded

Aloe bowieana Salm-Dyck: Fasc. 5, t. 9 [Sect. 29, t. 3] (1849). A species of Gasteria [G. picta Haw. sensu Stearn (1938); G. bicolor Haw. var. bicolor sensu Van Jaarsveld (1989)] which

Jacobsen (1954, 1974, 1977, 1986) inexplicably placed in the synonymy of A. bowiea.

Herbaceous perennial; acaulescent, with leaves in a basal rosette ± 150 mm in diameter; proliferous from the base and forming closely packed clusters; roots fusiform, up to 10 mm in diameter. Leaves rosulate-multifarious, flaccid, ± 25, dull green to glaucous green, spreading to recurved, the young erect, the old spreading, subulate, narrowly linear, ± 140 mm long, diameter ± 4 mm, dilating and becoming amplexicaul at or below ground level, thickness ± 2 mm; upper surface green with 1--2 centrally positioned white to light green nerves, canaliculate, immaculate or with very few white spots near base; lower surface convex, green with white spots, more copiously spotted near base, the spots tuberculate--subspinulescent; margins armed with firm, white, deltoid or recurved teeth, ± 1 mm long, larger low down, smaller and becoming obsolescent upwards, 4--5 mm distant throughout. Inflorescence up to 410 mm tall; peduncle simple, diameter ± 2 mm, up to 280 mm long, sterile bracteate in upper two-thirds, sterile bracts membranous, caudate, abruptly long acuminate, ± 6 mm long, erect, keeled with a yellowish vein; raceme elongate, lax, up to 130 mm long, 20 mm wide, ± 20 spirally arranged flowers and buds, 3--4 open simultaneously; floral bracts membranous, 5 mm long, cuspidate, keeled, clasping the pedicels, longer than the pedicels; pedicels erect to slightly recurved, persistent, dull green, 1--2 mm long throughout, diameter 1 mm. Flowers sub-erect, slightly zygomorphic, greenish-white, basally substipitate; perianth cylindric-trigonous, ventricose, narrowing slightly at the mouth, the mouth trigonous upturned, tube slightly constricted 3 mm from the base, 8--15 mm long, ± 5 mm across; outer segments free to base, with sub-acute apices, greenish-white, 1 broad, green nerve from base to apex; inner segments free, broader than the outer, greenish-white, 1 narrow green nerve from base to apex, apices more obtuse, tips very slightly flared; bud narrow, straight, slightly up-curved at tip; stamens 6 usually of unequal length; filaments white, filiform-flattened, longer than perianth; anthers bright yellow, exserted 2--4 mm; ovary olive green, 3 mm long, diameter 2 mm, finely 6-grooved; style light green, straight, capitate, up to 13 mm long, much exserted. Fruit trilocular capsule, cylindric, apically retuse, dull glaucous green, up to 12 mm long, diameter 4 mm. Seed light brownish-grey, angled, shortly winged, 3 mm long. Chromosome number: 2n = 14 (Brandham 1969, 1971). Figure 8.

Flowering asynchronous throughout the year with a peak during the summer months, December to March (southern hemisphere).

[INSERT FIGURE 8 NEAR HERE]

SPECIMENS EXAMINED

The localities of the collections are listed according to the grid reference system of Leistner & Morris (1976). The abbreviations of herbarium names are according to Holmgren et al. (1981).

SOUTH AFRICA, CAPE PROVINCE. -- 3325 (Port Elizabeth): 5 km from Uitenhage (-CD), Reynolds 1206 (PRE); the farm "Jachtvlakte" between Uitenhage and Despatch, 4 km from Uitenhage, Smith 1 (PEU, PUC); Despatch railway station, Hardy 2184 (PRE); the farm "Zwartkoppen" near Coega (-DC), Smith 160 (PUC); Maasward Private Nature Reserve near Coega, Smith 4, Smith 173 (PUC).

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TABLE 1: Morphological features used by Berger (1905, 1908) to establish the monotypic genus, _Chamaealoe_. A selection of taxa of _Aloe_ which share the respective characters are listed in the second column.

Characters used as diagnostic for _Chamaealoe_ (Berger 1905, 1908)	Species and infrageneric taxa of _Aloe_ sharing the characters
Dense, grass-like rosettes	Section _Leptoaloe_ Berger
Small, narrowly linear leaves (Figure 2)	Section _Graminialoe_; dwarf Madagascan species
Slender, lax inflorescence	Dwarf Madagascan species
Small, greenish-white flowers	_A. inconspicua_ Plowes
Subsessile flowers	_A. modesta_ Reynolds
Free perianth segments	_A. pictifolia_ Hardy
Exserted filaments (Figure 3)	Widespread in _Aloe_, but usually not as prominent as in _A. bowiea_

CAPTIONS TO FIGURES

FIGURE 1: Location of populations of Aloe bowiea (*) investigated in this study. The three localities shown are the only ones known for the species.

FIGURE 2: Growth form of Aloe bowiea showing rosette of small, linear leaves. Photograph taken in habitat near Kariega. Diameter of lens cover = 50 mm.

FIGURE 3: Aloe bowiea bears a laxly-flowered raceme with small, subsessile flowers. The anthers and style are much exserted. Specimen from Coega.

FIGURES 4-7: Scanning electron micrographs of pollen of Aloe bowiea. (4) Group of pollen grains showing uniform symmetry and aperture shape and length within a sample. (5) Distal face showing elongated aperture (sulcus). (6) Proximal surface displaying some degree of sculpturing. (7) Detail of tectum surface in the apertural region showing minute perforations and smooth muri. Figure 4 from Smith 173, prepared for SEM using the osmium tetroxide technique; Figures 5 and 7 from Smith 4 and Figure 6 from Smith 160, all prepared for SEM using the filtering technique. Scale bar = 20 µm in Figure 4; 5 µm in Figures 5 and 6 and 1 µm in Figure 7.

FIGURE 8: Aloe bowiea Schult. & J.H. Schult. A. Habit; B. Single flower in lateral view, showing the position of the peduncle and bract; C. Fruit, trilocular capsule. All drawings were made from live material of Smith 4. Scale line = 50 mm in Figure 8A and 5 mm in Figures 8B and 8C.

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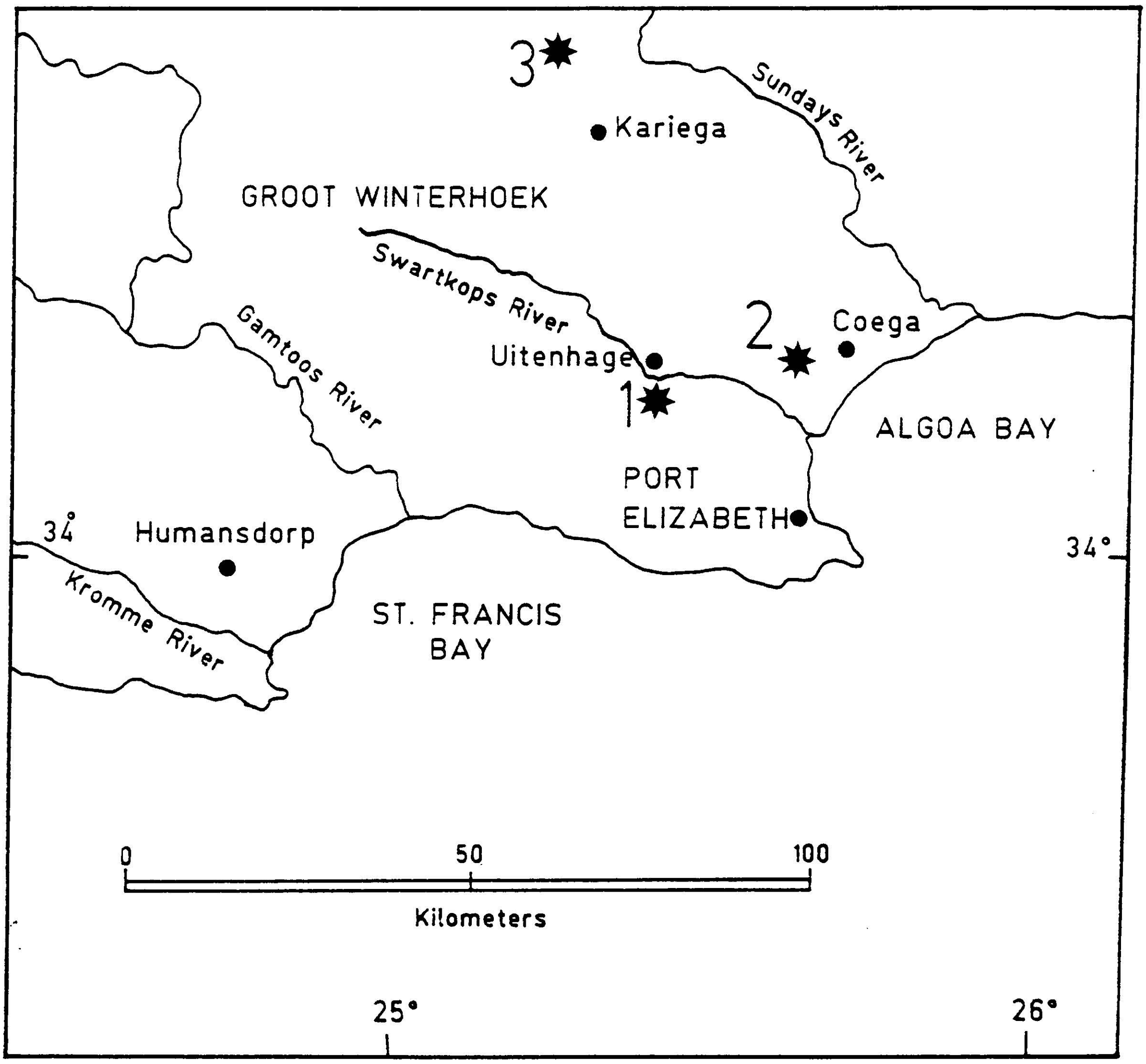
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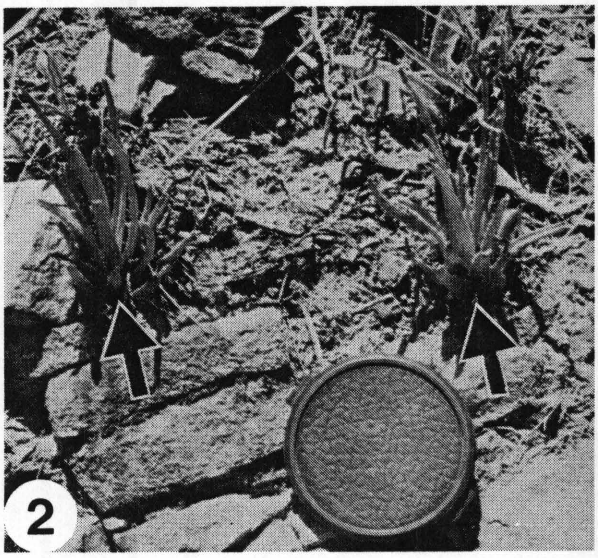
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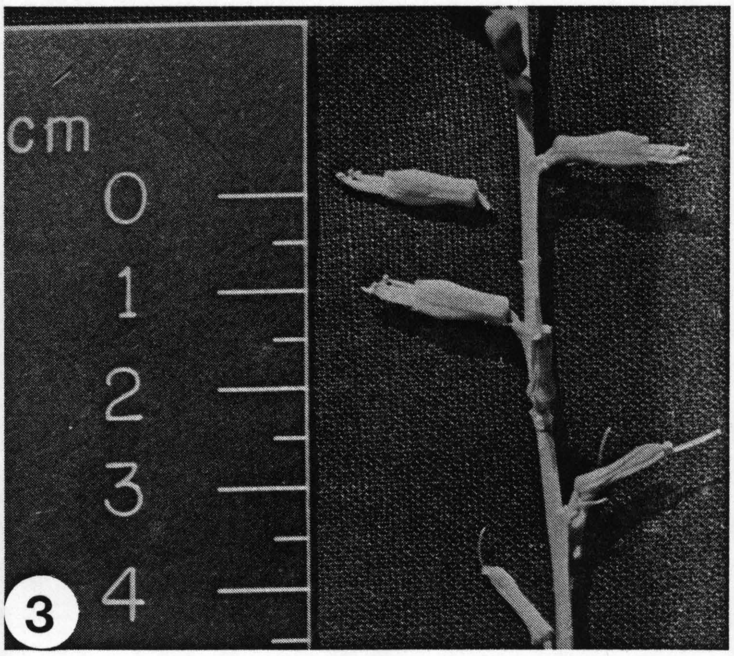
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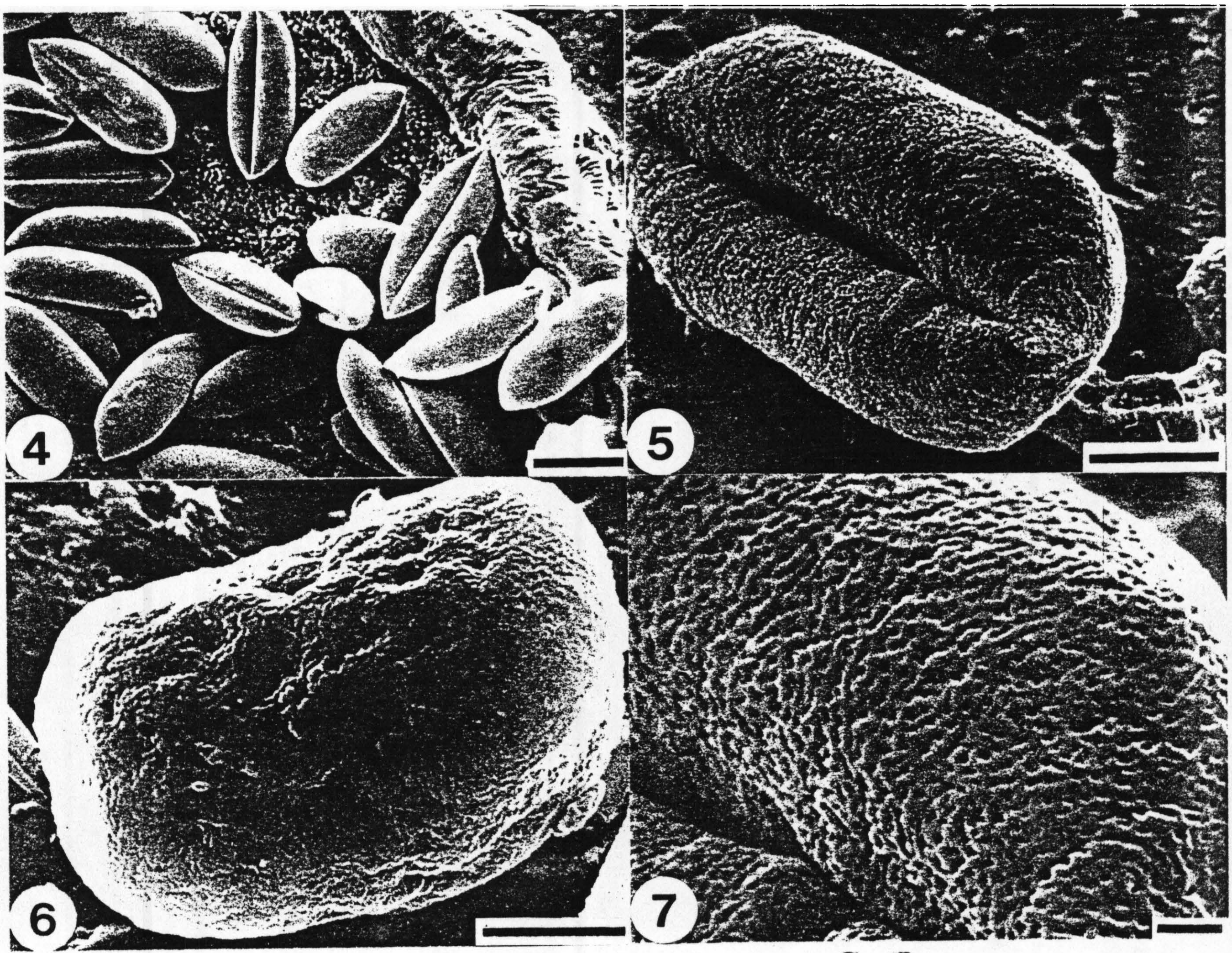

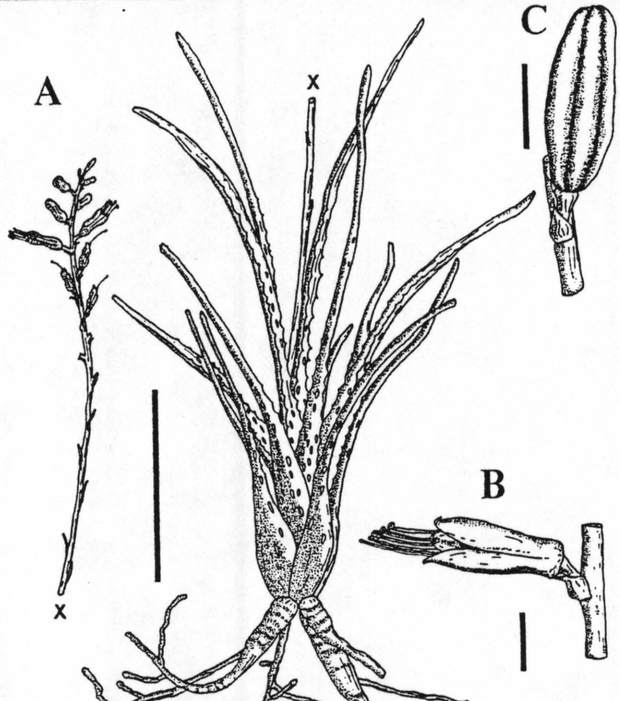

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Neotypification of *Bowiea myriacantha*, basionym of *Aloe myriacantha* (Asphodelaceae: Alooideae)

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Abstract. *Aloe myriacantha* (Haw.) Schult. & J. H. Schult. is a taxonomically little known species. A detailed taxonomic and biosystematic study of the smaller genera of the Asphodelaceae, subfamily Alooideae, which includes the genus *Bowiea* Haworth *non* W. H. Harvey *ex* J. D. Hooker in which *A. myriacantha* was originally described, has revealed that this species name has never been typified. *Bowiea myriacantha*, the basionym of *A. myriacantha*, is here neotypified by an unpublished Thomas Duncanson painting which is kept in the herbarium of the Royal Botanic Gardens, Kew.

Key words: *Aloe myriacantha* (Haw.) Schult. & J. H. Schult.; Asphodelaceae; Typification.

Introduction

While conducting biosystematic investigations toward a revision of the smaller genera of the subfamily Alooideae of the Asphodelaceae (Dahlgren *et al*., 1985) in southern Africa, I became aware that Haworth (1827) did not cite any specimens or drawings when he described *Bowiea myriacantha*, the second species name to be published in the genus *Bowiea* Haw. *non* W. H. Harvey *ex* J. D. Hooker (Haworth, 1824; Hooker, 1867). This species was transferred to *Aloe* by Schultes & Schultes (1829), whereas Stapf (1933) referred it to a segregate genus, *Leptaloe*. The species is currently treated as *A. myriacantha* (Reynolds, 1950, 1954). *Aloe bowiea*, the only other species of *Bowiea* Haw. has been dealt with in more detail elsewhere (Smith, 1983).

Aloe myriacantha is acaulescent and of slender growth with its narrow, linear, unkeeled leaves being borne in a flaccid rosette. The margins of the dull-green leaves are armed with minute white teeth. The inflorescence, produced during the summer months, is a densely capitate raceme with small, cylindric-trigonous flowers. The mouth of the perigone is bilabiate (Obermeyer, 1973).

A. myriacantha has a very wide geographic distribution. It ranges from Grahamstown and Port Alfred in the eastern Cape Province, South Africa, northwards to Kenya and Uganda, including Zimbabwe, Malawi and Tanzania, a distance of *ca*. 5,000 km (Bornman and Hardy, 1971). *A. myriacantha* was originally described by Haworth (1827) from material received at Kew from Mr. James Bowie from the then Cape of Good Hope. Bowie contributed much to our knowledge of aloes and succulents in general. During his initial residence at the Cape he visited the eastern parts of the Cape Colony during his third and fourth collecting trips into the southern African interior. These journeys lasted from early 1820 to 29 January 1821 and 24 May 1821 to 4 December 1822, respectively (Hutchinson, 1946; Smith & Van Wyk, 1989). The furthest westerly locality in southern Africa where *A. myriacantha* grows is in the eastern Cape, Grahahamstown and surroundings (Albany district). It was most probably here that Bowie collected living material of *A. myriacantha* for the first time. Since this species was discovered some time between 26 February 1822 and 29 March 1822 it could only have been collected on Bowie's fourth journey

(West, 1974). Bowie left the Cape early in 1823 and arrived back in England on 23 May 1823. Since living specimens of *A. myriacantha* were introduced to Kew in the same year (1823) it is likely that he took these specimens back with him aboard the "Earl of Egremont".

Previous monographs and synoptic works including revisions by Kunth (1843), Baker (1880, 1896), Berger (1905, 1908) Groenewald (1941) and Reynolds (1947, 1966) have avoided precise type designation for the name *B. myriacantha*. Nowhere in the literature could any reference to the typification of this species name be traced, from which I have concluded that it had never been typified. In this paper I present the results of my attempt to establish a type of *A. myriacantha*.

The Neotypification of *Bowiea myriacantha*

According to the ICBN (Chapter II, Section 2, Articles 7.1 and 7.2) all taxa of the rank of family or below must have a nomenclatural type. Furthermore, Article 7.4 of the same section clearly specifies that if no holotype was indicated by the author who described a taxon, or if the type has been lost or destroyed, a lectotype or, if permissible (Articles 7.9 and 7.10) a neotype, must be designated as a substitute for it (Greuter *et al.*, 1988). A lectotype is a specimen or illustration selected from the original material to serve as a nomenclatural type (Article 7.5). However, the protologue of *B. myriacantha* does not include any citation of specimens or reference to published or unpublished illustrations or descriptions. In addition, Haworth did not supply his description with illustrations nor did he mention any plant material which he used in establishing this taxon. Since no "original material" thus exists, *A. myriacantha* (=*B. myriacantha*) is here neotypified. Since a type must be a specimen or illustration, Haworth's (1827) description of *B. myriacantha* cannot serve as a lectotype (Greuter *et al.*, 1988).

Haworth assembled a herbarium which, after his death, was sold to Henry Barron Fielding (1805-1851) of Oxford. Fielding used it for study, but not realizing its immense value threw away most of the specimens (Stafleu and Cowan, 1979). Although some of Haworth's specimens are still in the Fielding-Druce Herbarium at the University of Oxford (Holmgren *et al.*, 1981), none of *A. myriacantha* (=*B. myriacantha*) which could be designated as type of this name have survived (S. K. Marner, personal communication). It is also likely that Haworth did not always make herbarium material of the novelties he described. Haworth also cultivated at his home in Chelsea many of the succulents that he described (Rowley, 1951, 1985; Roan, 1948). However, it is unlikely that any of these specimens have survived to the present day (Roberts, 1983).

Haworth was a friend of W. T. Aiton (1766-1849) of Kew and many of the new species which he described originated from this institution. Through this friendship he no doubt received many of the novelties sent to Kew from the then Cape of Good Hope by James Bowie. One of these, a small aloeoid specimen collected in the eastern Cape Province was described as *Bowiea myriacantha* (Haworth, 1827).

In 1822, a year before specimens of *A. myriacantha* (=*B. myriacantha*) were received at Kew, Thomas Duncanson, a young gardener from the Royal Botanic Garden Edinburgh was appointed as the first artist with the objective of drawing the new and unfigured plants in the garden at Kew (Hunt, 1988). Duncanson had a special talent for drawing plants and from 1822 to 1826 he executed more than 700 drawings, 350 of which are of succulent plants. A mental illness put an end to his drawing in the summer of 1826 (Daniels, 1974). Duncanson's drawings were indexed and numbered in systematic order and the catalogue numbers inscribed on the drawings by Richard Cunningham in 1826-1827 (Hunt, 1988).

Of Duncanson's drawings of succulent plants over 70 are of Alooideae species, one of them *Bowiea myriacantha* (G. Ll. Lucas, personal communication) (Fig. 1). This unsigned drawing of a flowering specimen bears the number "296" in its right upper corner, the number "181" in the left upper corner and a capital letter "B" in the bottom left corner, but appears to be uncatalogued. The name "Bowiea myriacantha", without author citation, is written at the bottom of the drawing and, in what appears to be the same handwriting (possibly that of Duncanson) a note reading "Imported in 1823 from the Cape of Good Hope by Mr. Bowie" has been added. Since Haworth usually wrote "A. H." or "Nob." and not "Haw." after his name on index cards of the *nomina nova* that he published (Haworth, 1965), it is unlikely that he added the latter name and inscription to the drawing. This handwriting also differs from that of James Bowie, the discovered of *A. myriacantha*. Good examples of Bowie's hand-

Fig. 1. *Bowiea myriacantha* Haw. at present included in the synonymy of *Aloe myriacantha* (Haw.) Schult. & J. H. Schult.: Iconotype. [Reduced photograph of an unpublished painting by Thomas Duncanson at Kew, of James Bowie's material. The inscription reads "Imported in 1823 from the Cape of Good Hope by Mr. Bowie"]. Copyright of the Trustees of the Royal Botanic Gardens, Kew (C) 1990. Reproduced with permission.

writing are included in six unpublished volumes which were his personal diaries and sketch and note books now in the Mary Gunn Library, National Botanical Institute, Pretoria (Smith and Van Wyk, 1989). After Stapf (1933) transferred *B. myriacantha* to *Leptaloe*, the name "Leptaloë myriacantha Stapf" was attached to the drawing by means of a Determinavit label initialed by Stapf ("O. S.") and dated "6-10-32". There is no indication that any of the names attached to the painting is in Haworth's hand and none of the handwritings compare favourably with his handwriting as reproduced in Clokie (1964). Although J. A. Schultes, one of the authors who transferred *B. myriacantha* to *Aloe* as *A. myriacantha*, knew Haworth and visited him at Chelsea (Stearn, 1971), there is thus no evidence that Haworth supported the latter taxonomic reclassification. The third and final annotation attached to the drawing is "*A. myriacantha* (Haw.) R & S", made by G. W. Reynolds on 11 September 1960. The name *A. myriacantha* reflects the current classification of this taxon in the genus *Aloe*.

In many cases drawings of the novelties received at Kew were made before their descriptions were published (for example: *A. gracilis* Haw. : drawn 1824, described 1825; *A. pluridens* Haw. : drawn 1823, described 1824; *A. striatula* Haw. : drawn 1824, described 1825 and *Haworthia altilinea* Haw. : drawn July 1824, described October 1824). It is thus likely that Haworth had seen Duncanson's drawing of *B. myriacantha* before the description of this species was published.

Since the protologue of *B. myriacantha* does not contain any cited specimens, descriptions or illustrations, a type should be chosen with other factual evidence (in this case the description only) as basis. After considering the description and associated circumstantial evidence I have concluded that Duncanson's undated drawing should be chosen to serve as neotype of the name *B. myriacantha* for the following reasons:

1. Duncanson's drawing is conspecific with the species nowadays known as *A. myriacantha* (=*B. myriacantha*) and clearly identifiable with field populations of this species.
2. This drawing is in accordance with the protologue of *B. myriacantha* (Haworth, 1827).
3. Through Haworth's friendship with W. T. Aiton of Kew and because drawings of novelties received at Kew were in many cases made before they were formally described, it is likely that Haworth had seen the drawing prior to the name *B. myriacantha* appearing in print.
4. In the case of succulents, a drawing is often more "diagnostic" than a dried specimen, hence the selection of a drawing rather than a specimen as neotype. Furthermore, the typification of species names in the Alooideae with iconotypes is not uncommon (Wijnands, 1983, 1985).

By implication the Duncanson drawing of *B. myriacantha* also typifies sect. *Graminialoe* Reynolds subsect. *Graminialoe* for which it is the type species.

The type of *Bowiea myriacantha* therefore is:

SOUTH AFRICA.—Cape of Good Hope without precise locality, unpublished drawing by Thomas Duncanson, neotype (iconotype), here chosen (K)!

Acknowledgements. The author wishes to thank Professor A. E. van Wyk for the constructive interest he has shown in this project. Grateful thanks are due to the Directors of the herbaria BM, K and OXF for the loan of material, or for permission to study their specimens *in situ*, and for hospitality extended while doing so. I am also indebted to Dr. H. F. Glen and Miss S. K. Marner for supplying examples of the handwritings of G. W. Reynolds and A. H. Haworth, respectively, and to Mms E. Potgieter and B. F. Lategan for supplying copies of scarce publications and illustrations. Permission granted by the Director of K to use copyright material in this article is gratefully acknowledged.

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Aloe myriacantha (Asphodelaceae: Alooideae) 之基本名, *Bowiea myriacantha* 新模式之指定

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Aloe myriacantha (Haw.) Schult. & J. H. Schult. 的分類稀爲人知，它的原始記載是發表在 *Bowiea* 屬，但並未指定模式標本。本文據英國皇家植物園標本館典藏之 Thomas Duncanson 所繪圖幅，指定爲 *Bowiea myriacantha* 之新模式。

Bothalia 20,2: 207–222 (1990)

Notes on African plants

VARIOUS AUTHORS

LILIACEAE/ASPHODELACEAE

THE TYPE OF *CHORTOLIRION BERGERIANUM* (ALOOIDEAE)

Berger (1908) erected the genus *Chortolirion* to accommodate the four bulbous species of *Haworthia* known at the time. Six years after this genus was established, Dinter (1914) described a fifth species as *C. bergerianum* from specimens which he collected near Windhoek in Namibia. Obermeyer (1973) sank the four *Chortolirion* species recognized by Berger (1908) in the synonymy of *H. angolensis* Baker. However, she did not mention *C. bergerianum* in her treatment of *Chortolirion*.

A revision of the smaller genera of the subfamily Alooideae of the Asphodelaceae currently under way has shown that *Chortolirion* represents a natural, monotypic entity which should be afforded separate generic recognition (Smith 1985, 1988). In an attempt to establish the identity of *C. bergerianum*, I became aware that Dinter failed to designate a type specimen when he described this species. In this paper I present the results of my efforts to typify the name *C. bergerianum*.

According to the International Code of Botanical Nomenclature (Articles 7.1 and 7.2) all taxa of the rank of family or below must have a nomenclatural type (Greuter *et al.* 1988). However, no Dinter material collected in January 1913 from the type locality ('Voigtland', 20 km east of Windhoek) could be traced in any of the herbaria listed by Holmgren *et al.* (1988), Stafleu & Cowan (1976) or Gunn & Codd (1981). The following discussion should clarify the typification of *C. bergerianum*:

1, Dinter (1914) did not cite any herbarium specimens nor did he mention any plant material which he used in establishing this taxon; 2, no specimens collected in January 1913 at the type locality and used (Article 7.3) or annotated by Dinter in preparing the description, but not cited or designated as type, could be found; 3, Dinter (1914) included a single reference to an illustration (Fig. 12) which was published along with the original description of *C. bergerianum* in *Neue und wenig bekannte Pflanzen Deutsch-Südwest-Afrikas* (1914); 4, this figure, which therefore forms part of the protologue, is of a sterile specimen, but clearly agrees with Dinter's description; 5, Article 7.3 and Note 1 of this article clearly specify that any designation made by the original author, if definitely expressed at the time of the original publication of the name of a taxon, is final. Furthermore, the type of a name may be either a specimen or an illustration.

After considering the existing evidence, I concluded that Dinter's illustration, as an element included in the protologue, is the type of *C. bergerianum*. Since it is the only element cited, and no specimens used or annotated by Dinter can be found, the illustration should be referred to as the holotype and not treated as a lectotype. The type of *C. bergerianum* is:

TYPE.—K. Dinter, Neue und wenig bekannte Pflanzen Deutsch-Südwest-Afrikas t. 12 (1914) (icono.).

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Mitt. Inst. Allg. Bot. Hamburg Band 23b S. 593 - 594 Hamburg 1990
PROCEEDINGS OF THE TWELFTH PLENARY MEETING OF **aetfat** SYMPOSIUM **VI**

A MULTIDISCIPLINARY APPROACH TO A REVISION OF *CHORTOLIRION* (*ASPHODELACEAE, ALOOIDEAE*)

GIDEON F. SMITH

KEY WORDS: *Chortolirion, Asphodelaceae*, taxonomy.

Chortolirion BERGER is a monotypic genus in the subfamily *Alooideae*, family *Asphodelaceae*, and has a history of taxonomic confusion. This taxon is a perennial, deciduous herb with a subterranean bulb and is widely distributed in the summer rainfall region of southern Africa. The aim of this investigation was to clarify the synonymy of *Chortolirion* and to expand its circumscription. The large number of synonyms of *Chortolirion angolense* (BAKER) BERGER provides a misleading reflection of the relatively uniform morphology of this taxon. Its synonyms were described by overseas botanists who often had only a single plant or herbarium specimen at their disposal. Scant regard was paid to natural variation and species were often based on characters which later proved to be insufficient for recognition at any level in the hierarchical classification system.

Chortolirion angolense displays obvious floral affinities with the subgenus *Hexangulares* of the genus *Haworthia* DUVAL. However, the subterranean bulb of *Chortolirion* BERGER is not encountered in the latter genus. A comparative investigation of the leaf surface sculpturing of *Chortolirion angolense* and *Haworthia graminifolia* G.G. SM. revealed that sharp discontinuity exists between these two taxa as far as stomatal elevation and micropapillate fine structure is concerned. Furthermore, with regard to symmetry, size of pollen from diploid specimens and the perforation of the surface bordering the sulcus, certain fine structural differences exist between pollen of *Chortolirion* and *Haworthia*. Chromosome counts were made of *Chortolirion angolense*. This taxon is diploid and has a karyotype of 2n = 14. It has a bimodal complement of eight long and six short acrocentric chromosomes. A similar karyotype is encountered for most species in the subfamily *Alooideae*.

An evaluation of the examined characters was carried out with reference to *Chortolirion angolense*. Along with an analysis of previously published morphological, geographical and phylogenetic information it was concluded that *Chortolirion* is best regarded as a monotypic genus within the subfamily *Alooideae* with *C. angolense* (BAKER) BERGER as the only species.

This paper was published in full in South African Journal of Science under the following title:

SMITH, G.F., 1988: A scanning electron microscopic investigation of the pollen morphology of *Chortolirion* BERGER (*Aloineae*; *Liliaceae*). - S. Afr. J. Sci. **84**: 428-430.

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1029a

CHORTOLIRION

by G.F. SMITH

Chortolirion *A. Berger* in Engl., Das Pflanzenreich IV, 38, III, II (Heft 33): 72 (1908); Phillips: 149 (1926); Obermeyer: 119 (1973). Type species: *Haworthia angolensis* Baker, i.e. *Chortolirion angolense* (Baker) A. Berger.

Herbaceous perennial; acaulescent, with leaves originating from a short, simple (rarely once branched), cylindrical, subterranean butt ± 9 mm in diameter; roots few, fusiform, fleshy, up to 8 mm in diameter; bulb with few, loosely packed, membranous scales covering the inner, slightly fleshy leaf bases, ovoid-oblong, 30--40 mm long, ± 20 mm in diameter. *Leaves* rosulate, slender, grass-like, flaccid, erect, ± 10, light green to glaucous green, usually once or twice twisted, upper 5--10 mm of leaves often dry, ± 150 mm long, diameter ± 2 mm; *upper surface* green, canaliculate, immaculate or with very few white spots near base; *lower surface* green, convex, copiously white spotted near base, the spots often slightly tuberculate-subspinulescent; *margins* armed with soft, white, decurved teeth, ± 0,5 mm long, larger low down, smaller upwards, 1--2 mm distant throughout. *Inflorescense* ± 360 mm tall; *peduncle* simple, diameter ± 2 mm, ± 205 mm long; *sterile bracts* membranous, ovate, abruptly long acuminate, erect, clasping the peduncle, keeled with 1--3 reddish brown vein(s), ± 8 mm long; *raceme* ± 155 mm long, ± 14 spirally arranged flowers and buds, 3 open simultaneously; *floral bracts* membranous, mucronate, keeled, clasping the pedicels, longer than the pedicels, 5 mm long; *pedicels* erect, persistent, brownish-green, 1--2 mm long, diameter 1 mm. *Flowers* erect, zygomorphic, greenish, brownish or pinkish white with greenish keels to the segments, base obtuse; perianth funnel-shaped, tube straight, constricted to 3 mm above, 14 mm long, ± 2 mm across; *segments* greenish white with darker green veins, not free to the base, closely adhering for two thirds of the length, limb bilabiate; upper-outer segments strongly recurved, retuse, spoon-shaped at tips; upper-inner segment slightly recurved, obtuse, spoon-shaped at tip, lower-outer segments recurved, lower-inner segment strongly recurved, tips flared; bud narrow, straight, decurved and pinkish at tip; *stamens* 6 of ± equal length, inserted within the perianth tube, attached below ovary, ± 7 mm long; *filaments* white, thinner towards apex; *anthers* yellow, dorsifix, dehiscing longitudinally and introrsely; *ovary* green, sessile, 3 mm long, diameter 2 mm; *style* white, straight, capitate, 4 mm long. *Fruit* light green, trilocular capsule, cylindric, apically acute, dehiscing loculicidally, chartaceous when dry, ± 15 mm long, diamter 5--6 mm. *Seed* dark brown to black, angled, shortly winged, ± 3 mm long. *Chromosome number*: $2n = 14$. Fig. 9.4.3.1.

Monotypic. Also in Angola and Zimbabwe. In southern Africa it occurs in Namibia, Botswana, Lesotho and in all four provinces of the Republic of South Africa. The general habitat of *Chortolirion* is the climatically severe southern African inland above the Great Escarpment. The genus is adapted to sparse or dense grasslands in which a wide variety of graminoids and forbs dominate. These grasslands are usually subject to natural or deliberate seasonal burning. *Chortolirion* is found from near sea level up to altitudes of more than 2000 m. Map 9.4.3.1.

Chortolirion is morphologically quite distinct from *Haworthia,* especially with regard to the presence of an underground bulbous rootstock. Furthermore, it is the only haworthioid taxon of which the leaves are deciduous and die back to ground level after fires or frost.

The name *Chortolirion* means "heath lily" and refers to the fact that the genus usually occur in grassland and, especially when not in flower, can easily be mistaken for small tufts of grass.

Chortolirion angolense *(Baker) A. Berger* in Engl. Das Pflanzenreich IV, 38, III, II (Heft 33): 73 (1908). Type: Angola, Huilla, regio subtemperata, in dumetis arenosis, *Welwitsch* 3756 (BM, holo.!, PRE, photo!).

Description as for the genus.

Haworthia angolensis Baker: 263 (1878); Baker: 210 (1880); Baker: 469 (1898) Obermeyer: 119 (1973). Type: as above.

Haworthia tenuifolia Engl: 2 (1888); Baker: 355 (1896). *Chortolirion tenuifolium* (Engl.) A. Berger: 73 (1908). Type: Betschuanaland, Manjering pr. Kuruman, in arenosis alt. 1200 m, *Marloth* 1049 (B, holo.!).

Haworthia stenophylla Baker: t. 1974 (1891); Baker: 355 (1896). *Chortolirion stenophyllum* (Baker) A. Berger: 72 (1908); R.A. Dyer: t. 932 (1944). Type: Transvaal, grassy mountain slopes of the Saddleback range near Barberton, *Galpin* 858 (K, holo.!).

Haworthia saundersiae Baker: t. 1974 (1891), *nom. nud.*

Haworthia subspicata Baker: 998 (1904). *Chortolirion subspicatum* (Baker) A. Berger: 74 (1908). Type: Transvaalkolonie, Modderfontein, *Conrath* 645 (Z, holo.!).

Chortolirion bergerianum Dinter: 24 (1914). Type: Deutsch-Südwest-Afrikas (Namibia), the farm "Voigtland", 20 km to the east of Windhoek, K. Dinter, Neue und wenig bekannte Pflanzen Deutsch-Südwest-Afrikas t. 12 (1914) (holo.!, icono.!).

Icones: Dyer: t. 932 (1944); Fabian & Germishuizen: t. 13a.

Vouchers: *Dinter* 4295 (B); *Hanekom* 1843 (PRE); *Smith* 8 (PRU); *Smith* 12 (PUC); *Ubbink* 318 (PUC).

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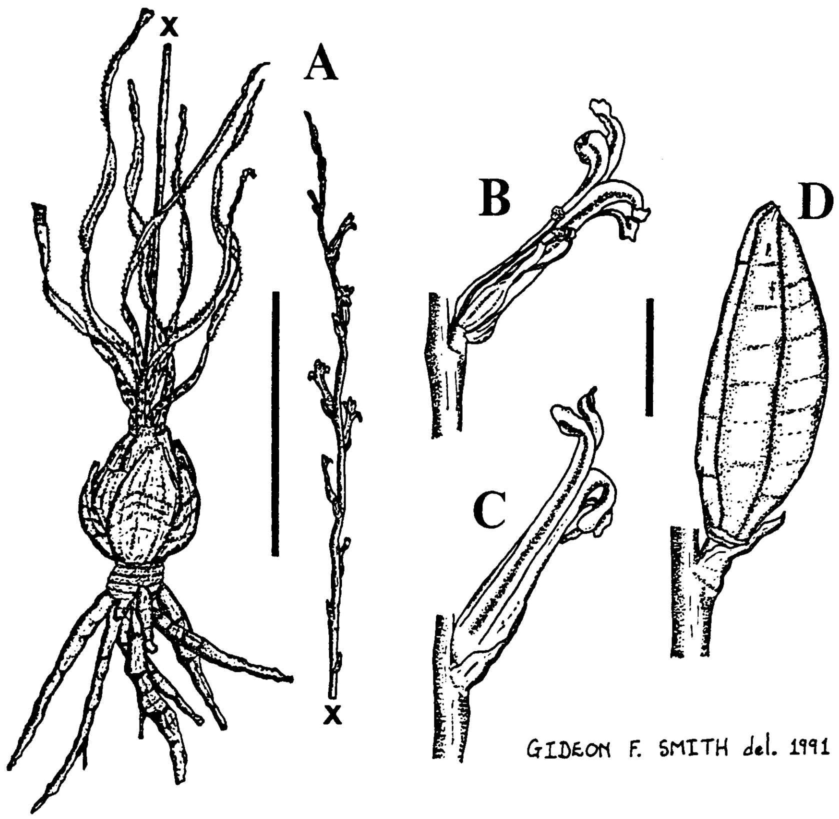
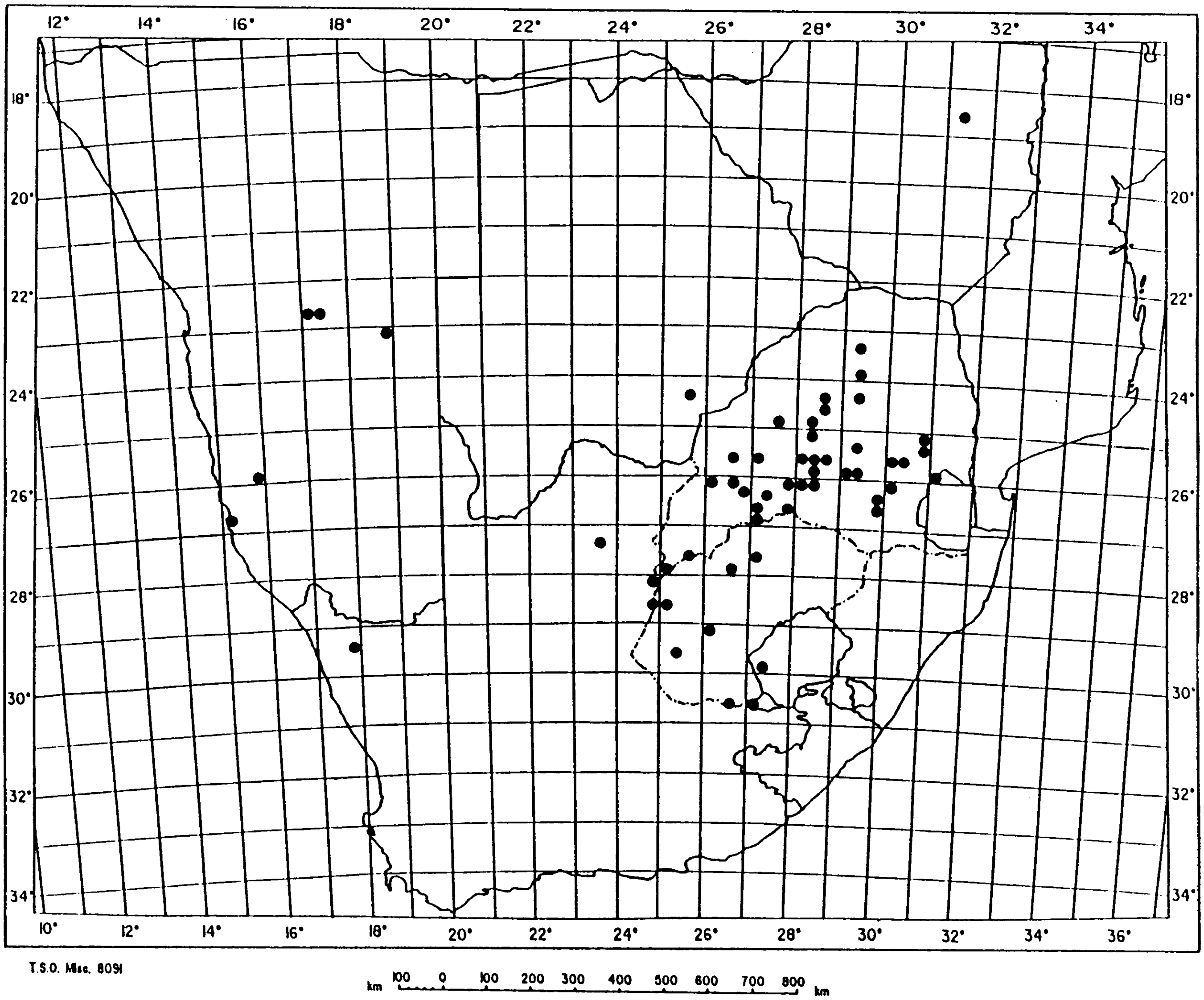


FIG. 9.4.3.1. --- **Chortolirion angolense**: A, habit; B, longitudinal section of flower (three stamens removed); C, lateral view of flower, showing the position of the peduncle and bract; D, fruit, acuminate capsule. All drawings were made from live material of *Smith 14* (PUC). Scale line = 50 mm in Fig. 9.4.3.1A and 5 mm in Fig. 9.4.3.1B -- Fig. 9.4.3.1D.



MAP 9.4.3.1 --- **Chortolirion angolense**

1028a

POELLNITZIA

by G.F. SMITH

Poellnitzia *A.J.A. Uitewaal* in Succulenta 22: 61 (1940); Hunt: t. 804 (1981). Type species: *Apicra rubriflora* H.M.L. Bolus, i.e. *Poellnitzia rubriflora* (H.M.L. Bolus) A.J.A. Uitewaal.

Herbaceous perennial; caulescent, offsetting at and near the base, stems erect when young, ascending when old, up to 250 mm long, diameter ± 10 mm; roots terete, diameter 2--3 mm. *Leaves* thick, hard, usually four-ranked in spirally arranged rows, squarrose-imbricate, ovate-squamiform, apex triquetrous, pungent-acuminate, dark green to glaucous green, coated with a waxy layer, 20--40 mm long, ± 20 mm broad near base, up to 5 mm thick; *upper surface* green, concave or flat, immaculate or with very few lighter green spots near base; *lower surface* green, convex, keeled towards the tip, usually with few lighter green spots, spots sometimes confluent to form longitudinal lines; *margins* and keel-apex minutely scabrid. *Inflorescence* up to 500 mm long; *peduncle* simple, erect, slender, ± 300 mm long, diameter ± 3 mm; *sterile bracts* membranous, lanceolate-acuminate, keeled with 1 reddish brown vein, ± 7 mm long; *raceme* borne horizontally, ± 200 mm long, ± 28 spirally arranged flowers and buds, 3--8 accessible simultaneously; *floral bracts* membranous, lanceolate, keeled, clasping the pedicels, shorter than the pedicels, 3--5 mm long; *pedicels* erect, persistent, brown, 6--8 mm long, diameter ± 1 mm. *Flowers* borne secundly-erect, narrowly tubular, elongate, slightly constricted above the ovary and below the segment lobes, upper one-third decurved, tube red to orange, upper one-tenth of perigone members dark green, connivent, reduplicate-valvate, tips of segments scarcely separated, ± 20 mm long, diameter 3 mm; *segments* red to orange with brownish midveins, not free to the base, fused, closely adhering where free, apically spoon-shaped, outer segments slightly larger than the inner, margins apically minutely crenulate-erose, yellow; *stamens* 6, subequal, inserted within the perianth tube, attached below ovary, ± 18 mm long; *filaments* light green; *anthers* yellow, dorsifix, dehiscing longitudinally; *ovary* green, sessile, 6--7 mm long, diameter 3 mm; *style* white, straight, capitate, ± equalling the anthers, ± 12 mm long. *Fruit* green, trilocular capsule, cylindric, apically retuse, dehiscing loculicidally, chartaceous when dry, ± 16 mm long, diameter 3--4 mm. *Seed* dark brown to black, angled, shortly winged, ± 4 mm long. *Chromosome number*: $2n = 14$. Fig. 9.5.1.

Monotypic. *Poellnitzia* is endemic to the Robertson Karoo (districts of Robertson, Bonnievale and McGregor) which is one of the drier, predominantly winter rainfall areas bordering the Fynbos Biome. The vegetation in the habitat of *Poellnitzia* can be broadly classified as Karroid Shrublands and the entire range of distribution of the genus falls within the Succulent Karoo Biome. *Poellnitzia* is found between altitudes of approximately 150 and 250 m above sea level. Map 9.5.1.

On vegetative morphological grounds *Poellnitzia* shows affinities with some representatives of *Aloe, Astroloba* and *Haworthia*. However, the flower morphology of *Poellnitzia* is unique in the subfamily Alooideae in that the dark green, free portion of the segment lobes are connivent and reduplicate-valvate with the very tips of the segments scarcely separated.

The genus name *Poellnitzia* honours Dr. Joseph Karl Leopoldt Arndt von Poellnitz (4 May 1896 -- 15 February 1945). He was a German agriculturist and botanist and had a general interest in succulent plants, particularly the subfamily Alooideae. Both Von Poellnitz and his only daughter died tragically in bombing raids during World War II.

Poellnitzia rubriflora *(H.M.L. Bolus) A.J.A. Uitewaal* in Succulenta 22: 61 (1940); Hunt: t. 804 (1981). Type: Cape Province: South-Western Region; Swellendam Div., Bonnie Vale, *Smith* s.n. (National Botanic Gardens, No. 2/17) (Herbarium Bolusianum 45213) (BOL, holo.!).

Description as for the genus.

Apicra rubriflora H.M.L. Bolus: 13 (1920); Uitwaal: 28 (1939). *Astroloba rubriflora* (H.M.L. Bolus) E. Lamb: 230 (1955) *nom. illeg.*. *Haworthia rubriflora* (H.M.L. Bolus) Parr: 196 (1971). *Aloe rubriflora* (H.M.L. Bolus) G.D. Rowley: 2 (1981). Type: as above.

Apicra jacobseniana J.K.L.A. von Poellnitz: 95 (1939). *Poellnitzia rubriflora* var. *jacobseniana* (Poelln.) Uitewaal *in* Jacobsen & Rowley: 80 (1955). *Haworthia rubriflora* var. *jacobseniana* (Poelln.) Parr: 89 (1972) *nom. illeg.* Type: Kapland: Worcester, leg. Mrs. Florence Morris; Typ (=Triebner 34) im Botanishen Garten Kiel kultiviert, no specimen preserved (unnumbered photograph in Kakteenkunde (1939): 95 lecto.!, here designated).

Icones: Hunt: t. 804 (1981); Court: 140 (1981).

Vouchers: *Acocks* 14098 (PRE); *Burgers* 78 (PRE); *Smith* 9 (PRU); *Smith* 174 (PUC); *Smith* 177 (PUC).

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UITEWAAL, A.J.A. 1939. Het geslacht *Apicra* (Willd.) Haw. c.m. (Vervolg). *Succulenta* 21: 25-29.

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VON POELLNITZ, J.K.L.A. 1939. *Apicra jacobseniana* v. P. *Kakteenkunde* (1939): 95.

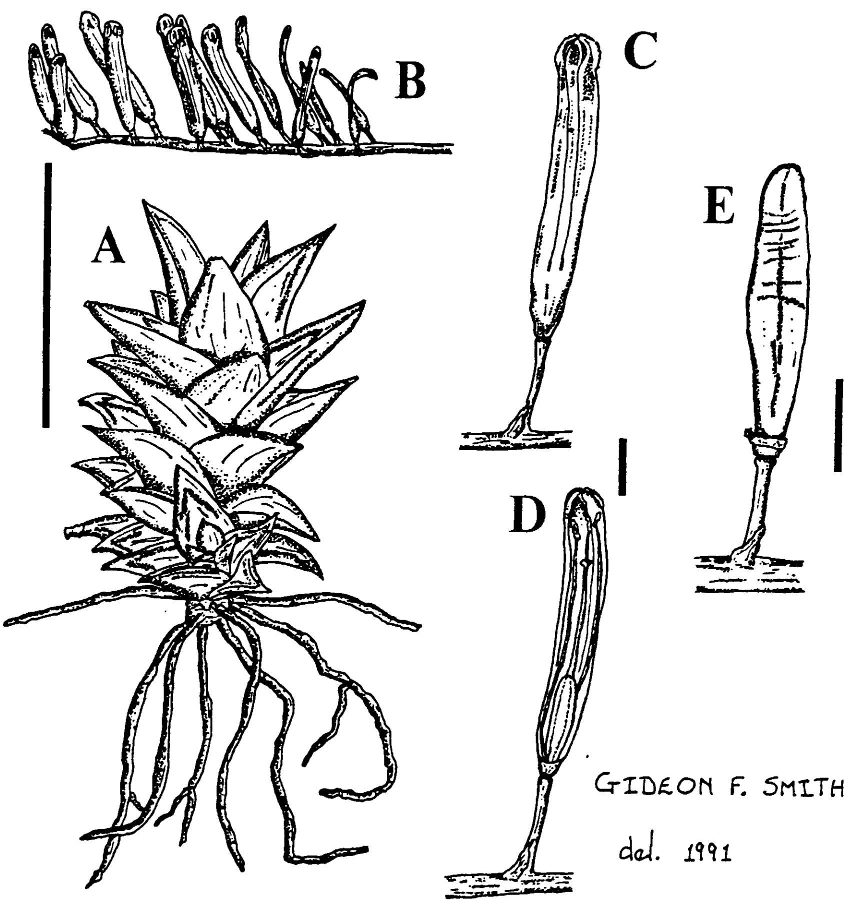
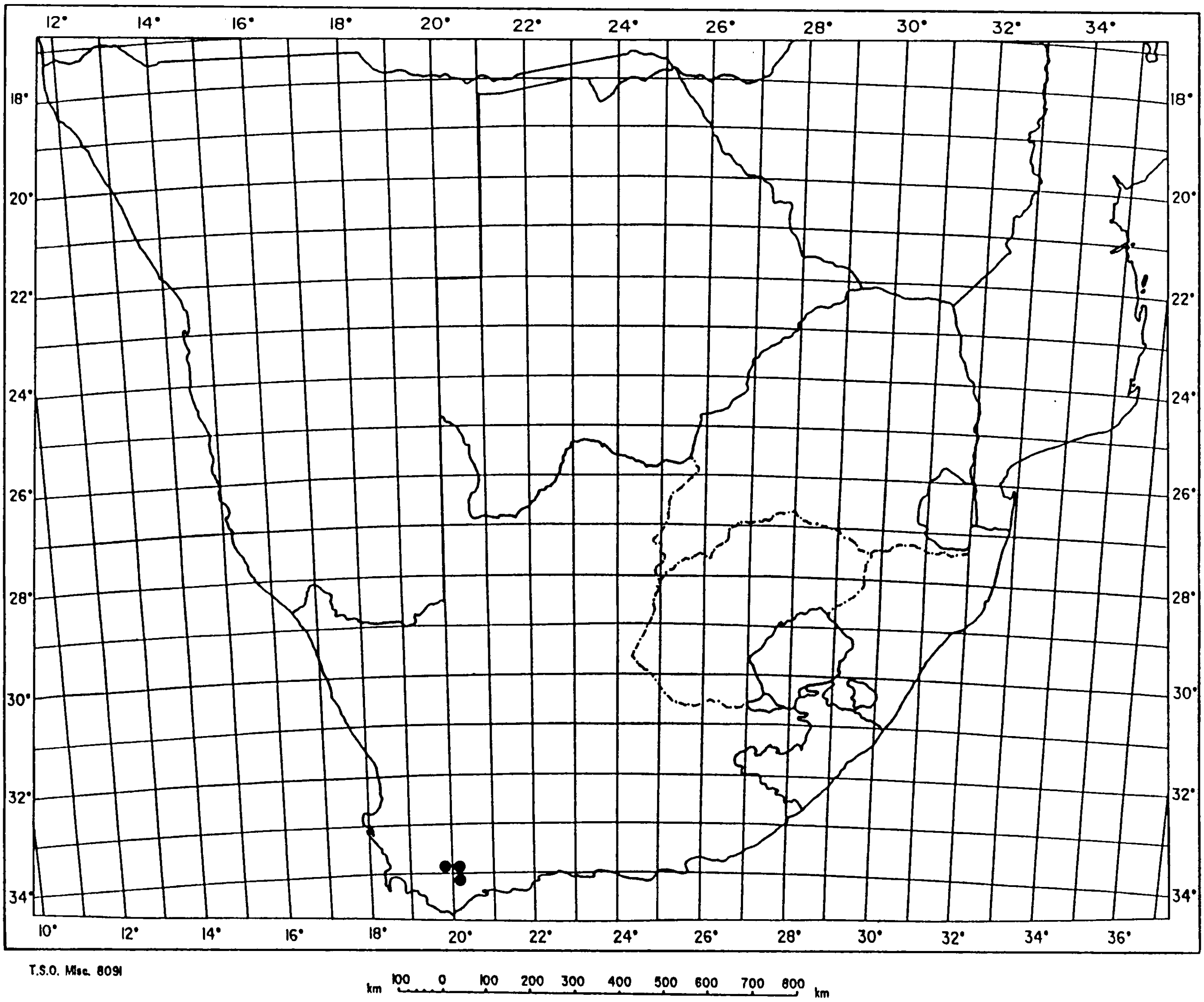


FIG. 9.5.1. --- **Poellnitzia rubriflora:** A, habit; B, terminal portion of raceme; C, lateral view of flower, showing the position of the peduncle and bract; D, longitudinal section of flower (three stamens removed); E, fruit, trilocular capsule. All drawings were made from live material of *Smith 174* (PUC). Scale line = 50 mm in Fig. 9.5.1A & 9.5.1B and 5 mm in Fig. 9.5.1C -- Fig. 9.5.1E.



MAP 9.5.1 --- **Poellnitzia rubriflora**

SUMMARY

CONTRIBUTIONS TO THE SYSTEMATICS OF SELECTED GENERA OF THE ALOOIDEAE (ASPHODELACEAE)

by

GIDEON FRANCOIS SMITH

Promoter: Prof. Dr. A.E. van Wyk

DEPARTMENT OF BOTANY
UNIVERSITY OF PRETORIA

July 1991

PHILOSOPHIAE DOCTOR

This study extends the work on the taxonomy of the genus *Chamaealoe*, which was considered by the author in a B.Sc. project (1983), and the taxonomy of the genera *Chortolirion* and *Poellnitzia*, which the author presented as a B.Sc.(Hons.) scription (1985). A wide variety of potential sources of taxonomic evidence was studied in the light of the classification system for the smaller aloeoid genera proposed by the earlier studies. The principal objective was to evaluate comparatively the taxonomic significance of various characters as an aid towards a revision of these taxonomically difficult genera.

Contributions are presented on generic concepts, botanical biography and bibliography, palynology and reproductive biology, scanning electron microscopic methodology, leaf anatomy, karyology, ecology, conservation and phylogeny. The dissertation is a compilation of 26 papers published in various journals over a period of about three years. It also contains comprehensive introductions to the various aspects investigated, a synthesis of the principal findings and a key to the genera of Alooideae, supplemented by notes on diagnostic characters, synonymy and typification and various other plant nomenclatural topics.

The revision of *Chamaealoe* Berger revealed that it should best be regarded as a synonym of *Aloe* L. However, *Aloe bowiea* Schult. & J.H. Schult. [=*C. africana* (Haw.) Berger] is a distinctive species which is clearly distinct from its nearest congeners by the combination of its dense, grass-like rosettes, lax, elongated racemes, shortly pedicellate flowers and much exserted anthers and style. By virtue

of these characters the genus *Bowiea* Haw. *non* Harv. *ex* Hook *f. pro parte quoad A. myriacantha* (Haw.) Schult. & J.H. Schult. was reinstated as a subsection in the section *Graminialoe*, namely, *Bowieae* (Haw.) G.F. Smith, with *A. bowiea* the only species.

Chortolirion and *Poellnitzia* also have histories of taxonomic confusion. *Chortolirion*, is a perennial, deciduous herb and is widely distributed in the summer rainfall region of southern Africa. *Poellnitzia*, a caulescent herb with rigid, acuminate leaves has a very restricted distribution in the Robertson region of the south-western Cape Province, which receives its precipitation mainly in winter. *Chortolirion* has obvious floral affinities with the subgenus *Hexangulares* of the genus *Haworthia* Duval. However, the subterranean bulb and deciduous leaves of *Chortolirion* is not encountered in the latter genus. The flower morphology of *Poellnitzia* is unique in the Alooideae in that the free portion of the segment lobes are connivent and reduplicate-valvate with the very tips of the segments scarcely separated. Along with its two closest congeners, *Astroloba* and *Haworthia, Chortolirion* is phylogenetically one of the most derived aloeoid genera. *Poellnitzia* and *Gasteria* occupy an intermediate position between the basal *Aloe/Lomatophyllum*-group and the derived haworthioid genera.

An evaluation of all the examined characters was carried out with reference to *Chortolirion* and *Poellnitzia*. Along with an analysis of morphological , geographical and phylogenetic information it was concluded that both taxa are best regarded as monotypic genera within the subfamily Alooideae with *C. angolense* (Bak.) Berger and *P. rubriflora* (L. Bol.) Uitew. the only species, respectively.

OPSOMMING

BYDRAES TOT DIE SISTEMATIEK VAN GESELEKTEERDE GENUSSE VAN DIE ALOOIDEAE (ASPHODELACEAE)

deur

GIDEON FRANCOIS SMITH

Promotor: Prof. Dr. A.E. van Wyk

DEPARTEMENT PLANTKUNDE
UNIVERSITEIT VAN PRETORIA

Julie 1991

PHILOSOPHIAE DOCTOR

Die huidige ondersoek is 'n voortsetting van die werk op die taksonomie van die genus *Chamaealoe* wat as 'n B.Sc.-projek (1983) aangebied is, en werk op die taksonomie van die genusse *Chortolirion* en *Poellnitzia* wat as 'n B.Sc.(Hons.)-skripsie (1985) voorgelê is. 'n Verskeidenheid bykomende bronne van potensiële taksonomiese getuienis is ondersoek in die lig van die klassifikasiestelsel vir die kleiner aalwynagtige genusse wat uit die vroeëre bevindings gespruit het. Die hoofdoelstelling was die vergelykende evaluering van die taksonomiese belangrikheid van verskillende kenmerke as hulpmiddels in 'n hersiening van hierdie taksonomies moeilike genusse.

Bydraes oor veral genuskonsepte, botaniese biografie en bibliografie, palinologie en voortplantingsbiologie, aftaselektronmikroskopiese metodologie, blaaranatomie, kariologie, ekologie, bewaring en filogenie word verskaf. Die proefskrif is uit 26 artikels saamgestel wat oor 'n tydperk van ongeveer drie jaar in 'n verskeidenheid tydskrifte gepubliseer is. Dit bevat ook omvattende inleidings tot die aspekte wat ondersoek is, 'n sintese van die belangrikste bevindings en 'n sleutel tot die Alooideae-genusse, aangevul deur aantekeninge oor diagnostiese kenmerke, sinonimie, tipifisering en verskeie ander plantnomenklatoriese onderwerpe.

Die hersiening van *Chamaealoe* Berger het aan die lig gebring dat hierdie genus 'n sinoniem van *Aloe* L. is. *Aloe bowiea* Schult. & J.H. Schult. [=*C. africana* (Haw.) Berger] is 'n eiesoortige spesie wat organografiese verwantskappe met *Aloe* seksie *Graminialoe* Reynolds toon. Hierdie spesie kan egter duidelik van verwante spesies

onderskei word op grond van 'n kombinasie van sy digte, grasagtige rosette, yl, verlengde raseme, kort-gesteelde blomme en uitgestote meeldrade en style. Op grond van hierdie kenmerke is die genus *Bowiea* Haw. *non* Harv. *ex* Hook. *f. pro parte quoad A. myriacantha* (Haw.) Schult. & J.H. Schult. heringestel as 'n subseksie in die seksie *Graminialoe*, naamlik *Bowieae* (Haw.) G.F. Smith, met *A. bowiea* die enigste spesie.

Chortolirion en *Poellnitzia* gaan beide gebuk onder taksonomiese verwarring. *Chortolirion* is 'n meerjarige, bladwisselende kruid en kom wydverspreid in die somerreënvalstreek van suidelike Afrika voor. *Poellnitzia*, 'n stingelvormende, meerjarige kruid met stywe, toegespitste blare, het 'n beperkte verspreiding in die Robertson-omgewing van die suidwestelike Kaapprovinsie. Die gebied is geleë in die winterreënvalstreek. *Chortolirion* toon opvallende blommorfologiese ooreenkomste met die subgenus *Hexangulares* van die genus *Haworthia* Duval. Die ondergrondse bol en bladwisselende blare van *Chortolirion* kom egter nie in laasgenoemde genus voor nie. Die blommorfologie van *Poellnitzia* is uniek in die Alooideae deurdat die vrye gedeelte van die segmentlobbe toegespits is, met die punte van die lobbe dig saamgesnoer. Tesame met *Astroloba* en *Haworthia*, waaraan *Chortolirion* die naaste verwant is, is laasgenoemde genus filogeneties een van die gevorderdste aalwynagtige genusse. *Poellnitzia* en *Gasteria* beklee 'n intermediêre posisie tussen die basale *Aloe/Lomatophyllum*-groep en die gevorderde haworthia-agtige genusse.

'n Evaluering van al die ondersoekte kenmerke is uitgevoer met betrekking tot *Chortolirion* en *Poellnitzia*. Tesame met 'n ontleding van morfologiese, geografiese en filogenetiese inligting is tot die slotsom gekom dat beide taksons erkenning as monotipiese genusse in die subfamilie Alooideae regverdig, met *C. angolense* (Bak.) Berger en *P. rubriflora* (L. Bol.) Uitew., onderskeidelik, die enigste spesies.

ACKNOWLEDGEMENTS

To my Creator, the Lord God, who has given me the opportunity to carry out this work.

I wish to express my sincere thanks to the many persons and institutions who have offered encouragement, assistance and co-operation in the preparation of this dissertation, namely:

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the Curators of the following herbaria for the loan of specimens and/or permission to study their collections during visits: B, BM, BOL, GRA, HBG, J, K, KMG, M, NBG, PRE, PRU, PUC, SAM, STE, WIND and Z;

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my parents and parents-in-law for support and encouragement, and also

the Potchefstroom University for Christian Higher Education for financial assistance.

Finally, to my wife El-marié and two daughters, Janine and Tanya, to whom I dedicate this work, a special word of thanks for the patience, sacrifices, support, unselfish love and unobtrusive but valued ways in which they made this task easier.

CURRICULUM VITAE

Gideon Francois Smith was born on 20 October 1959 in Uitenhage, a small, rural town situated some 20 km from Port Elizabeth in the eastern Cape Province and spent the first 18 years of his life in this, one of the richest succulent regions of the world. In 1977 he matriculated from Brandwag Secondary School with a B-aggregate and a distinction in his mother language, Afrikaans. During his school career he participated in the normal cultural activities, serving as a member of the pupils council, debating society and editorial staff of the school journal. He also represented the school at rugby, cricket and tennis and was awarded academic honours in 1975. In 1978 he enlisted in the South African Defence Force and completed 3 years of service as an instructor in the South African Armoured Corps at Bloemfontein. All the courses completed in the South African Defence Force were passed with distinction.

After having completed his initial compulsory military service (1978-1980), he registered at the University of Port Elizabeth for a B.Sc. degree and took up a bursary from the South African Bureau of Standards. During all three undergraduate study years he was awarded merit bursaries by the University of Port Elizabeth.

At the end of 1983 he graduated from the University of Port Elizabeth majoring in Botany (distinction) and Chemistry and, in 1984, took up a position as chemist in the Division Pharmaceutical Chemistry, Food Chemistry and Vitamin Products at the South African Bureau of Standards, Pretoria. At the same time he registered for the B.Sc. (Honours) degree in Botany at the University of Pretoria. After two years of part time study at the latter university he was awarded the B.Sc. (Hons.) degree with distinction and also became the first recipient of the Hans Schweickerdt medal.

In 1986, at the age of 26, he took up a position as lecturer in taxonomy and curator of the PUC herbarium at the Potchefstroom University for Christian Higher Education. During March 1988 he became one of only five lecturers in the Faculty of Natural Sciences to receive an award for excellence in tuition.

His interest in succulents started in his primary school days. However, his main research interest is centered on the aloeoid genera, *Aloe, Astroloba, Chortolirion, Gasteria, Haworthia, Lomatophyllum* and *Poellnitzia*. Gideon Smith has presented papers at numerous congresses both locally and abroad. He is the author or co-author of about 25 scientific and about 65 popular scientific papers.

APPENDIX

CORRECTIONS AND ADDITIONAL NOTES

Due to practical considerations, such as inadequate printing space and different letter types, the errors listed below could not be corrected on the reprints included in this thesis. They are recorded here for the attention of the reader. Page numbers are those of the original publications. Corrections and notes are supplied separately for each paper. The papers are listed under the heading of the chapter in which they appear in this thesis.

CHAPTER 3

3.3 TAXONOMIC HISTORY OF *ALOE BOWIEA*
SMITH, G.F. 1991. Additional notes on the taxonomic status and habitat of *Aloe bowiea* (Asphodelaceae: Alooideae). *Aloe* 28: 9-17.

CORRECTIONS

p. 16, middle column, ref. 20: 'ausgewählter', not 'ausgewhlter'
p. 17, right column, ref. 4: 'über', not 'ber'

CHAPTER 4

4.4.1 SMITH, G.F. 1988. A scanning electron microscopic investigation of the pollen morphology of *Chortolirion* Berger (Aloineae; Liliaceae). *South African Journal of Science* 84: 428-430.

CORRECTIONS

p. 430, right column, ref. 4: 'Engelmann', not 'Engelman'

CHAPTER 7

7.4 CONSERVATION STATUS OF *HAWORTHIA FASCIATA*

SMITH, G.F. 1991b. Populations of *Haworthia fasciata* (Willd.) Haw. are dwindling in urban Port Elizabeth, eastern Cape, South Africa. *British Cactus and Succulent Journal* 9: In press.

NOTES

This paper has since been published in volume 9(2): 42-44 of the journal. It appeared under the same title, bar the author citation of the species name. The text is also accompanied by two additional colour plates, viz. cover page and Fig. 1.

CHAPTER 8

SMITH, G.F. & VAN WYK, B-E. In press. Generic relationships in the Alooideae (Asphodelaceae). *Taxon.*

NOTES

This paper was accepted for publication in *Taxon* shortly before this thesis was submitted in partial fulfilment for the Ph. D. degree. Consequently the comments in the reviews could not be taken up in the version of the paper included in the thesis, i.e. as it was initially submitted for review. The major changes made to the manuscript can be summarized as follows:

1. The paper has been shortened to exclude evolutionary and biological data that are not directly relevant. Where exclusion of this type of information would have weakened our arguments on character polarization, we have, however, retained some of the evolutionary discussions.

2. The *Kniphofia* hypothesis has been excluded until a detailed analysis of the family as a whole can be made.

3. The descriptive geographical information for the genera has been summarized in the form of an area cladogram (an additional figure, Fig. 8) to show that the phylogenetic sequence of the genera is congruent with two major biogeographical events, but that it is not possible to reconstruct the sequence of these events from the proposed phylogeny.

4. Fig. 2 of the paper highlights basic problems around the monophyly of some genera. We were unable to find convincing apomorphies for these genera and have explicitly stated this. [See for example the top of page 296 of the thesis "... The controversy that has surrounded generic delimitation in the Alooideae is reflected by the lack of autapomorphies for some of the genera upheld in this study. Only *Gasteria* (three distinct apomorphies), *Chortolirion*, *Lomatophyllum* and *Poellnitzia* (one distinct apomorphy each) are reasonably well defined."] The weaknesses in the present classification system are clearly displayed in the proposed hypothesis and this may be helpful in showing others where to focus their attention.

CHAPTER 9

9.2.4. SMITH, G.F. 1990. Nomenclatural notes on the subsection *Bowieae* in *Aloe* (Asphodelaceae: Alooideae). *South African Journal of Botany* 56: 303-308.

CORRECTION

p. 306, Key, line4: '*Graminialoe*', not '*Graminaloe*'

ERRATA

Following the examination process it was brought to my attention that the dissertation contains a number of minor typographical and grammatical errors and some inconsistencies with regard to, e.g., the spelling of author citations. Many of these appeared anew or were not corrected between the time proofs left my hands and the time of printing. However, none of these errors should cause any confusion to the reader and only the following points warrant further elaboration.

1. Differences in the number of species included in a particular genus are due to different references being cited as authority (see e.g. *Aloe* and *Gasteria*, pp. 26 and 307).

2. p.146 para. 2 line 2: "33° 58'S not "34° 06'S".

3. p.157 insert after ref. 16:

   O'DOWD, D.J. & WILLSON, M.F. 1989. Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biological Journal of the Linnean Society* 37: 191—236.

4. p.174 para. 1 line 3: insert "Madagascan and" before "Mascarene".

5. p.337 Table 1 column 2: "4—16" not "14—16"; insert "dense," before "capitate".

6. p.337 column 2 Description line 5: insert ", rarely sessile" after "pedicellate".

7. p.338 column 1 Key..... line 3: insert "or very shortly exserted" after "included".

8. For Natal *Chortolirion* is known from a single accession only (Grid ref. unknown: Zululand, *Anon. s.n.* (K)!). For obvious reasons this vague collection record cannot be shown on Map 9.4.3.1 (p. 382). The presence of the genus in Natal is, however, reflected in Fig. 7, p. 315.