CHAPTER 1 INTRODUCTION

1.1 Background

The leaf succulent genus *Aloe* L. (Asphodelaceae; order Asparagales) is an iconic lilioid monocotyledonous group, owing to its popularity among succulent plant collectors and a long history of medicinal use. It is represented by 448 species (Newton 2001) throughout sub-Saharan Africa, the Arabian Peninsula and islands in the western Indian Ocean, including the Comoros, Madagascar, Mauritius, Reunion, Seychelles and Socotra (Figure 1.1).

Asphodelaceae and the related family Xanthorrhoeaceae are estimated to have evolved approximately 90 million years ago (Janssen & Bremer 2004). Emergent views of the biogeographical and evolutionary history of *Aloe*, which is absent from the fossil record, suggest the genus radiated from the highland region of South-East Africa (Holland 1978). It is likely that *Aloe* was introduced to Madagascar by an early dispersal event, and subsequent speciation on the island resulted in the 80 species of *Aloe* known on Madagascar today. The presence of approximately 40 species of *Aloe* on the Arabian Peninsula may be explained by vicariance associated with the separation of Arabia from Africa ca. 15 million years before present.

Species richness in *Aloe* has been positively correlated to diversity in available habitats (Holland 1978). Modes of speciation and factors such as hybridisation and ploidy in the evolution of *Aloe* are not fully understood. However, leaf succulence is thought to have contributed significantly to the adaptive success of *Aloe* in xeric environments. Succulence facilitates enhanced water regulation, together with anatomical adaptations such as sunken stomata and a thick cuticle, and physiological features such as Crassulacean acid metabolism (CAM) (Scott 2008). Available evidence supports the hypothesis that leaf succulence is an advanced state in *Aloe*, while barely succulent, diminutive forms and woody, tree-like forms are primitive (Smith 1991, Zonneveld 2002).

Besides the extraordinary endemism of *Aloe* on Madagascar, endemism is typically high elsewhere, ranging from about 60% in the *Flora of Tropical East Africa* region (Carter 1994) to 87% in the *Flora of Ethiopia and Eritrea* region (Demissew et al. 2001). A relative minority of species of *Aloe* are widespread. Checklist data (Newton 2001) show that an estimated 70% of accepted species of *Aloe* spp. occur within the political boundaries of only one country. The genus is well represented in floristic units of exceptional diversity, such as the Succulent Karoo (van Wyk &

Smith 2001) and Somalia-Masai regional centre (White 1983). Many species of *Aloe* occur in regions recognised as biodiversity hotspots, where high rates of endemism are coupled with high threat status (Myers 2000), including the Horn of Africa, Maputaland-Pondoland-Albany, Cape Floristic Region and Succulent Karoo hotspots (Myers 2000; Mittermeier 2004). In addition to habitat loss, the greatest specific threats to *Aloe* are collecting for horticultural purposes and wild harvesting for the extraction of natural products. About 4% of *Aloe* species have been assessed according to International Union for Conservation of Nature (IUCN) Red List criteria, and the level of national protection afforded to the genus varies widely. Threats and conservation status have been most thoroughly considered for *Aloe* spp. in South Africa (e.g. van Jaarsveld & Smith 1997; Smith et al. 2000). However, the trade in all species of *Aloe* (with the exception of *A. vera*, a domesticated species) is monitored by the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Newton 2001).

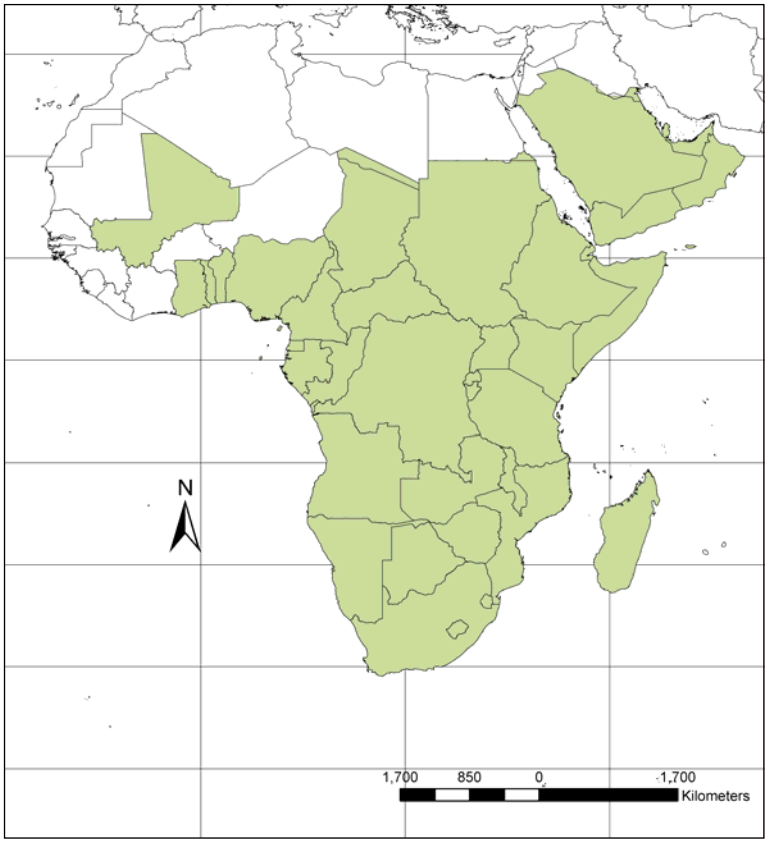

Figure 1.1 Recorded political distribution of *Aloe* L.

The use of *Aloe* for horticulture and medicine has been recorded throughout ancient history. In particular, *A. vera* (L.) Burm.f. (also known under the persistent synonym, *A. barbadensis* Mill.) has, at times, been of great economic value as a source of natural products. The major commodity from *Aloe* spp. was historically a concentrated, dried preparation of the leaf exudate known as 'drug aloes' or, more recently, 'bitter aloes'. However, the leaf mesophyll ('aloe gel') of *Aloe* spp., notably *A. vera*, is of greater economic importance today; the dried, powdered tissue is used globally in foods, cosmetics and numerous other commercial products. While *A. vera* is cultivated and is no longer known in the wild, many other species of *Aloe* continue to be wild harvested for natural products. A plethora of traditional uses of *Aloe* (Grace et al. 2009; Chapter 3 of the present study) and global popularity as a collectable succulent group, dating to 16th century Europe, have been recorded.

Due to its popularity, *Aloe* has received considerable research attention that has often added to, rather than resolved, the complex taxonomy of the group. Species delineation is remarkably inconsistent, exaggerated and geographically biased. The systems of Berger (1908) and later Reynolds (1950, 1966) provide a framework for the arrangement of *Aloe.* A resolved classification reflecting postulated evolutionary relationships is required to facilitate the conservation, opportunities for use in arid environments, and research into the biology and biodiversity of *Aloe*.

A lack of predictive power in the classification poses difficulties for identification of *Aloe* spp., particularly of species in problematic and neglected infrageneric groups such as section *Pictae* Salm-Dyck (= section *Maculatae* Baker, series *Saponariae* Berger), the so-called maculate species complex. The section is distinguished by patterned leaf surfaces, a basally inflated corolla and perianth constriction above the ovary (Fig. 1.2). However, it is a "heterogeneous and frequently most exasperating group, and it is often impossible to know where one species ends and the next begins" (Reynolds 1966). Putative hybridisation, active speciation (Reynolds 1966; Glen and Hardy 2000) and a paucity of phylogenetic information have precluded a conclusive classification of section *Pictae*.

Figure 1.2 Maculate aloes: 1, 2 *Aloe maculata*; 3 *A. longibracteata*; 4 *A. umfoloziensis*; 5 *A. parvibracteata*; 6 *A. monotropa*; 7 *A. dewetii*; 8 *A. immaculata*; 9 *A. affinis*. Photographs O.M. Grace except 1, Mr. E van Wyk.

1.2 Taxonomic history

Asphodelaceae are an Old World family comprising 15 genera and approximately 700 species, of which *Aloe* is the oldest and largest. Two unresolved subfamilies are recognised: Alooideae, concentrated in southern Africa, and Asphodeloideae, which extend to the Mediterranean, Asia, Australia and New Zealand. *Aloe* was first circumscribed according to the Latin binomial system in *Species Plantarum* (Linneaus 1753), but was already a widely known medicinal and horticultural subject. The original circumscription of *Aloe* included 12 accepted species now recognised in *Agave* L., *Aloe*, *Gasteria* Duval., *Haworthia* Duval. and *Kniphofia* Moench; the generic boundaries of these genera in Asphodelaceae have remained uncertain, particularly among polyphyletic alooid genera. A detailed pre-Linnean history of *Aloe* was given by Reynolds (1950).

Significant innovations in the taxonomic history of *Aloe* in the 250 years since it was published have included the circumscription of Alooideae (Batsch 1802) (Figure 1.3) and the first comprehensive infrageneric classification of the genus into series and sections (Berger 1908). Earlier workers, including Duval (1809), Haworth (1801, 1812), Salm-Dyck (1836–1863) and Baker (1896) had introduced infrageneric groups to *Aloe*, but Berger's (1908) system presented a solution to dealing with the considerably expanded genus, in which 170 species were recognised. A multi-volume revision (Reynolds 1950, 1966) was likewise necessitated by the ongoing proliferation of species recognised in *Aloe* (to 324 species) which led Reynolds (1950) to conclude that "There is almost as much individuality and variation among species of *Aloe* as there is among human beings". *Aloe* has since been the subject of several Flora treatments, including the *Flora of Southern Africa* (Glen and Hardy 2000) in which the authors introduced new infrageneric groups, whereas Carter (1994) did not include groups in her treatment for the *Flora of Tropical East Africa* (Carter 1994), as "it has proved virtually impossible to arrange the species of the Flora in a sensible phylogenetic sequence."

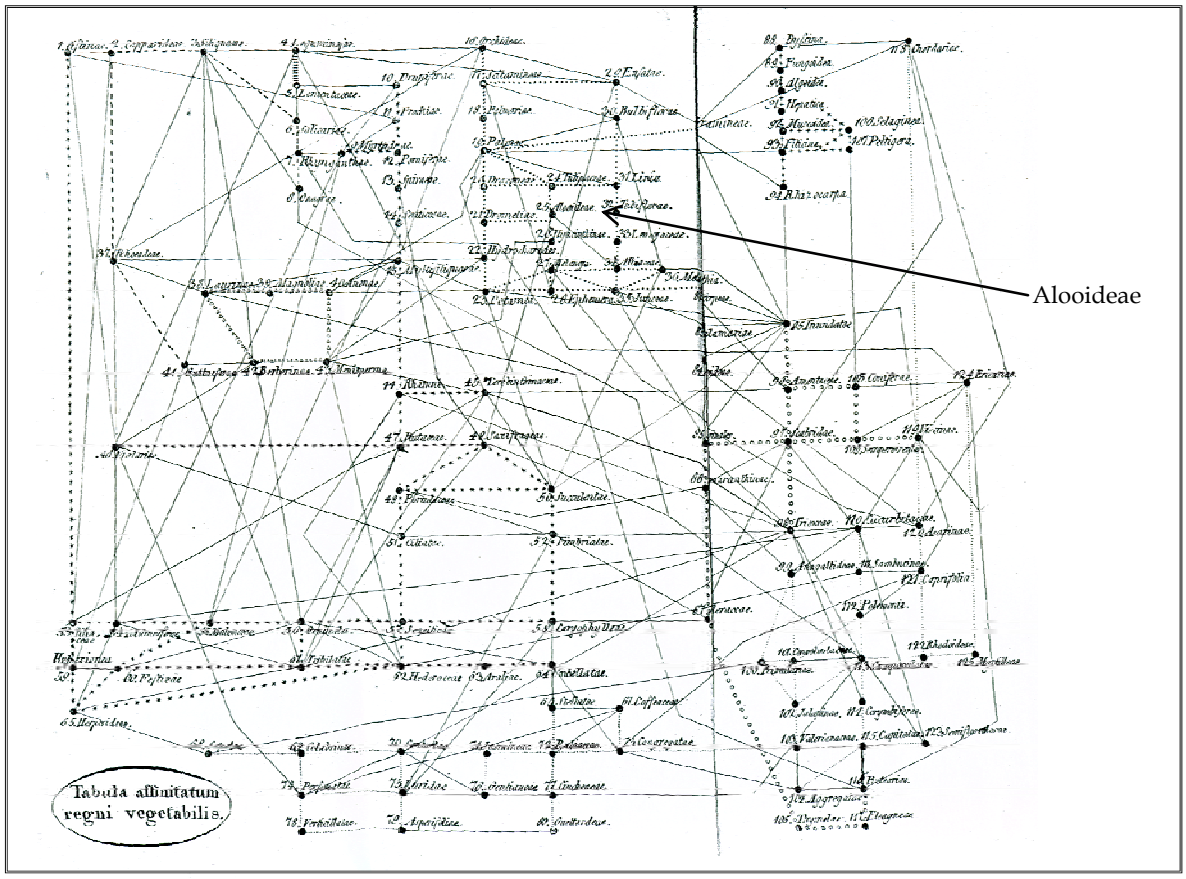

Figure 1.3 Batsch's (1802) family scheme including the first circumscription of Alooideae.

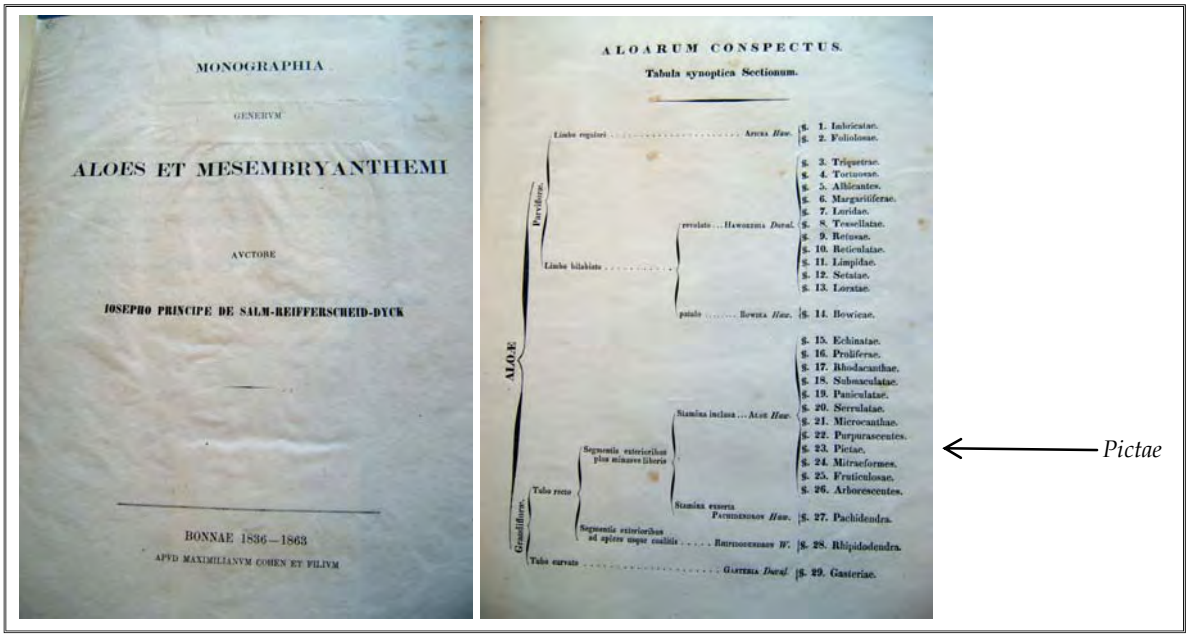

Figure 1.4 Salm-Dyck's (1836–1863) treatment of *Aloe* including section *Pictae*.

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The maculate group has been largely overlooked in studies of *Aloe*, and innovations in the infrageneric arrangement of *Aloe* have had minor influences on it. However, the delineation of species has not escaped the inconsistencies and nomenclatural confusion that affect the taxonomy of *Aloe*. Maculate taxa have variously been circumscribed at the ranks of section (*Pictae* Salm-Dyck; *Maculatae* Baker) and series (*Saponariae* Berger) (Table 1.1).

Although Berger's (1908) was the first comprehensive treatment, priority lies with *Pictae* Salm-Dyck as the sectional name for the maculate group (Figure 1.4). There is little support for the names *Maculatae* Baker or *Saponariae* Berger to be upheld. Baker (1896) neglected to identify a type specimen for his section, while the type of series *Saponariae* Berger, *Aloe saponaria* (Ait.) Haw., has subsequently been reduced to a synonym of *A. maculata* All., the type of section *Pictae* Salm-Dyck. The name, which Salm-Dyck (1836–1863) presumably elected as a reference to the prominent leaf markings of maculate taxa, was reinstated by Glen and Hardy (2000) in their account of *Aloe* in the *Flora of Southern Africa*. The taxonomic attention afforded *Aloe* is reflected in the number of maculate species recognised by Berger (1908) and Groenewald (1941), but the section *Pictae* could be reduced in size were proposals by Glen and Hardy (2000) and Wabuyele (2006) accepted.

Table 1.1 Classification of the maculate species complex

Author	Infrageneric taxon	Type	Taxa included	Currently accepted names
Salm-Reifferscheidt-Dyck (1837)	Section *Pictae* Salm-Dyck	*A. maculata* All.	4	2
Baker (1896)	Section *Maculatae* Baker	Not cited.	10	3
Berger (1908)	Series *Saponariae* A.Berger	*A. saponaria* (Aiton) Haw.	27	16
Groenewald (1941)	Section *Maculatae* Baker	Not cited.	42	35
Reynolds (1950)	Series *Saponariae* A.Berger	*A. saponaria* (Aiton) Haw.	31	30
Reynolds (1966)	Series *Saponariae* A.Berger	*A. saponaria* (Aiton) Haw.	10	9
Glen & Hardy (2000)	Section *Pictae* Salm-Dyck	*A. maculata* All.	14	14

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Table 1.2 Taxa in the maculate species complex, as recognised by various authors

Taxon	Accepted name[1]	Author[2]						
		Salm-Dyck (1836–1863)	Baker (1896)	Berger (1908)	Groenewald (1941)	Reynolds (1950)	Reynolds (1966)	Glen & Hardy (2000)
Aloe affinis A.Berger	*A. affinis* A.Berger			•×	×	×		×
A. ammophila Reynolds	*A. zebrina* Baker				×	×	•×	
A. amudatensis Reynolds	*A. amudatensis* Reynolds						•×	
A. angolensis Baker	*A. angolensis* Baker		•×		×			×
A. barbertoniae Pole-Evans	*A. barbertoniae* Pole-Evans				*×	×		
A. boehmii Engl.	*A. lateritia* Engl. var. *lateritia*			*×				
A. branddraaiensis Groenew.	*A. branddraaiensis* Groenew.				•×	×		×
A. burgersfortensis Reynolds	*A. burgersfortensis* Reynolds				×	•×		
A. chimanimaniensis Christian	*A. swynnertonii* Rendle				*×	×		
A. commutata Engl.	*A. macrocarpa* Tod.			*×				
A. comosibracteata Reynolds	*A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy				*×	×		
A. constricta A.Berger	–			•×				
A. davyana Schönland	*A. greatheadii* var. *davyana* (Schönland) Glen & D. S. Hardy			*×	×	×		
A. davyana var. *subolifera* Groenew.	*A. greatheadii* var. *davyana* (Schönland) Glen & D.S. Hardy				•×			
A. decurvidens Groenew.	*A. parvibracteata* Schönland				•×			
A. deflexidens Groenew.	–				•×			
A. dewetii Reynolds	*A. dewetii* Reynolds				*×	×		×
A. duckeri Christian	*A. duckeri* Christian						*×	

Table 1.2 *(continued)*

Taxon	Accepted name[1]	Author[2]						
		Salm-Dyck (1836–1863)	Baker (1896)	Berger (1908)	Groenewald (1941)	Reynolds (1950)	Reynolds (1966)	Glen & Hardy (2000)
A. dyeri Schönland	*A. dyeri* Schönland			*×	×	×		×
A. ellenbeckii A.Berger	*A. ellenbeckii* A.Berger			•×			×	
A. fosteri Pillans	*A. fosteri* Pillans				*×	×		×
A. gasterioides Baker	–		•×	×				
A. graciliflora Groenew.	*A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy				•×	×		
A. grahamii A.Berger	–			•×				
A. graminicola Reynolds	*A. lateritia* var. *graminicola* (Reynolds) S.Carter						•×	
A. grandidentata Salm-Dyck	*A. grandidentata* Salm-Dyck	•×	×	×	×	×		×
A. greatheadii Schönland	*A. greatheadii* Schönland			*×	×	×	×	×
A. greenii Baker	*A. greenii* Baker		•×	×	×	×		×
A. greenwayii Reynolds	*A. leptosiphon* A.Berger						•×	
A. hereroensis Engl.	*A. hereroensis* Engl.			*×				
A. heteracantha A.Berger	–			•×				
A. immaculata Pillans	*A. immaculata* Pillans				*×	×		
A. keithii Reynolds	*A. keithii* Reynolds				*×	×		
A. kilifensis Christian	*A. kilifensis* Christian						*×	
A. komatiensis Reynolds	*A. parvibracteata* Schönland				*×	×		

Table 1.2 *(continued)*

Taxon	Accepted name[1]	Author[2]						
		Salm-Dyck (1837–1863)	Baker (1896)	Berger (1908)	Groenewald (1941)	Reynolds (1950)	Reynolds (1966)	Glen & Hardy (2000)
A. labiaflava Groenew.	A. greatheadii var. davyana (Schönland) Glen & D.S.Hardy				•×			
A. lateritia Engl.	A. lateritia Engl.			*×			×	
A. latifolia Haw.	*A. maculata* All.	*×	×	×				
A. laxissima Reynolds	*A. zebrina* Baker				*×			
A. leptophylla N.E.Br. ex Baker	*A. maculata* All.		*×	×				
A. leptosiphon A.Berger	*A. leptosiphon* A.Berger			•×				
A. lettyae Reynolds	*A. lettyae* Reynolds				*×	×		
A. longibracteata Pole-Evans	*A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy				*×	×		
A. lusitanica Groenew.	*A. parvibracteata* Schönland				*×			
A. macracantha Baker	–		•×	×				
A. macrocarpa Tod.	*A. macrocarpa* Tod.			*×			×	
A. maculata All.	*A. maculata* All.							*×
A. menyharthii Baker	*A. menyharthii* Baker			*×				
A. monotropa I. Verd.	*A. monotropa* I.Verd.							*×
A. mudenensis Reynolds	*A. mudenensis* Reynolds				*×	×		×

Table 1.2 *(continued)*

Taxon	Accepted name[1]	Author[2]						
		Salm-Dyck (1837–1863)	Baker (1896)	Berger (1908)	Groenewald (1941)	Reynolds (1950)	Reynolds (1966)	Glen & Hardy (2000)
A. mutans Reynolds	A. greatheadii var. davyana (Schönland) Glen & D. S. Hardy				*×	×		
A. obscura Baker	–		•×	×				
A. parvibracteata Schönland	A. parvibracteata Schönland				*×	×		×
A. petrophila Pillans	A. petrophila Pillans				*×	×		
A. picta Salm-Dyck	–	×						
A. pongolensis Reynolds	*A. parvibracteata* Schönland				*×			
A. pongolensis var. *zuluensis* (Reynolds) (Reynolds)	*A. parvibracteata* Schönland				*×			
A. prinslooi I.Verd.	*A. prinslooi* I.Verd.							*×
A. pruinosa Reynolds	*A. pruinosa* Reynolds				*×	×		×
A. runcinata A.Berger	–			•×				
A. saponaria (Ait.) Haw.	*A. maculata* All.	*×	×	×	×	×	×	
A. saponaria var. *ficksburgensis* Reynolds	*A. maculata* All.				*×			
A. serrulata Baker	–		•×					
A. simii Pole-Evans	*A. simii* Pole-Evans				*×	×		×
A. spuria Berger	–			*×				
A. striata Haw.	*A. striata* Haw.			*×				
A. suffulta Reynolds	*A. suffulta* Reynolds				*×			

Table 1.2 *(continued)*

Taxon	Accepted name[1]	Author[2]						
		Salm-Dyck (1837–1863)	Baker (1896)	Berger (1908)	Groenewald (1941)	Reynolds (1950)	Reynolds (1966)	Glen & Hardy (2000)
A. swynnertonii Rendle	*A. swynnertonii* Rendle						*×	×
A. transvaalensis Kuntze	*A. zebrina* Baker			*×	×	×		
A. tricolor Baker	–		•×					
A. umfoloziensis Reynolds	*A. umfoloziensis* Reynolds				*×	×		
A. vandermerwei Reynolds	*A. vandermerwei* Reynolds					•×		
A. verdoorniae Reynolds	*A. greatheadii* var. *davyana* (Schönland) Glen & D. S. Hardy				*×	×		
A. vogtsii Reynolds	*A. vogtsii* Reynolds				*×	×		
A. zebrina Baker	*A. zebrina* Baker		•×	×		×	×	×

[1]Sensu Newton (2001).
[2]Key: ×, author recognised species in maculate group; •, species named by this author prior to/in this treatment; *, first recognition in maculate group of a species not named by this author.

1.3 Rationale

The complex taxonomy and unresolved classification of *Aloe* affect its conservation, opportunities for future use, and hinder research into their biology. The rationale for the present research lay in addressing these obstacles. The research intended to advance the understanding of the contemporary uses and value of *Aloe*, and to contribute comparative data for resolving taxonomic uncertainties in problematic species.

A substantial body of literature recounts the long history of *Aloe* in traditional use, horticulture and the natural products trade. Indeed, the uses, properties, economic and social importance of *A. vera* have been recorded for thousands of years, whereas the documented history of less widely used species of *Aloe* is comparatively limited. The ways in which *Aloe* spp. are used and valued have implications for their conservation and future utility. An ethnobotanical literature review of the genus (with the exception of *A. vera*) was undertaken to provide a baseline for an assessment of modern uses and value.

Systematic studies of *Aloe* undertaken in recent decades have largely neglected problematic groups such as section *Pictae.* Potentially informative aspects of the phytochemistry, morphology and anatomy of *Aloe*, identified in previous studies, were selected for evaluation in section *Pictae.* Novel investigations into the molecular biology of the section were conducted. Findings from the present research were used to draw conclusions on systematic relationships among maculate species of *Aloe* and to propose a natural (evolutionary) concept of section *Pictae.*

1.4 Research approach

This research project was approached from a multidisciplinary perspective, combining a variety of methods and theoretical reasoning to test the formulated hypotheses.

Among the novel contributions intended from the research were the first comprehensive assessment of the ethnobotany of *Aloe*, and the first systematic study of maculate species in *Aloe*

section *Pictae*. The objectives of the research were, therefore, achieved using intensive literature studies, field sampling and laboratory techniques. Research concepts are presented below.

Ethnobotany

- Intensively search varied information resources for uses of *Aloe* documented since the nineteenth century; consult as widely as possible the printed and electronic resources accessible in the extensive libraries of the Royal Botanic Gardens, Kew.

- Compile a dataset of these records following the Economic Botany Data Collection Standard (Cook, 1995) and use accepted methods to quantify these utility data (Chapter 3).

- Evaluate the literature-based method for ethnobotanical survey using a case study of the medicinal uses of *Aloe* spp. in southern Africa (Chapter 3).

Systematics

- Conduct a thorough survey of potentially informative taxonomic characters in the problematic section *Pictae*, by sampling widely within the group using plant material gathered from natural populations and curated living collections in South Africa and the United Kingdom.

- Generate novel comparative data for species in section *Pictae*, including DNA sequences (Chapter 4), phytochemical chromatograms (Chapter 5) and digital micrographs (Chapter 6).

- Analyse these data to assess the infrageneric status of section *Pictae* and infraspecific relationships among maculate species.

1.5 Objectives

- To advance the understanding of the value and diversity of the succulent-leaved monocot genus *Aloe*.

- To assess the uses and biocultural value of *Aloe*, and the influence of these factors on the conservation of the group.

- To test the literature as a surrogate for ethnobotanical field study, using the medicinal uses of *Aloe* in southern Africa as a case study.

- To address a paucity in comparative data available for maculate species of *Aloe*.

- To determine the systematic significance of DNA sequence data, leaf chemistry and leaf surface morphology in section *Pictae*.

- To survey the leaf chemistry of species in section *Pictae* and identify constituents of systematic relevance in the group.

- To identify and test the systematic significance of an anthrone *C*-glycoside previously speculated to be unique to maculate species of *Aloe* occurring in East Africa.

- To compare micromorphological features of leaf surfaces among species in section *Pictae* and identify characters of systematic significance.

- To evaluate, using available evidence, species relationships and circumscription of section *Pictae* to inform a future taxonomic revision of *Aloe*.

1.6 Hypotheses

- *Aloe* is a popular succulent genus of considerable economic importance, but is threatened by non-sustainable collecting. Understanding of the contemporary uses, value and diversity of the genus *Aloe* could inform effective its conservation and opportunities for sustainable use.

- The literature is an acceptable surrogate for resource-intensive ethnobotanical field study to evaluate the uses and value of *Aloe*.

- Documented uses of *Aloe* reflect the biocultural value of the group and can be quantified using consensus analysis methods.

- The contemporary use of species of *Aloe* in southern Africa is reflected by recorded uses.

- The present circumscription and species delineation does not reflect evolutionary relationships among maculate species of *Aloe*.

- Phylogenetic interpretations of nuclear and plastid data have indicated the current infrageneric classification of *Aloe* includes artificial (paraphyletic) elements. A phylogenetic study of nuclear and plastid data will confirm monophyly in section *Pictae.*

- Certain secondary metabolites are indictors of relatedness among species in *Aloe.* Relationships among maculate species are reflected by UV-absorbing compounds.

- An anthrone *C*-glycoside provides a chemical marker for maculate species of *Aloe.*

- Variation in leaf surfaces and stomata in *Aloe* correlate with certain taxonomic units. Leaf surface morphology and stomatal anatomy reflect species relationships in section *Pictae*.

- Systematic data can be used to clarify evolutionary relationships in section *Pictae* , its circumscription and the delineation of maculate species.

1.7 Thesis structure

This thesis comprises a series of multidisciplinary contributions and three general sections, including an introduction to the research and arguments (present Chapter), an overview of general materials and methods used (Chapter 2) and discussion and overall conclusions drawn from the research (Chapter 7).

A study of the ethnobotany and biocultural value of *Aloe* is presented in Chapter 3. The complete list of references consulted during the preparation of Chapter 3 is given as supplementary material in Appendix A. Three systematic studies of comparative characters in the taxonomically problematic section *Pictae*, the maculate species complex, are presented. These deal with the phylogeny (Chapter 4), leaf phytochemistry (Chapter 5) and leaf micromorphology (Chapter 6) of the group. Additional phytochemical data are presented in Appendix B and spectral data of species studied are included on a supplementary CD.

Papers published or submitted for publication in the peer reviewed literature are included in relevant Chapters. Hence, the format and styles required by different journals are reflected in the appearance of the thesis, and some unavoidable repetition in introductory and discursive remarks is evident. Tables of contents and references are given for each Chapter.

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