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Contributions to the systematics and biocultural value of *Aloe* L. (Asphodelaceae)

by

Olwen Megan Grace BSc, BSc (Hons), MSc (Natal)

Submitted in partial fulfilment of the requirements for the degree

PHILOSOPHIAE DOCTOR

in the Faculty of Natural and Agricultural Sciences (Department of Plant Science)

University of Pretoria

March 2009

Supervised by Prof. Dr. A. E. van Wyk

Co-Supervised by Prof. Dr. G. F. Smith

"I don't know of any tribe of plants which afford a more pleasing variety than these, for the odd shape of their leaves and manner of spotting, and being some of them covered as it were with pearls."

(Richard Bradley, *Dictionarium Botanicum* [T. Woodward & J. Peele, London, 1728], cited by Adrian Haworth, [1801] *A new arrangement of the genus* Aloe. *Transactions of the Linnean Society* 7: 1–28).

DECLARATION

I, Olwen Megan Grace, declare that the thesis which I hereby submit for the degree Philosophiae Doctor at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

3 March 2009

ABSTRACT

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Aloe L. (Asphodelaceae) is a monocotyledonous group of considerable popularity among succulent plant collectors and with a long history of medicinal use. It comprises ca. 500 species occurring throughout Africa, the Arabian Peninsula and western Indian Ocean islands. The first comprehensive ethnobotanical study of *Aloe* (excluding the cultivated *A. vera*) was undertaken using the literature as a surrogate for data gathered by interview methods. Over 1400 use records representing 173 species were collated, the majority (74%) of which described medicinal uses, including species used for natural products. In southern Africa, 53% of approximately 120 *Aloe* species in the region are used for health and wellbeing. Consensus ratios indicated that the uses of *Aloe* spp. for medicine and pest control are of the greatest biocultural importance.

Utility has contributed to the recognition of diversity, taxonomic complexity, and conservation concerns, in *Aloe*. A systematic evaluation of the problematic maculate (spotted) species complex, section *Pictae*, was undertaken. New sequences were acquired of the nuclear ribosomal internal transcribed spacer (ITS), chloroplast *trnL* intron, *trnL–F* spacer and *matK* gene in 29 maculate species of *Aloe*. A well supported monophyletic (holophyletic) maculate group was recovered in phylogenetic trees of comparable topology generated by parsimony analysis and Bayesian inference. A representative of the related section *Paniculatae*, *A. striata*, was recovered in the maculate group, whereas doubtful maculate species with unusual floral morphology (*A. leptosiphon* and *A. suffulta*) comprised a sister group. Analogous patterns were identified in chemosystematic and comparative morphological studies of 34 and 36 maculate species, respectively, and insights were gained into interspecific relationships. The flavonoids isoorientin and isovitexin, and a new *C*-glycosylanthrone, 6′-malonylnataloin, were characterised using hyphenated chromatographic techniques and nuclear magnetic resonance (NMR) spectroscopy. Leaf surface sculpturing, stomata and lobes surrounding the epistomatal pore observed under a scanning electron microscope (SEM) are of potential taxonomic significance. Available evidence indicates that floral characters, namely a basally swollen perianth with constriction above the ovary, are of greater significance than maculate leaves as synapomorphies for section *Pictae*. An evolutionary hypothesis for section *Pictae* excludes marginal maculate species with unusual flowers.

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KEYWORDS: *Aloe*, Asphodelaceae, biocultural value, *C*-glycosylanthrone, consensus analysis, epistomatal pore, ethnobotany, flavonoid, leaf surface, maculate, molecular data, *Paniculatae*, phylogeny, *Pictae*, spotted, stomata, synapomorphy, systematics, taxonomy.

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CONTENTS

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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).

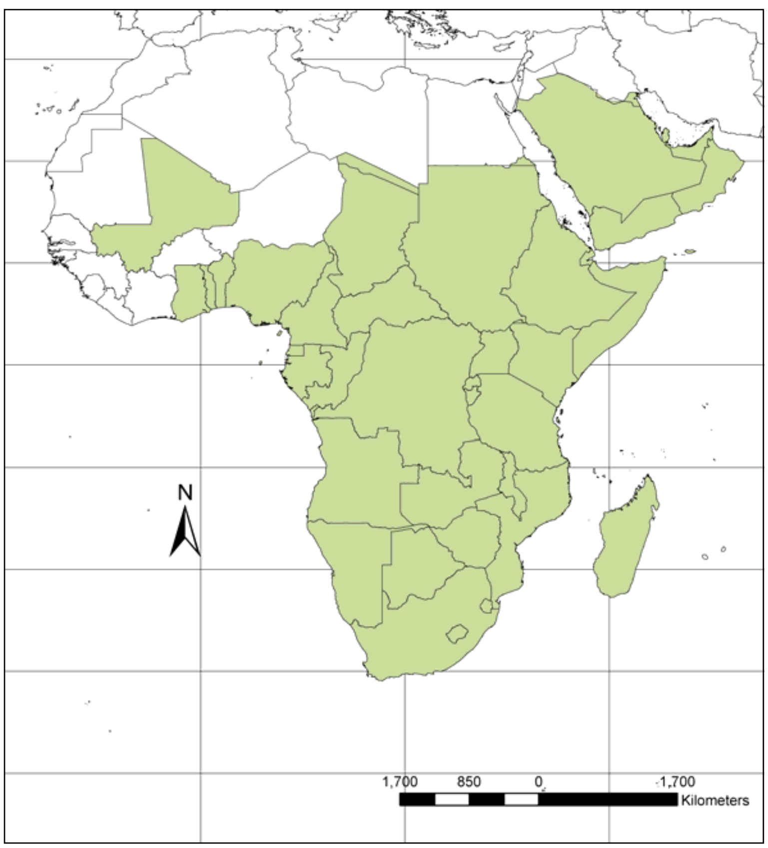

Figure 1.1 Recorded political distribution of *Aloe* L.

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 16^{th} 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."

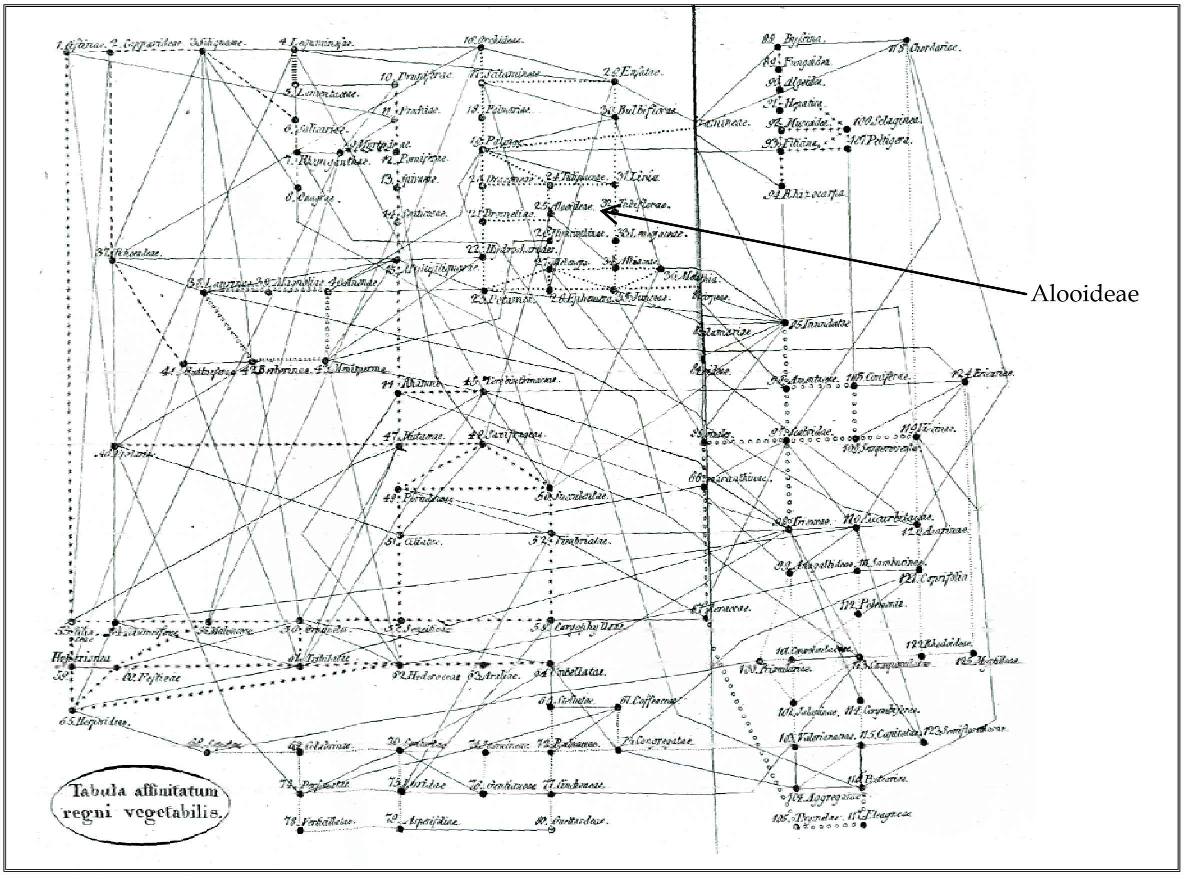

Figure 1.3 Batsch's (1802) family scheme including the first circumscription of Alooideae.

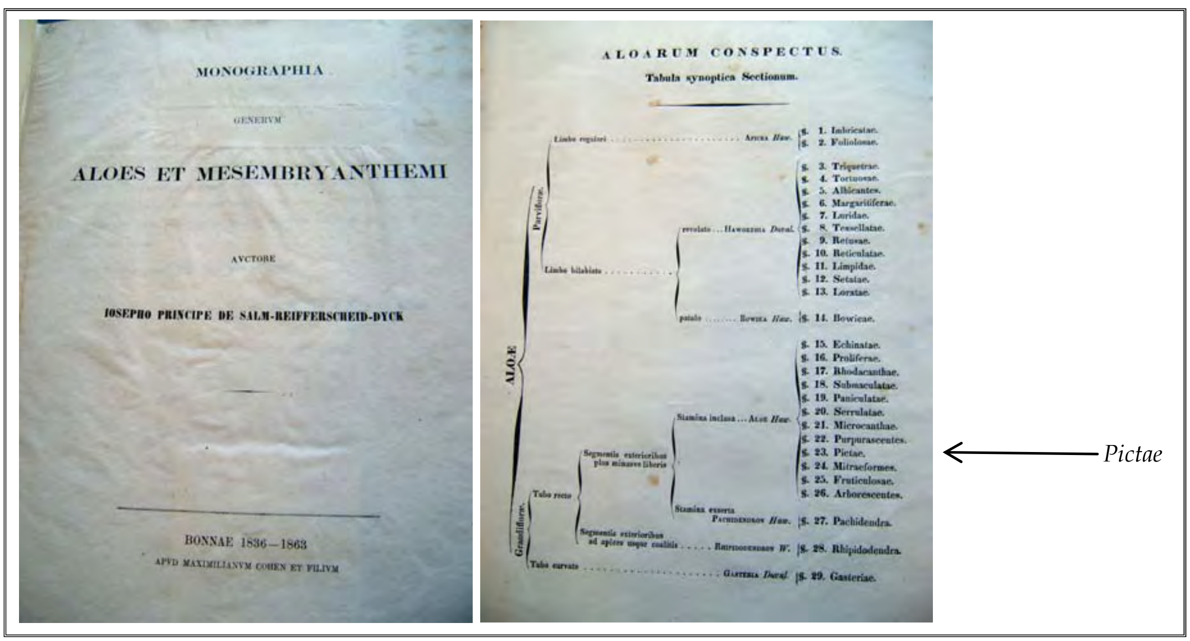

Figure 1.4 Salm-Dyck's (1836–1863) treatment of *Aloe* including section *Pictae*.

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*	*A. greatheadii* var. *davyana*				•×			
Groenew.	(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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Chapter 2 Materials and Methods

2.1 Material

An overview of materials used during this research project is presented. Comparatives studies undertaken during this research were primarily concerned with section *Pictae*, and effort was made to sample thoroughly within this taxonomic unit and associated species in the so-called maculate species complex. Species classified in other infrageneric groups within *Aloe* and neighbouring genera were included as outgroups. Material for experimental purposes was collected from plants of field provenance kept in glasshouses at the Royal Botanic Gardens, Kew, from natural populations in South Africa or from pressed herbarium specimens. Voucher specimens of field collections were deposited in the National Herbarium in South Africa (PRE) and the herbarium at Kew (K), where voucher specimens of *ex hort* material were deposited (Table 2.1). Localities (Figures 2.1 and 2.2) are given on a large scale due to the sensitivity of locality data for certain rare species threatened by plant collectors.

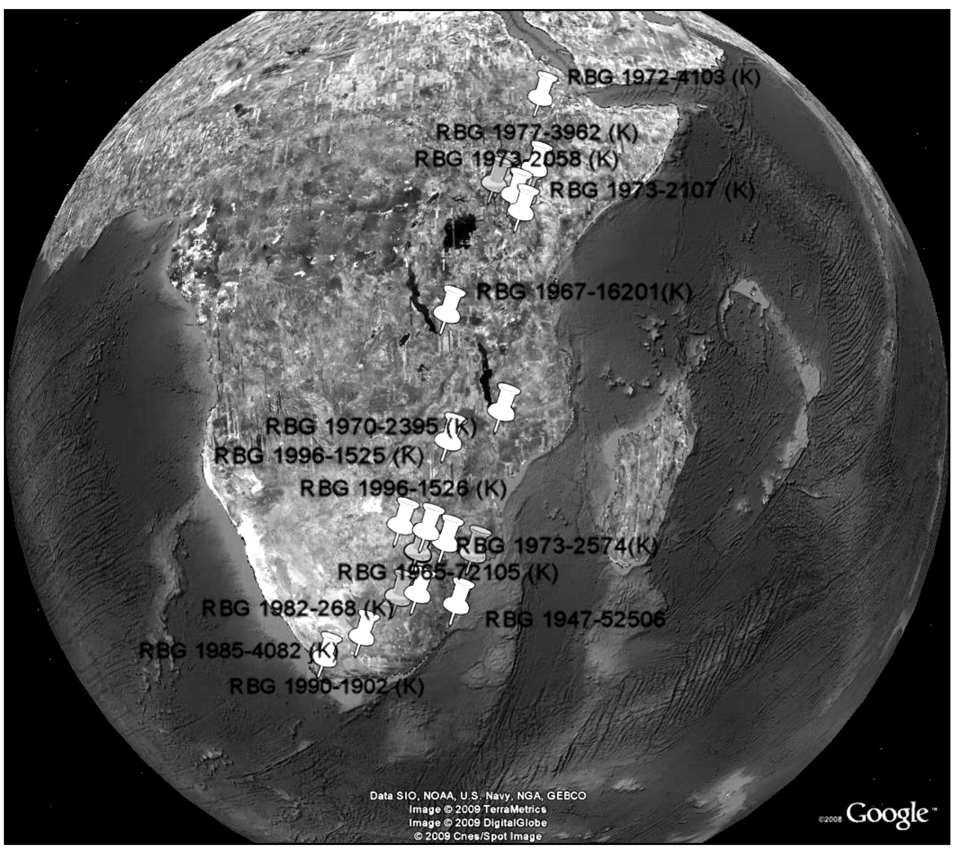

Figure 2.1 Approximate origin localities of plant material at Kew used in this study, labels are Kew Living Collection accession numbers (see Table 2.1).

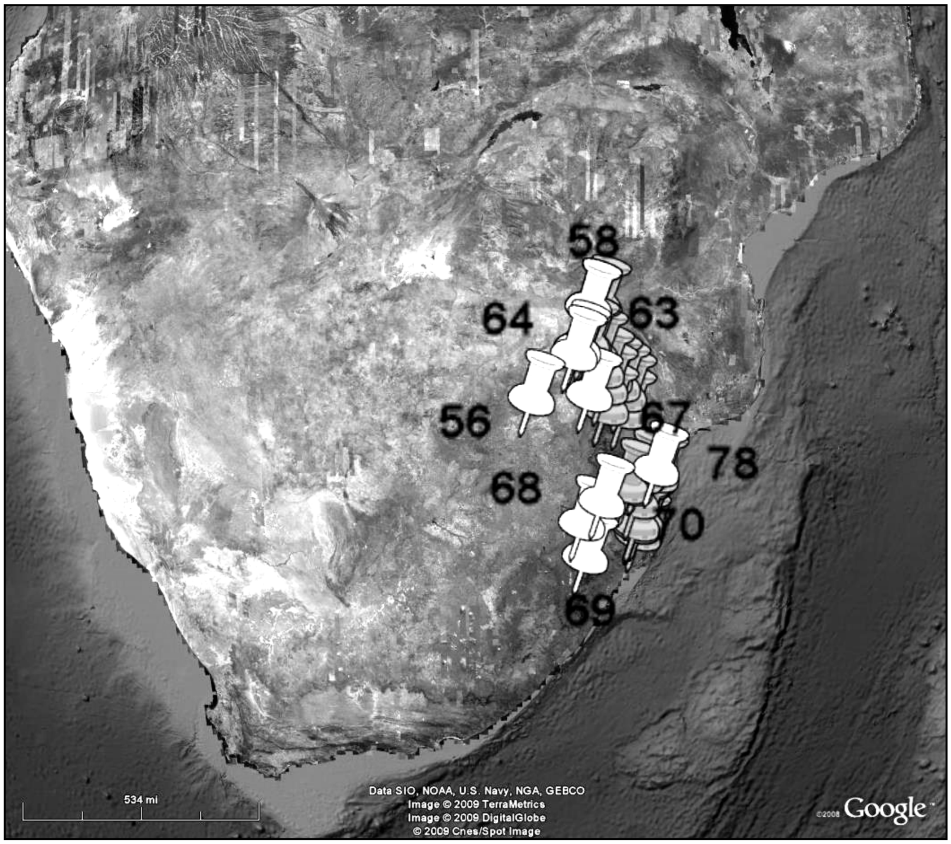

Figure 2.2 Approximate localities of plant material collected for this study, labels are Grace collector's numbers (see Table 2.1).

2.2 Methods

An overview of methods used during this research project is presented. Detailed methods used for comparative studies are described in respective Chapters.

Ethnobotany

The biocultural and economic value of *Aloe* L. was assessed using the literature as a surrogate for ethnobotanical field study (Chapter 3). Approximately 500 references were surveyed by searching library catalogues and information repositories, and by browsing library shelves. Most sources were located in the Library, Art and Archives collections of the Royal Botanic Gardens, Kew. Documented uses and useful properties of species of *Aloe* were recorded. Data were analysed and subjected to consensus analysis, where a mathematical formula is applied to quantify the relative importance of use categories.

Phylogenetics

DNA sequences were obtained for representatives of section *Pictae*, supplemented by published sequences available for ingroup and outgroup species. The plastid *trnL–F* intron and spacer, and *matK* gene and the nuclear ribosomal Internal Transcribed Spacer (ITS) were amplified and sequenced. Phylogenetic reconstructions from these data were obtained with statistical models for parsimony supported by bootstrap and consensus tests, as well as maximum likelihood using Bayesian inference (Chapter 4).

Phytochemistry

The leaf chemistry of species in section *Pictae* was surveyed using hyphenated chromatographic techniques (Chapter 5). Qualitative comparative data were analysed by quantifying the peak area of constituents shown on chromatograms from high performance liquid chromatography (HPLC). Mass spectrometry was used to identify known flavonoids, while nuclear magnetic resonance spectroscopy was used to characterise a novel anthrone *C*-glycoside.

Micromorphology

Leaf material of species in section *Pictae* were fixed and mounted appropriately for examination under scanning electron microscope (SEM) and light microscope. Digital micrographs of leaf surfaces and transverse sections were recorded (Chapter 6).

Table 2.1 Plant material used for comparative studies (synonyms recognised at time of collection shown in parentheses)

Taxon	Voucher and herbarium[1]	Collection locality[2]
Aloe affinis A.Berger	Grace 87	Mac Mac Falls, South Africa
A. amudatensis Reynolds	RBG 1977-6734 (K)	Weiwei, Kenya
A. barbertoniae Pole-Evans	Grace 85	Barberton, South Africa
A. branddraaiensis Groenew.	RBG 1957-14502 (K)	South Africa
A. burgersfortensis Reynolds	RBG 1965-72105 (K)	Lydenburg, South Africa
A. burgersfortensis Reynolds	Grace 89	Burgersfort, South Africa
A. chabaudii Schönland	RBG 1996-1526(K)	Buffel's Drift, Zimbabwe
A. dewetii Reynolds	Grace 83	Alpha, South Africa
A. ellenbeckii A.Berger	RBG 1973-2107(K)	Nairobi, Kenya
A. ellenbeckii A.Berger	RBG 1977-2441 (K)	Marsabit, Kenya
A. ellenbeckii A.Berger (= *A. dumetorum*)	RBG 1977-3962 (K)	Marsabit, Kenya
A. fosteri Pillans	RBG 2003-1796 (K)	South Africa
A. fosteri Pillans	Grace 88	Ohrigstad, South Africa
A. grandidentata Salm-Dyck	RBG 1973-2520(K)	Orange Free State, South Africa
A. greatheadii Schönland	RBG 1996-1525 (K)	Harare, Zimbabwe
A. greatheadii var. *davyana* (Schönland) Glen & D.S. Hardy (= *A. graciliflora* Groenew.)	Grace 67	Tonteldoos, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S. Hardy (= *A. longibracteata* Pole-Evans)	Grace 66	Lydenburg, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy	RBG 1965-12201 (K)	Pretoria, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy (= *A. davyana*)	RBG 1973-2542 (K)	Pretoria, South Africa
A. greatheadii var. *greatheadii*	Grace 58	Louis Trichardt, South Africa
A. greatheadii var. *greatheadii*	Grace 61	Boyne, South Africa
A. greenii Baker	Grace 74	Eshowe, South Africa
A. immaculata Pillans	Grace 62	Chuniespoort, South Africa
A. immaculata Pillans	Grace 64	Chuniespoort, South Africa

Table 2.1 *(continued)*

Taxon	Voucher and herbarium[1]	Collection locality[2]
A. lateritia var. *graminicola* (Reynolds) S.Carter	RBG 1973-2058 (K)	Thompson's Falls, Kenya
A. lateritia var. *graminicola* (Reynolds) S.Carter (= *A. lateritia* var. *solaiana*)	RBG 1973-2070 (K)	Nanyuki, Kenya
A. leptosiphon A.Berger (= *A. greenwayi)*	RBG 1967-16201 (K)	Abercorn, Zambia
A. lettyae Reynolds	Grace 60	Haenertsburg, South Africa
A. macrocarpa Tod.	RBG 1972-4103 (K)	Adamitulla, Ethiopia
A. maculata All.	Grace 82	Ngome, South Africa
A. maculata All.	Grace 84	Carolina, South Africa
A. maculata All. (= *A. saponaria* var. *ficksburgensis*)	RBG 1982-268 (K)	Ficksburg, South Africa
A. maculata All. (= *A. saponaria*)	RBG 1990-1902 (K)	Cape Province, South Africa
A. monotropa I.Verd.	Grace 65	Mmafefe, South Africa
A. mudenensis Reynolds	RBG 1947-52506 (K)	Natal, South Africa
A. parvibracteata Schönland	Grace 77	Jozini, South Africa
A. parvibracteata Schönland	Grace 78	Ingwavuma, South Africa
A. parvibracteata Schönland	Grace 79	Pongola, South Africa
A. parvibracteata Schönland	Grace 80	Pongola, South Africa
A. petrophila Pillans	RBG 1973-2501 (K)	Transvaal, South Africa
A. prinslooi I.Verd. & D.S.Hardy	Grace 68	Colenso , South Africa
A. pruinosa Reynolds	Grace 69	Ashburton, South Africa
A. simii Pole-Evans	Grace 86	White River, South Africa
A. striata Haw.	RBG 1985-4082 (K)	Karoo, South Africa
A. suffulta Reynolds	RBG 1961-56203 (K)	Mozambique
A. swynnertonii Rendle	RBG 1970-2395 (K)	Livingstone Falls, Malawi
A. swynnertonii Rendle	Grace 59	Thohoyandou, South Africa
A. umfoloziensis Reynolds	Grace 71	Eshowe, South Africa

Table 2.1 *(continued)*

Taxon	Voucher and herbarium[1]	Collection locality[2]
A. umfoloziensis Reynolds	Grace 72	Eshowe, South Africa
A. umfoloziensis Reynolds	Grace 73	Eshowe, South Africa
A. umfoloziensis Reynolds	Grace 75	Eshowe, South Africa
A. umfoloziensis Reynolds	Grace 76	Eshowe, South Africa
A. vanbalenii Pillans	Grace 81	Nongoma, South Africa
A. vanrooyenii G.F.Sm. & N.R.Crouch	Grace 70	Muden, South Africa
A. vogtsii Reynolds	Grace 57	Louis Trichardt, South Africa
A. wollastonii Rendle (= *A. lateritia* var. *kitaliensis*)	RBG 1973-1982 (K)	Kitale, Kenya
A. zebrina Baker (= *A. ammophila* Reynolds)	Grace 63	Chuniespoort, South Africa
A. zebrina Baker (= *A. ammophila*)	RBG 1973-2574 (K)	Potgietersrus, South Africa

[1]K, Herbarium at Kew, United Kingdom; PRE, National Herbarium, Pretoria, South Africa.

[2]Original locality data may reflect historical or vague geographical names

CHAPTER 3 UTILITY

3.1Documented utility and biocultural value of *Aloe* L. (Asphodelaceae): a review

GRACE, O. M., SIMMONDS, M. S. J., SMITH, G. F. & VAN WYK, A. E. 2009. Documented utility and biocultural value of *Aloe* (Asphodelaceae): a review. *Economic Botany* 63: 167–178.

NOTES

The paper presented in 3.1 uses current names from Newton (2001). In a limited number of cases, this has resulted in anomalous use records such as the preservation of *A. elegans* with salt in India (Watt 1889), despite *A. elegans* being a species endemic to the Horn of Africa region described only in 1882 (Walker 2009 pers. comm.). The species cited in the source document (Watt 1889) was, in fact, *A. abyssinica*, now reduced to a synonym of *A. elegans.*

The ethnobotany of *Aloe* spp. on Socotra has been authoritatively documented in the following reference not cited in this Chapter:

MILLER, A. G., MORRIS, M. 2004. Ethnoflora of the Soqotra archipelago. Royal Botanic Gardens, Edinburgh.

ERRATUM

The correct reference for Pole-Evans (1919) is:

Pole-Evans, I. B. 1919. Our aloes: their history, distribution, and cultivation. *Journal of the Botanical Society of South Africa* 5: 11–16.

Documented Utility and Biocultural Value of *Aloe* L. (Asphodelaceae): A Review[1]

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Documented Utility and Biocultural Value of *Aloe* L. (Asphodelaceae): A Review. The genus *Aloe* L. (Asphodelaceae) comprises 548 accepted species, of which at least one-third are documented as having some utilitarian value. The group is of conservation concern due to habitat loss and being extensively collected from the wild for horticulture and natural products. Cultural value is increasingly important in the effective conservation of biodiversity. The present study evaluated the biocultural value of the known uses of *Aloe*, excluding the domesticated and commercially cultivated *A. vera*. Over 1,400 use records representing 173 species were collated from the literature and through personal observation; this paper presents a synopsis of uses in each of 11 use categories. Medicinal uses of *Aloe* were described by 74% of the use records, followed by social and environmental uses (both 5%). Species yielding natural products, notably *A. ferox* and *A. perryi*, were most frequently cited in the literature. Consensus ratios indicate that the most valued uses of *Aloe* are in medicine and pest control against arthropods and other invertebrates.

Key Words: *Aloe*; Asphodelaceae; biocultural value; conservation; Ethnobotany; medicine; Uses.

Introduction

The genus *Aloe* L. (Asphodelaceae), here used in a broad sense to include the segregate genus *Lomatophyllum* Willd., comprises 548 accepted species occurring in Africa, the western Indian Ocean Islands, and the Arabian Peninsula (Newton 2001). Like the related succulent-leaved genera *Gasteria* Duval and *Haworthia* Duval, *Aloe* enjoys popularity among succulent enthusiasts and horticulturalists. Furthermore, *A. vera* L. (= *A. barbadensis* Mill.) is cultivated globally as a source of natural products derived from the leaf exudate and mesophyll. Species such as *A. ferox* Mill. (Figs. 1, 2 and 3) and *A. secundiflora* Engl. support wild harvesting industries in South Africa and Kenya, respectively, supplying unprocessed natural products to export markets, particularly in Europe and Asia (Newton and Vaughan 1996; Oldfield 2004). The literature contains numerous references to the traditional uses of *Aloe* spp., but a comprehensive analysis of the biocultural value and documented uses of the genus has been lacking. Consequently, information on the ethnobotanical significance of *Aloe* has remained largely inaccessible, despite this knowledge being of potential importance in biodiversity conservation and ecotourism (Cocks 2006).

About 4% of *Aloe* species have been assessed according to the International Union for Conservation of Nature (IUCN) Red List criteria; the most endangered species are narrow endemics such as *A. suzannae* Decary and *A. helenae* Danguy on Madagascar and *A. pillansii* L.Guthrie in the Northern Cape, South Africa (IUCN 2007). These assessments identified habitat loss, plant collectors, and leaf exudate tappers as

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Economic Botany, 63(2), 2009, pp. 167–178.

Fig. 1. *Aloe ferox*, South Africa. Photograph Gideon Smith.

the principal threats to species of *Aloe*. Due to concerns regarding unsustainable harvesting from the wild for the horticulture and natural products industries, coupled with the difficulty of identifying sterile plant material of members of the group, trade in all species of *Aloe*, except the commercially cultivated *A. vera*, is regulated by the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Newton 2001).

The present study evaluated the biocultural value of the uses of *Aloe* by means of a synthesis of the uses documented in the literature, supplemented by personal observations. We previously reported on the therapeutic uses of *Aloe* in southern Africa, where most species are used medicinally (Grace et al. 2008). Here, we provide the first assessment of documented uses of *Aloe* throughout its range and across all categories. The results are discussed in the context of biocultural value and conservation, highlighted by selected examples of documented plant use to avoid unnecessary repetition of information published in the literature.

Materials and Methods

Literature Survey

Over 350 multidisciplinary publications, mostly in the English language, were surveyed for the uses and useful properties of *Aloe* spp. within their natural range, with the exception of the domesticated *A. vera* (Grace et al. 2008). The sources consulted spanned a period of over 169 years and included ethnographic accounts, Floras, peer-reviewed literature, theses, and the popular press.

The earliest reference consulted, Brande (1839), was among 32 references published prior to 1900 that generally referred to the provenance of drug aloes, their authentication, and commercial uses. References published later in the 19th century included several regional ethnobotanical accounts, such as those of Smith (1888) and Bryant (1909) on southern African ethnobotany and Holland (1922) on Nigerian useful plants. More recently, the uses of *Aloe* spp. have been documented in publications on various subjects, notably medicinal plants (e.g., Githens 1979; Kokwaro 1993) and horticulture (e.g., Jex-Blake 1934; De Wet 1996).

Fig. 2. The succulent leaves of *Aloe ferox* are used for their leaf exudate and mesophyll. Photograph Olwen Grace.

Fig. 3. The traditional method of collecting leaf exudate and mesophyll from *Aloe ferox* continues in South Africa today. Photograph Gideon Smith.

Monographs on *Aloe* published during the 20th century included those of Pole-Evans (1919) and the important contributions of Dr. G. W. Reynolds (e.g., Reynolds 1950, 1966).

Each documented use constituted a "use record" for a species; these were arranged in categories according to the Biodiversity Data Standard (formerly TDWG, the Taxonomic Database Working Group) on economic botany (Cook 1995). Accepted Latin binomial plant names are based on a checklist of the genus (Newton 2001). Nearly 800 vernacular plant names were gathered in 125 languages, of which 86% are in African languages, using the *Ethnologue* language compendium as a standard (Gordon 2005). In total, 1,467 use records for 173 accepted species and infraspecific taxa of *Aloe* were collated (Table 1).

Consensus Analysis

The utility value or biocultural significance of a species generally lies in the extent to which it is used. Culturally important plants are used by many people for the same purpose and are identifiable in the homogeneity of ethnobotanical information (Heinrich et al. 1998). Numerous methods have been developed to quantify this homogeneity as a measure of a taxon's value (for a detailed account, see Tardío and Pardo-de-Santayana [2008]). In the present study, consensus analysis was used to quantify homogeneity in the literature—a surrogate for ethnobotanical field study—in order to express the biocultural value of the known uses of *Aloe*.

The Informant Agreement Ratio derived by Trotter and Logan (1986) is a function of n_{ur}, the total number of use records per use category, and n_i, the total number of plant taxa recorded for that category:

$$\text{Consensus ratio} = \frac{n_{ur} - n_i}{n_{ur} - 1}$$

The formula was originally applied to quantify homogeneity among use records and identify medicinal plants possessing desired bioactivity among the household remedies of Mexican Americans in the state of Texas (Trotter and Logan 1986). The formula has since been applied to datasets that have ranged in volume and geographical extent from 2,260 records of 328 species in Tanzania (Schlage et al. 2000), four datasets each comprising up to 3,059 records of 445 species in Mexico (Heinrich et al. 1998), to 25,000 records of 2,735 species in North America (Moerman 2007). The present dataset differed principally from previous examples in that data were collected from the literature and referred to the known uses of plant species in a single genus throughout its range.

Results and Discussion

Medicines

The majority (73%) of documented uses refer to the use of about one-quarter of recognized species of *Aloe* in medicine. Excluding *A. vera*, the most frequently cited species is *A. ferox* (158 use records), a source of natural products known as Cape aloes, followed by *A. arborescens* Mill. (47 use records), *A. perryi* Baker (53), and *A. marlothii* A.Berger (45). Leaf exudate tapping on Socotra has been identified as a potential threat to the endemic *A. perryi*, the source of Socotrine aloes (Miller 2004). Four hundred and eighty-five use records referred to unspecified medicinal uses of 121 species, while the remainder could be

Table 1. CONSENSUS IN THE LITERATURE ON USES OF *Aloe spp.* (excluding *A. vera*).

Category	Sub-Category	Number of Use Records	Number of Taxa	Consensus Ratio
Medicines	Not recorded	485	121	0.75
	Infections and parasites	136	35	0.75
	Digestion	119	39	0.68
	Injuries	67	22	0.68
	Skin	42	17	0.61
	Pregnancy	33	17	0.50
	Sensory system	33	14	0.59
	Genito-urinary system	30	16	0.48
	Respiratory system	25	16	0.38
	Inflammation	19	11	0.44
	Poisonings	14	11	0.23
	Pain	14	10	0.31
	Muscular-skeletal system	14	8	0.46
	Undefined illness	13	9	0.33
	Endocrine system	8	7	0.14
	Blood system	6	4	0.40
	Nutrition	6	3	0.50
	Circulation	5	5	0
	Neoplasms	2	2	0
	Mental health	2	2	0
	Immune system	1	1	0
	Nervous system	1	1	0
	Abnormalities	1	1	0
Social uses		83	35	0.59
Vertebrate poisons		80	37	0.54
Environmental uses		78	44	0.44
Food		51	24	0.54
Materials		46	23	0.51
Non-vertebrate poisons		18	5	0.76
Animal food		16	10	0.40
Bee plants		8	6	0.29
Food additives		5	3	0.50
Fuel		2	2	0

classified in the subcategories of medicinal use discussed below.

Infections and Parasites. The use of *Aloe* spp. to treat infections and parasites was the most frequently cited of the medicinal uses for the genus; 136 use records were collected for 35 species. In particular, their widespread use as anthelmintic agents was recorded in history (e.g., *A. succotrina* All. in Lindley [1869]) and in contemporary sources (e.g., *A. dhufarensis* Lavranos in Ghazanfar [1994]). *A. dichotoma* Masson, an endangered species occurring in arid regions of Namibia and South Africa, is used to treat tuberculosis (van Damme and van den Eynden 2000; van den Eynden et al. 1992).

Besides medical uses against infections and parasites, 12 species are recorded in ethnoveterinary medicine against foot and mouth disease, lice, rabies, and African horse sickness (Watt and Breyer-Brandwijk 1962; ITFG and IITR 1996; van Damme and van den Eynden 2000).

Digestion. The literature contains numerous references to the use of *Aloe* spp. for digestive ailments, since this is the principal application of commercial preparations containing aloe products. In general, concentrated preparations of the leaf exudate ("drug aloes") are taken for laxative effects attributed to anthraquinones, while the polysaccharide rich mesophyll ("aloe gel") is taken as a source of fiber (Steenkamp and Stewart 2007).

Including possible uses of commercial products, 119 use records for 39 species of *Aloe* were identified in the literature, including *A. ballyi*

Reynolds (Kokwaro 1993; Oketch-Rabah 1996), a species vulnerable to extinction (IUCN 2007).

Injuries. We collected 67 use records that described the use of 22 species of *Aloe* for treating injuries. Leaf mesophyll is commonly applied directly to burns and wounds, such as sunburned skin (*A. marlothii*; Rood 2008b). In Togo, the leaves of *A. buettneri* A.Berger are warmed prior to application (Adjanohoun 1987). Less frequently, leaves of species such as *A. maculata* All. are used in poultices, while *A. ferox* is used to treat tooth abscesses (Powell 1868; Reynolds 1950; Githens 1979). In Kenya, *A. lateritia* Engl., *A. kedongensis* Reynolds, and *A. secundiflora* are used to heal castration wounds in cattle (ITFG and IITR 1996).

Skin. The use of *Aloe* leaves to treat skin conditions was described in 42 use records referring to 17 species. The high polysaccharide and water content of the leaf mesophyll may account for its soothing effect on the skin; the efficacy of *A. arborescens*, *A. ferox*, and *A. vera* in wound healing has been attributed to the skin healing and antimicrobial properties of leaf tissues (Jia et al. 2008; Steenkamp and Steward 2007).

The emollient properties of the leaves were described in therapy of rashes, and the leaf exudate for skin irritations (Ghazanfar 1994; Njoroge and Bussmann 2007; van Wyk et al. 1997). Two species with spotted leaves, *A. greatheadii* var. *davyana* and *A. maculata*, are taken orally and applied topically to heal skin ailments (Hutchings et al. 1996; Watt and Breyer-Brandwijk 1962), although it is unclear if they are selected specially for their leaf markings.

Pregnancy. Seventeen species of *Aloe* (33 use records) were documented for uses in pregnancy, labor, and postnatal care, including the toxic species *A. chabaudii* Schönland in Zimbabwe (Gelfand et al. 1985). Preparations are taken to induce or ease labor and promote expulsion of the placenta. The most common use, however, is of the bitter leaf exudate as a weaning aid.

The use of *A. ferox* may cause purging in infants when taken by nursing mothers (Wren 1975), whereas *A. buettneri* is reportedly given to mothers to stop purging in breast-fed infants (Gill 1992). Despite records of their traditional use, additional records have contraindicated the use of *A. chabaudii* (Gelfand et al. 1985), *A. cooperi* Baker (Hutchings et al. 1996), and *A. ferox* (van Wyk et al. 1997) by pregnant women due to a risk of inducing early labor (see *Vertebrate poisons*).

Sensory System. *Aloe* spp. are commonly used to treat the sensory system (33 use records for 14 species), frequently as eye drops to treat conjunctivitis. An infusion of the leaves of *A. chabaudii* is used to treat ear infections (Morris 1996), while *A. broomii* Schönland is used similarly for ear ailments in sheep (Reynolds 1950).

Genito-Urinary System. We found that 16 species of *Aloe* (30 use records) were cited as medicines used to treat disorders of the genito-urinary system, notably menstruation and infertility. *Aloe hereroensis* Engl. is used to treat urinary incontinence and *A. zebrina* Baker for treating kidney and urinary complaints (van Koenen 2001). A leaf of *A. dawei* A.Berger, warmed on the fire, is used to massage the back for sore kidneys (Olembo et al. 1995).

Respiratory System. Sixteen species of *Aloe* are known to be used in therapy of respiratory ailments, including the common cold, coughs, influenza, and associated symptoms. *Aloe kedongensis* is administered to cattle in East Africa for the same purpose (ITFG and IITR 1996). Species such as *A. asperifolia* A.Berger, *A. dichotoma*, and *A. excelsa* A.Berger are used for asthma (Gelfand et al. 1985; van den Eynden et al. 1992), while *A. volkensii* Engl. is used for whooping cough (Olembo et al. 1995).

Inflammation. Smith (1888) noted that *A. maculata* [= *A. saponaria* (Aiton) Haw.] was "perhaps the best of all the plants which have virtue in healing an inflamed wound." Nineteen topical remedies containing *Aloe* spp. were recorded, while other medicines containing *Aloe* spp. are reportedly ingested, such as *A. sinkatana* Reynolds for tonsillitis (Marshall 1998).

Poisoning. Eleven species were recorded in 14 use records for the treatment of poisoning caused by snake and insect venom. In Namibia, *A. asperifolia* is given to donkeys that have eaten poisonous plants (van Damme and van den Eynden 2000).

Pain. Analgesic applications were documented for 10 species of *Aloe*, commonly for toothache. The Herero people in Namibia use *A. hereroensis* for chest and stomach pains, while *A. secundiflora* is used in Kenya and Tanzania to relieve chest pain and headaches (Kokwaro 1993; van den Eynden et al. 1992).

Muscular-Skeletal System. Historical and contemporary references referred to the use of *A.*

ferox and *A. perryi* for arthritis and rheumatism (Hocking 1997; Powell 1868; van Wyk et al. 1997). *A. maculata* was traditionally used in ethnoveterinary medicine in Lesotho to treat sprains and fractured bones (Reynolds 1950).

Undefined Illness. Use records describing the use of *Aloe* spp. to treat ailments of an unspecified nature included *A. humilis* (L.) Mill. and *A. aristata* Haw. for bathing, to impart tonic effects (Reynolds 1950; Watt and Breyer-Brandwijk 1962).

Endocrine System. References to the use of *Aloe* spp. for hormonal disorders were infrequent in the literature. In total, eight use records referred to the use of *A. massawana* Reynolds (Heine and Legére 1995), *A. maculata* (Maliehe 1997), *A. dhufarensis*, and *A. inermis* Forssk. (Ghazanfar 1994) for diabetes; *A. excelsa* is used for jaundice (Gelfand et al. 1985; Iwu 1993).

Blood System. *Aloe buettneri* (Gill 1992), *A. ferox* (Powell 1868), and *A. rabaiensis* Rendle (Kokwaro 1993) were cited as medicines for ailments of the spleen, while *A. lateritia* is administered for anaemia in Tanzania (Neuwinger 1996).

Nutrition. Food products and commercial preparations containing *A. ferox* have gained popularity in health food markets (Kleinschmidt 2004). Sap sucked from the leaves of *A. secundiflora* is a traditional remedy in Kenya for appetite loss and nausea (Kokwaro 1993). In contrast, the bitter exudate of *A. ferox* and other species has traditionally been painted on children's fingernails to discourage nail biting (Rood 2008b). The leaf exudate of *A. volkensii* has been used as a bitter paint to deter animals from gnawing on objects (Watt and Breyer-Brandwijk 1962).

Circulation. Arteriosclerosis, hypertension, and stress are among the circulatory ailments reportedly treated with *Aloe* spp. For example, a mixture of *A. arborescens* and *A. maculata* is administered for heart problems in Swaziland (Amusan et al. 2002).

Neoplasms. Although several species of *Aloe* have been included in laboratory studies for anticancer potential (e.g., Kametani et al. 2007), only *A. maculata* has been used in traditional medicine to treat tumors (Johnson 1999).

Mental Health. Historically, leaf exudate preparations of *A. perryi* and *A. succotrina* were taken for hysteria (Watt 1889).

Immune System. Hutchens (1994) noted that *A. ferox* is "soothing" to the lymphatic system.

Nervous System. A single use record described *A. asperifolia* as an ingredient in traditional medicine in Namibia for epilepsy (van den Eynden et al. 1992).

Abnormalities. A single use record referred to the use of *A. maculata* to treat unspecified scleroses (Johnson 1999).

Social Uses

The social uses of 35 species of *Aloe* were documented in 83 use records. Magical and ritual uses were frequently cited among these, including uses in fertility and initiation ceremonies (Reynolds 1950), charms for good fortune (Watt and Breyer-Brandwijk 1962), safety at funerals (Morris 1996), and protection for the home (Dold and Cocks 2000). *Aloe gracilis* Haw., a species vulnerable to extinction (TSP 2007), is used as a protective charm (Hutchings et al. 1996). Some 20 use records referred to snuff prepared from the dried or burned leaves of various species. The nectar of *A. ferox* was speculated to possess narcotic properties (Smith 1888). Two southern African species, *A. christianii* Reynolds and *A. chabaudii*, are used to induce abortion (see *Vertebrate Poisons*), although the latter is also known as a medicine taken during pregnancy (Gelfand et al. 1985; van Wyk and Gericke 1999).

The cultural importance of some species of *Aloe* has been conveyed in various media besides the literature. Examples include rock art motifs of *A. broomii* and *A. ferox* in South Africa (Reynolds 1950), illustrations of species such as *A. aculeata* Pole-Evans and *A. lutescens* Groenew. on postal stamps in Zimbabwe and Botswana (Steffens 1991; Smith and Glen 1993), and *A. aculeata* on the first decimal 10-cent coin of South Africa (Smith and Glen 1993). In the landscape, Reynolds (1950) noted in the Congo region that *A. dawei* was planted around the flagpole of a chief, while *A. buettneri*, *A. rivae* Baker, and *A. sinkatana* were reportedly planted on graves (Holland 1922; Reynolds 1966).

Vertebrate Poisons

Aloe buettneri, *A. lateritia*, *A. rabaiensis*, *A. secundiflora*, and *A. zebrina* have been documented as ingredients in arrow poisons throughout Africa (Holland 1922; Neuwinger 1996). Meat painted with *A. ruspoliana* Baker is used as bait to kill hyenas (Newton 1972) and *A.*

volkensii is used as a rodenticide to kill moles (Olembo et al. 1995).

Anecdotal evidence of severe or fatal poisoning in humans, typically caused by an overdose of preparations taken for constipation or to induce abortion, was recorded for 14 species. Risks of poisoning were noted for *A. ferox*, the source of Cape aloes, which is contraindicated in high doses and during pregnancy (Roberts 1990), as are species used to induce labor such as *A. perryi* (Khory and Katrak 1999) and *A. christianii* (Gelfand et al. 1985). While toxicity may be due to the presence of alkaloids in some species (e.g., *A. chabaudii*, *A. globuligemma* Pole-Evans, and *A. ortholopha* Christian & Milne-Redh.), the toxic principles in other species are not documented.

Environmental Uses

The spiny foliage and hardiness of many species of *Aloe* are exploited as living hedges, commonly for livestock enclosures; such hedges may be evident in the landscape for decades after a homestead has been vacated. The environmental uses of 44 species and infraspecific taxa were described in the literature, including *A. striata* Haw. (Glen and Hardy 2000), a species vulnerable to extinction (TSP 2007) although common in some parts of its range. At the ecological level, expansive populations of *A. greatheadii* var. *davyana* are an indicator of heavy overgrazing by domestic livestock in southern Africa (Glen and Hardy 2000). The soil-binding properties of the roots of this species are important in the stabilization and reclamation of eroded or otherwise degraded areas (Smith and Correia 1988, 1992). In Kenya, *A. secundiflora* is an important facilitator species in rangeland plant communities, promoting increased vegetation cover (King 2007; King and Stanton 2007). The Vhavenda of southern Africa use *A. marlothii* as a seed primer; seeds are soaked in the liquid from pounded leaves to make them more resilient and productive when sown (Mabogo 1990).

Food

The literature referred to 51 species of *Aloe* that are locally valued as vegetables, famine food, and occasional food. Most commonly, the flowers are cooked as a vegetable, sometimes with groundnuts (*Arachis hypogaea* L., Fabaceae) (e.g., *A. maculata*), in soup (e.g., *A. buettneri*), porridge (e.g., *A. esculenta* L.C.Leach), or in sweetmeats (e.g., *A. zebrina*) (Rodin 1985; FAO 1988). Immature inflorescences of *A. krausii* Baker and *A. minima* Baker are eaten raw (Heine and Legére 1995; Reynolds 1950; Silberbauer 1981). However, the floral buds of *Aloe greatheadii* var. *greatheadii* may cause vomiting if incorrectly prepared (Hyde and Wursten 2008). The leaves of some species may be cooked as a leafy vegetable or eaten as salad leaves.

Although undocumented, it is probable that the exudate-containing green leaf tissues are peeled from the mesophyll to remove the source of the extremely bitter taste and potential toxins. The peeled leaf mesophyll of *A. ferox* is used to make jam in South Africa (Roberts 1990; Rood 2008a; Smith and van Wyk 2008; Watt and Breyer-Brandwijk 1962). In India, the leaves of *A. elegans* Tod. were historically pickled with salt (Watt 1889). The flowers of *A. volkensii* have been used to preserve butter (Watt and Breyer-Brandwijk 1962). The sweet floral nectar of *A. ferox* and *A. secundiflora*, and perhaps other undocumented species, is favored as a snack food (Maundu et al. 1999; Watt and Breyer-Brandwijk 1962). The roots of *A. kedongensis*, *A. ngongensis* Christian, *A. secundiflora*, and *A. volkensii* are used in brewing traditional beer in East Africa (Maundu et al. 1999). As a famine food, the flowers of *A. angolensis* Baker and *A. zebrina* are cooked and dried or made into a paste for later use (Rodin 1985; Leffers 2003).

Materials

Dyes and ink of various hues from *Aloe* spp. were recorded in the literature. Yellow dyes from *A. maculata* and *A. zebrina* are used to dye sisal and palm fiber for basketry (FAO 1988; van Wyk and Gericke 1999); red-brown, purple, blue-black, and black dye are obtained from six other species (Ghazanfar 1994; Newton 1972; Reynolds 1950; van Wyk and Gericke 1999). Black ink was historically produced from *A. littoralis* Baker (Drury 1858).

Notes were collated on an adhesive prepared from *A. inermis* (Ghazanfar 1994); soap from *A. duckeri* Christian (Lane 2004), *A. maculata* (Newton 1972), and *A. secundiflora* (Wabuyele 2006); cordage from *A. ferox* (Grime 1976); and birdlime from the leaf exudate of *A. lateritia* (Heine and Legére 1995). The spiny leaves of *A. maculata*, *A. marlothii*, and possibly other species have been used to prepare hides for tanning (Morton 1961; Reynolds 1950). In the Eastern

Cape, we have observed short sections of the stem of *A. ferox* mechanically hollowed out and used as decorative containers for household utensils and dried flower arrangements. Explorers in southern Africa documented the use of hollowed branches of *A. dichotoma* as quivers by the San in the 17th century (Reynolds 1950).

The diversity in form among *Aloe* spp. has attracted keen horticultural interest. *Aloe succotrina* was recorded as an ornamental in Europe as early as 1697 (Pole-Evans 1919) and the genus continues to interest plant collectors today (Rowley 1976; De Wet 1996). Indiscriminate collecting for horticulture is of particular concern regarding threatened species including the endangered *A. peglerae* Schönland (Pfab and Scholes 2004) and the Lesotho endemic, *A. polyphylla* Schönland (Marshall 1998).

Non-Vertebrate Poisons

The principal application of *Aloe* spp. for pest control is in dips for poultry (*A. chabaudii*, *A. secundiflora*) and livestock (*A. broomii*, *A. ferox*) (Gelfand et al. 1985; ITFG and IITR 1996; Kokwaro 1993; Roberts 1990). The dried leaves of *A. castanea* Schönland, *A. ferox*, and *A. secundiflora* are burned and the ash from them is used to repel insects (Watt and Breyer-Brandwijk 1962; Timberlake 1987; Spring and Diederichs 2006). Ash from the dried, burned leaves of *A. castanea* is also recommended for pest control when mixed with stored grain (National Department of Agriculture, South Africa 2008). The dried, powdered leaves of *A. ferox* are reportedly an effective pesticide for plants (Spring and Diederichs 2006).

Animal Food

Aloe fulfills important ecosystem functions; 18 use records regarding animal food were gathered for 11 species. The copious floral nectar of *A. marlothii* is an important source of sustenance for many bird species (Symes et al. 2008). Wildlife, including antelope, baboon (*Papio* spp., Cercopithecidae), and rock hyrax (*Procavia capensis* Pallas, Procaviidae), browse on the leaves, fruits, and flowers particularly during droughts, and species recover at different rates. However, concerns have been recorded over damage caused by livestock to populations of *A. arenicola* Reynolds and the critically endangered *A. bowiea* Schult. & Schult.f. (Bornman and Hardy 1971; Smith 1989).

Bee Plants

A. greatheadii is regarded as the most superior species for honey production (Bornman and Hardy 1971). However, bees reputedly become vicious when kept exclusively on *A. greatheadii* var. *davyana* or on *A. zebrina* (Watt and Breyer-Brandwijk 1962).

Food Additives

The leaf exudate of *A. arborescens* is used as a bittering agent in Kenya (Duri et al. 2004), while Cape aloes from *A. ferox* was historically used as such in beer (Robertson 1979). "*Aloe* juice" prepared from the leaves of *A. ferox* is used as a food additive (Kleinschmidt 2004); *A. ferox* and *A. perryi* are approved for use as flavorings in the United States (Review of Natural Products 2004).

Fuel

The dried leaves of *A. ferox* are known to burn quickly (Maliehe 1997). It is likely that other undocumented species are used for kindling since many species accumulate dried leaves at the base of the crown. In East Africa, *A. lateritia* is a substitute for fuel wood and is used for lime burning (Heine and Legére 1995).

Consensus Analysis

Consensus ratios (CR) for the categories of uses documented for *Aloe* ranged from 0–0.76 (Table 1), where consensus increases as the ratio approaches 1.0 (Trotter and Logan 1986). The medicinal uses of *Aloe* spp. for which data were most abundant, were supported by high consensus ratios for both uncategorized medicinal uses (CR 0.75) and those for which detail in the literature allowed them to be classed in subcategories.

Consensus was most convincing for subcategories of medicinal use in which data were numerous, such as against infections and parasites (CR 0.75), digestive complaints, and injuries (both CR 0.68). However, there was no consensus (CR 0) in data-poor categories, such as on the use of *Aloe* spp. for fuel nor on their use to treat abnormalities, neoplasms, mental health, circulation, and disorders of the immune and nervous systems. Non-comparative data comprising a single mention of a single species may be excluded from analyses of large datasets without affecting consensus analyses (Moerman 2007). The volume of data and aim to compare homogeneity and biocultural value between use categories, however, required that all use categories were analyzed in the present study.

Besides the robust consensus ratios for their medicinal uses, the use of *Aloe* spp. to control invertebrate pests was supported by a consensus ratio of 0.76. Homogeneity among the recorded utility of *Aloe* spp., therefore, indicates that uses for medicine and pest control are of the greatest biocultural importance.

Conclusions

Evaluation of the literature has illustrated the multi-utility value of the genus *Aloe*, in particular for the medicinal uses of 25% of species. Homogeneity among use records indicated the uses of *Aloe* spp. for medicine and invertebrate pest control are of the greatest biocultural importance. Cultural value, in the broad sense, is a necessary consideration for effective conservation of biodiversity (Cocks 2006). It is particularly important for utility species that may be threatened by unsustainable rates of use; the biocultural value placed upon them is reflected by homogeneity among ethnobotanical data (Pardo-de-Santayana 2008).

Despite possible limitations in the detail and accuracy of data recovered, ethnobotanical records gathered by proxy from the literature afforded novel insights into the biocultural importance of utility in *Aloe*. Taking into consideration utility value and commercial demands biocultural importance may be anticipated to sustain the need for and add to the efficacy of the conservation of *Aloe*.

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3.2 Therapeutic uses of *Aloe* L. (Asphodelaceae) in southern Africa

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NOTE

The paper presented in 3.2 is a discussion of a data subset compiled for 3.1 focused on the medicinal uses of *Aloe* spp. in southern Africa.

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Therapeutic uses of *Aloe* L. (Asphodelaceae) in southern Africa

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ABSTRACT

Ethnopharmacological relevance: The African-Arabian succulent genus *Aloe* L. (Aloaceae/Asphodelaceae) is represented by approximately 120 infrageneric taxa in southern Africa, including *A. ferox* Mill., a species long used in commercial natural products.
Aims of the study: To assess the documented ethnobotanical knowledge and biocultural value of utility in the genus in southern Africa.
Materials and methods: A survey of over 350 multidisciplinary publications was undertaken.
Results: Local uses for medicine and wellbeing were identified for over half the species of *Aloe* occurring in the *Flora of Southern Africa* region. The most frequently cited medicinal uses were the treatment of infections and internal parasites, digestive ailments and injuries. Numerous species were recorded for their social uses, notably as ingredients in tobacco snuff.
Conclusion: The exceptional infrageneric diversity of *Aloe*, and extensive therapeutic uses in southern Africa, indicate its cultural importance in the subcontinent. These factors highlight the need for the conservation of the species as well as their potential as a source of natural products.

1. Introduction

Southern Africa is celebrated for its biological and ethnic diversity. More than three centuries of botanical exploration in South Africa and neighbouring countries have revealed astonishing floristic diversity – approximately 25,000 plant species and >50% endemism – in the region (Cowling and Hilton-Taylor, 2004; Steenkamp and Smith, 2006). More recently, the cultural value of biodiversity and its importance in effective biodiversity conservation planning and ecotourism, have been recognised (Cocks, 2006). The need for ethnobotanical research and the importance of existing accounts of utility in the flora of southern Africa have grown as a result. In this paper, we present an analysis of documented uses for medicine and wellbeing in southern Africa of the genus *Aloe* L. (Aloaceae/Asphodelaceae), a group of leaf succulents used for medicine throughout its range on the African continent, the western Indian Ocean Islands and Arabian Peninsula.

Species such as *Aloe ferox* Mill. in South Africa and *Aloe secundiflora* Engl. in Kenya are wild-harvested for the internation trade in natural products prepared from the bitter leaf exudate ('drug aloes') and jelly-like mesophyll ('aloe gel') of aloes. However, the principal source of these products, *Aloe vera* L., a species native to the Arabian Peninsula, is extensively cultivated around the world (Newton and Vaughan, 1996; Oldfield, 2004). Unsustainable harvesting for the natural products industry is one of the major threats to *Aloe* (Oldfield, 2004), and consequently trade in all species except *Aloe vera* is regulated by the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES). Despite the demand for natural products from *Aloe* spp. and their suitability to cultivation in dryland regions, few species are utilised commercially.

The record of plant use in southern Africa is substantial (see Van Wyk, 2002 for a general review) and includes numerous, scattered references to the ethnomedicinal uses of *Aloe* spp. in the region. In the present contribution, these 'use records' were collated and analysed to postulate the cultural value of *Aloe* spp. used for wellbeing in southern Africa and to highlight species with promise as sources of commercial natural products. The literature-guided approach, using the ethnographic record as a surrogate for ethnobotanical field study to identify plants of pharmacological interest, has previously been used to identify candidates for research against illnesses such as schistosomiasis (Clark et al., 1997) and diabetes (Simmonds and Howes, 2006) or, as in the present study, within a taxon, e.g. *Plectranthus* (Lukhoba et al., 2006). Recent examples of this approach to identify promising candidates from the diverse flora of southern Africa include plants

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with antimalarial activity (Clarkson et al., 2004) and monoamine oxidase inhibitory effects (Stafford et al., 2007).

2. Literature survey

Records of the therapeutic uses and useful properties of *Aloe* spp. in the countries covered by the *Flora of Southern Africa* (FSA) (South Africa, Lesotho, Swaziland, Botswana and Namibia) were identified during a review of over 320 multidisciplinary, mostly English-language, publications. References were identified by searching the extensive library at the Royal Botanic Gardens, Kew, and the online repositories BioMed Central (www.biomedcentral.com), Blackwell Synergy (www.blackwell-synergy.com), CAB Abstracts (www.cabi.org), Elsevier ScienceDirect (www.sciencedirect.com), Ingenta Connect (www.ingentaconnect.com), ISI Web of Knowledge (www.isiknowledge.com), JSTOR (www.jstor.org) and Swetswise (www.swetswise.com). Sources of information included pertinent ethnographic accounts of southern Africa such as those of Bryant (1909), Watt and Breyer-Brandwijk (1962) and Van den Eynden et al. (1992), as well as the Flora, peer-reviewed literature and the popular press. However, fewer than 18% of the publications consulted referred plainly to the use of *Aloe* spp. for medicine and general wellbeing in southern Africa. Records of plant use in South Africa were more abundant than elsewhere in the region covered by the Flora.

The uses of *Aloe* spp. for preventative and rehabilitative therapy, magical and ritual purposes in southern Africa were collated. Accepted names were appended, where necessary, from Newton's (2001) checklist of names and synonyms for *Aloe*. The domesticated *Aloe vera* was omitted from this survey, as the substantial literature documenting its uses and properties has been reviewed frequently (e.g. Grindlay and Reynolds, 1986; Reynolds and Dweck, 1999; Eshun and He, 2004; Richardson et al., 2005). Some 20 use records that could not be attributed to a particular species were also omitted, for example "The Zulu apply a pinch of the ash from the leaf an aloe species and the root of a *Lasiosiphon* [=*Gnidia* L., Thymelaeaceae] species to the eye, in the treatment of opthalmia" (Watt and Breyer-Brandwijk, 1962).

Each documented use for a therapeutic purpose in southern Africa constituted a 'use record' for a species. Using the Biodiversity Information Standard (formerly TDWG, the Taxonomic Database Working Group) standard (Cook, 1995), these records were classified into categories: Medicines (including veterinary medicine), Social Uses and Vertebrate Poisons. Sub-categories were recorded for approximately 60% of the use records in the Medicines category, when detail in the literature allowed (Table 1). In total, 440 use records describing the therapeutic uses of 63 accepted species of *Aloe* in southern Africa were collected (Tables 2 and 3).

3. Documented uses

More than half of the species of *Aloe* recognised in the *FSA* treatment (Glen and Hardy, 2000) are known to be used for medicine and wellbeing in the region. Patterns in the ethnographic literature indicate that widespread, common species of *Aloe* in southern Africa are more likely to be popular, multi-use ethnomedicines than rare species with narrow ranges.

Species for which use records were most numerous included *Aloe maculata* All. (46 records) and *Aloe marlothii* A. Berger (29), two species common in the landscape where they occur in southern Africa (Van Wyk and Smith, 1996). Conversely, species about which little is documented included *Aloe pearsonii* Schönland (1 record), a species with a limited range on the Namibia–South Africa border, and *Aloe suprafoliata* Pole-Evans (2), which occurs in a narrow distribution on rocky slopes in the South Africa–Swaziland border region (Van Wyk and Smith, 1996). Exceptions, however, included the Namibian endemic *Aloe asperifolia* and the very restricted Cape species *Aloe succotrina* All., for which use records were relatively numerous (17 and 16 records, respectively).

Table 1
Frequency of citation of *Aloe* spp. for medicine and wellbeing in southern Africa

Use category[a]	Sub-category	Number of use records	Species cited
Medicine	Unspecified	167	45
Medicine	Infections/infestations	54	11
	Digestion	40	15
	Injuries	24	6
	Pregnancy	23	11
	Skin complaints	16	7
	Sensory system	10	6
	Inflammation	10	4
	Pain	7	5
	Respiratory system	7	4
	Genito-urinary system	6	5
	Muscular–skeletal system	5	3
	Poisoning	6	3
	Circulation	5	5
	Undefined illnesses	4	4
	Nutrition	2	1
	Endocrine system	1	1
	Nervous system	1	1
Social		63	28
Poisons		7	6

[a] After Cook (1995).

3.1. Medicine

The majority (85%) of use records describing the uses and properties of *Aloe* spp. in southern Africa for wellbeing refer to medicinal applications (Table 1). The most frequently cited species was *Aloe ferox*, for which 86 use records were gathered from 31 publications. This species is the source of a natural product known as Cape aloes prepared from the dried leaf exudate (see Hodge, 1953 for a detailed account). Cape aloes was a local traditional medicine adopted by colonists at the Cape of Good Hope and first exported to Europe in the late eighteenth century (Pole-Evans, 1919). Although demands for Cape aloes from *Aloe ferox* have fluctuated, some 600 tonnes of crystalline leaf exudate, collected almost entirely from natural populations, are exported annually from South Africa (Sachedina and Bodeker, 1999).

Cape aloes is most widely used for its potent laxative and cathartic effects, attributed to anthraquinones and in particular aloe-emodin (see Steenkamp and Stewart, 2007) in the leaf exudate. The literature, however, reflects numerous other ethnomedicinal applications of the leaf exudate of *Aloe ferox* in southern Africa, such as relieving arthritis, and, commonly, the use of leaf sap as eye drops for conjunctivitis and other eye ailments (Smith, 1888; Watt and Breyer-Brandwijk, 1962; Crouch et al., 2006).

3.1.1. Infections

The principal therapeutic uses of *Aloe* spp. in southern African ethnography are to treat infections, particularly sexually transmitted infections and internal parasites. Fifty four use records were collected for 11 species in the region, referring to a variety of preparations used for topical and internal administration; *Aloe ferox* and *Aloe maculata* were cited most frequently. Leaf pulp (mesophyll) may be applied directly to the skin, without preparation, to treat ringworm (Reynolds, 1950) or to dress wounds (Morton, 1961). Cape aloes from *Aloe ferox* is applied topically to sores caused by viral infections such as warts, herpes and shingles (Van Wyk

Table 2
Documented social uses and toxicity of *Aloe* spp. in southern Africa

Infrageneric taxon	Category[a]	
	Social use	Vertebrate poisons
Aloe aculeata Pole-Evans	Steffens (1991), Smith and Glen (1993), Glen and Hardy (2000)	
Aloe affinis A. Berger	Smith et al. (2005)	
Aloe angelica Pole-Evans	Steffens (1991)	
Aloe arborescens Mill.	Roberts (1990)	
Aloe aristata Haw.	Cunningham (1993), Mander et al. (1995), Hutchings et al. (1996), Glen and Hardy (2000), Crouch et al. (2006)	
Aloe broomii Schönland	Reynolds (1950)	
Aloe chabaudii Schönland	Van Wyk and Gericke (1999)	Van Wyk and Gericke (1999)
Aloe christianii Reynolds	Van Wyk and Gericke (1999)	
Aloe cooperi Baker	Glen and Hardy (2000)	
Aloe cryptopoda Baker	Steffens (1991)	
Aloe ecklonis Salm-Dyck	Watt and Breyer-Brandwijk (1962), Glen and Hardy (2000)	
Aloe esculenta L.C. Leach	Rodin (1985)	
Aloe ferox Mill.	Smith (1888), Pujol (1990), Hutchings et al. (1996), Maliehe (1997), Glen and Hardy (2000), Smith et al. (2005)	Roberts (1990)
Aloe globuligemma Pole-Evans	Steffens (1991), Glen and Hardy (2000)	Gelfand et al. (1985), Glen and Hardy (2000)
Aloe gracilis Haw.	Hutchings et al. (1996); Arnold et al. (2002)	
Aloe humilis (L.) Mill.	Reynolds (1950), Watt and Breyer-Brandwijk (1962), Dold and Cocks (2000)	
Aloe khamiesensis Pillans	Reynolds (1950)	
Aloe kraussii Baker	Reynolds (1950), Watt and Breyer-Brandwijk (1962)	
Aloe littoralis Baker	Glen and Hardy (2000)	
Aloe lutescens Groenew.	Steffens (1991)	
Aloe maculata All.	Reynolds (1950), Watt and Breyer-Brandwijk (1962), Johnson (1999)	
Aloe marlothii A. Berger	Reynolds (1950), Watt and Breyer-Brandwijk (1962), Bornman and Hardy (1971), Roberts (1990), Hutchings et al. (1996), Van Wyk et al. (1997), Glen and Hardy (2000), Smith et al. (2005)	Glen and Hardy (2000)
Aloe ortholopha Christian & Milne-Redhead		Gelfand et al. (1985)
Aloe peglerae Schönland	Bornman and Hardy (1971)	
Aloe plicatilis (L.) Mill.		Arnold et al. (2002)
Aloe polyphylla Schönland	Maliehe (1997)	
Aloe prinslooi I.Verd & D.S.Hardy	Bornman and Hardy (1971)	
Aloe spicata L.f.	Hutchings et al. (1996)	
Aloe tenuior Haw.	Hutchings et al. (1996), Dold and Cocks (2000)	
Aloe thraskii Baker	Pujol (1990), Hutchings et al. (1996), Smith et al. (2005)	

[a] After Cook (1995).

and Gericke, 1999). The sap and decoctions of the leaves were widely reported for bathing sores caused by sexually transmitted infections or taken orally: the Ndebele drink a preparation of *Aloe globuligemma* Pole-Evans (Gelfand et al., 1985) despite its reported toxicity, *Aloe zebrina* Baker is taken in Botswana (Hedberg and Staugard, 1989), and in Namibia the sap of *Aloe hereroensis* Engl. diluted in water (Van den Eynden et al., 1992) and a water extract of *Aloe littoralis* Baker (Van Koenen, 2001) are among the remedies used. Species such as *Aloe humilis* (L.) Mill., *Aloe marlothii* (Watt and Breyer-Brandwijk, 1962) and *Aloe tenuior* Haw. (Githens, 1979) are administered internally to treat tapeworm, roundworm and other parasites. *Aloe dichotoma* Masson is used in Namibia to treat tuberculosis (Van den Eynden et al., 1992; Van Koenen, 2001).

In addition to medical applications, numerous use records were identified in the literature describing the ethnoveterinary value of *Aloe* spp. in southern Africa, for example against African horse sickness, tick and flea infestations, and rabies in dogs (Van den Eynden et al., 1992; Hutchings et al., 1996; Van Koenen, 2001).

3.1.2. Digestion

The greatest number of *Aloe* species (15) was documented for the treatment of ailments of the digestive system. Among these, *Aloe maculata* and *Aloe marlothii* were cited most frequently. For example, water in which leaves of *Aloe maculata* are steeped was noted by Watt and Breyer-Brandwijk (1962) as a Zulu medicine taken for its laxative and purgative effects, while leaf preparations are known in ethnoveterinary medicine to relieve digestive disorders in animals (Hutchings et al., 1996). A tea of the chopped leaves of *Aloe marlothii* was recorded as a remedy for stomach ailments (Roberts, 1990). Examples of species recorded less widely include *Aloe ecklonis* Salm-Dyck in Lesotho as a purgative (Johnson, 1999), the roots of *Aloe tenuior* in South Africa (Githens, 1979) and a brandy infusion of *Aloe variegata* L. taken for haemorrhoids in South Africa (Watt and Breyer-Brandwijk, 1962).

3.1.3. Injuries

Twenty-four use records recounted the application of *Aloe* spp. to treat injuries, most commonly applied directly to wounds, burns and other injuries. For instance, *Aloe greatheadii* Schönland is used to treat burns, bruises (Van Wyk et al., 1997) and insect bites (Smith, 2003) in South Africa. Uses were often described with related complaints that are dealt with in other sub-categories, such as inflammation. *Aloe maculata*, for instance, was documented by Reynolds (1950) as an effective treatment for boils, sores, and acutely inflamed injuries. *Aloe esculenta* L.C. Leach is used in Namibia to treat cuts and burns (Rodin, 1985; Van Koenen, 2001).

3.1.4. Pregnancy

Pregnancy, labour and postnatal care are among the most frequently documented uses of *Aloe* spp. in southern Africa: 23 use records describing 11 species were identified. For instance, *Aloe arborescens* Mill. and *Aloe greatheadii* were historically recorded as purgatives taken during pregnancy (Reynolds, 1950; Watt and Breyer-Brandwijk, 1962) while more recently, *Aloe cooperi* Baker and *Aloe ecklonis* Salm-Dyck were documented as ethnomedicines taken to ease labour (Hutchings et al., 1996; Johnson, 1999). Most commonly, however, the bitter leaf sap of numerous species is recorded as a weaning aid.

Table 3
Records of the medicinal use of *Aloe* spp. in southern Africa

Infrageneric taxon	Medicine	Medicine sub-category[a]							
		Circulation	Digestion	Endocrine	Genito-urinary	Infection	Inflammation	Injury	Muscular–skeletal
Aloe affinis A. Berger	Arnold et al. (2002)								
Aloe africana Mill.	Pereira (1855), Wood and Bache (1854), Flückiger (1855), Sebire (1899), Thoms (1929), Reynolds (1950), Arnold et al. (2002)								
Aloe arborescens Mill.	Wills (1893), Thoms (1929), Reynolds (1950), Hodge (1953), Watt and Breyer-Brandwijk (1962), Githens (1979), Roberts (1990), Arnold et al. (2002),	Amusan et al. (2002)	Roberts (1990)					Schwegler (2003)	
Aloe aristata Haw.	Cunningham (1993), Arnold et al. (2002), Te Beest (2004)								
Aloe asperifolia A. Berger	Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000), Arnold et al. (2002)	Van den Eynden et al. (1992)	Van Damme and Van den Eynden (2000)		Van den Eynden et al. (1992)				
Aloe ballyi Reynolds									
Aloe barberae Dyer	Bruce (1974), Arnold et al. (2002)								
Aloe boylei Baker	Arnold et al. (2002)								
Aloe broomii Schönland	Arnold et al. (2002)								
Aloe buettneri A. Berger	Arnold et al. (2002)								
Aloe burgersfortensis Reynolds	Arnold et al. (2002)								
Aloe chabaudii Schönland	Arnold et al. (2002)								
Aloe ciliaris Haw.	Arnold et al. (2002)								
Aloe cooperi Baker	Cunningham (1993), Arnold et al. (2002), Te Beest (2004)								
Aloe cryptopoda Baker	Arnold et al. (2002)								
Aloe dewetii Reynolds	Arnold et al. (2002)								
Aloe dichotoma Masson	Reynolds (1950), Arnold et al. (2002)					Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000)			
Aloe ecklonis Salm-Dyck	Arnold et al. (2002)		Watt and Breyer-Brandwijk (1962), Johnson (1999), Glen and Hardy (2000)			Johnson (1999)			
Aloe esculenta L.C. Leach							Rodin (1985), Van Koenen (2001)	Rodin (1985), Van Koenen (2001)	
Aloe excelsa A. Berger	Arnold et al. (2002)								Gelfand et al. (1985)

Table 3 (*Continued*)

Infrageneric taxon	Medicine	Medicine sub-category[a]							
		Circulation	Digestion	Endocrine	Genito-urinary	Infection	Inflammation	Injury	Muscular–skeletal
Aloe ferox Mill.	Wood and Bache (1854), Pereira (1855), Simmonds (1865), Flückiger (1891), Sebire (1899), Humphrey (1921), Greenish (1929), Thoms (1929), Reynolds (1950), Hodge (1953), Watt and Breyer-Brandwijk (1962), Bruce (1974), Wren (1975), Githens (1979), Robertson (1979), Trease and Evans (1979), Roberts (1990), Hutchings et al. (1996), Van Wyk and Smith (1996), Van Wyk et al. (1997), Sachedina and Bodeker (1999), Glen and Hardy (2000), Arnold et al. (2002), Kleinschmidt (2004), Kambizi et al. (2005), Shackleton and Gambiza (2007)	Van Wyk et al. (1997)	Smith (1888), Greenish (1929), Roberts (1990), Hutchings et al. (1996), Maliehe (1997), Van Wyk et al. (1997), Kleinschmidt (2004), Van Wyk and Wink (2004)		Bryant (1909)	Smith (1888), Bryant (1909), Watt and Breyer-Brandwijk (1962), Githens (1979), Roberts (1990), Hutchings et al. (1996), Van Wyk and Gericke (1999), Glen and Hardy (2000), Kambizi et al. (2005), Crouch et al. (2006)	Bond (1995), Van Wyk et al. (1997), Van Wyk and Gericke (1999), Crouch et al. (2006)	Roberts (1990), Van Wyk et al. (1997)	Van Wyk et al. (1997), Crouch et al. (2006)
Aloe fosteri Pillans	Reynolds (1950), Arnold et al. (2002)								
Aloe globuligemma Pole-Evans	Arnold et al. (2002)					Gelfand et al. (1985)			
Aloe greatheadii Schönland	Gelfand et al. (1985), Arnold et al. (2002)		Mathabe et al. (2006)			Roberts (1990)		Roberts (1990), Van Wyk et al. (1997), Smith (2003)	
Aloe hereroensis Engl.	Arnold et al. (2002)	Van Damme and Van den Eynden (2000)	Van den Eynden et al. (1992), Van Koenen (2001)		Van Koenen (2001)	Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000), Van Koenen (2001)			
Aloe humilis (L.) Mill.	Arnold et al. (2002)		Watt and Breyer-Brandwijk (1962)			Watt and Breyer-Brandwijk (1962)			
Aloe keithii Reynolds	Arnold et al. (2002)								
Aloe kraussii Baker									
Aloe linearifolia A. Berger	Cunningham (1993), Hutchings et al. (1996), Arnold et al. (2002)								Reynolds (1950), Watt and Breyer-Brandwijk (1962)
Aloe littoralis Baker			Van Koenen (2001)			Van Koenen (2001)	Van Koenen (2001)		
Aloe maculata All.	Reynolds (1950), Watt and Breyer-Brandwijk (1962), Glen and Hardy (2000), Arnold et al. (2002)	Amusan et al. (2002)	Watt and Breyer-Brandwijk (1962), Hutchings et al. (1996), Glen and Hardy (2000)	Maliehe (1997)		Smith (1888), Reynolds (1950), Morton (1961), Watt and Breyer-Brandwijk (1962), Githens (1979), Hutchings et al. (1996), Sachedina and Bodeker (1999), Glen and Hardy (2000)	Smith (1888), Watt and Breyer-Brandwijk (1962)	Smith (1888), Reynolds (1950), Watt and Breyer-Brandwijk (1962), Githens (1979), Sachedina and Bodeker (1999), Glen and Hardy (2000)	

Aloe marlothii A. Berger	Hodge (1953), Bruce (1974), Cunningham (1993), Hutchings et al. (1996), Arnold et al. (2002), Te Beest (2004)	Watt and Breyer-Brandwijk (1962), Bredenkamp and Van Vuuren (1987), Roberts (1990), Hutchings et al. (1996), Glen and Hardy (2000)		Watt and Breyer-Brandwijk (1962), Bredenkamp and Van Vuuren (1987), Roberts (1990), Hutchings et al. (1996), Glen and Hardy (2000)	
Aloe micrantha Haw.	Arnold et al. (2002)				
Aloe mutabilis Pillans	Arnold et al. (2002)				
Aloe parvibracteata Schönland	Arnold et al. (2002)				Glen and Hardy (2000)
Aloe pearsonii Schönland	Arnold et al. (2002)				
Aloe pendens Forssk.	Sachedina and Bodeker (1999), Arnold et al. (2002)				
Aloe perryi Baker	Thoms (1929), Greenish (1929), Coimbra (1994)				
Aloe plicatilis (L.) Mill.	Wood and Bache (1854), Pereira (1855), Flückiger (1891), Dragendorff (1898), Sebire (1899), Thoms (1929), Hodge (1953), Arnold et al. (2002), Lindsey et al. (2002)				
Aloe rabaiensis Rendle		Johnson (1999)			
Aloe rupestris Baker	Arnold et al. (2002), Te Beest (2004)		Hutchings et al. (1996)		
Aloe speciosa Baker	Hodge (1953), Bruce (1974), Arnold et al. (2002)				
Aloe spicata L.f.	Wood and Bache (1854), Pereira (1855), Redwood (1857), Boulger (1889), Sebire (1899), Hodge (1953), Hutchings et al. (1996), Arnold et al. (2002), Te Beest (2004)	Watt and Breyer-Brandwijk (1962)			
Aloe striata Haw.		Glen and Hardy (2000)			
Aloe striatula Haw.	ITFG and IITR (1996), Arnold et al. (2002)				
Aloe succotrina All.	Von Mueller (1881), Boulger (1889), Hodge (1953), Bornman and Hardy (1971), Bruce (1974), Arnold et al. (2002)				
Aloe suprafoliata Pole-Evans	Arnold et al. (2002), Lindsey et al. (2002)				
Aloe tenuior Haw.	Arnold et al. (2002)	Githens (1979), Hutchings et al. (1996), Dold and Cocks (2001)		Smith (1888), Watt and Breyer-Brandwijk (1962), Githens (1979), Hutchings et al. (1996)	

Table 3 (*Continued*)

Infrageneric taxon	Medicine	Medicine sub-category[a]							
		Circulation	Digestion	Endocrine	Genito-urinary	Infection	Inflammation	Injury	Muscular–skeletal
Aloe thraskii Baker	Bruce (1974), Hutchings et al. (1996), Arnold et al. (2002)								
Aloe zebrina Baker	Arnold et al. (2002), Leffers (2003)		Leffers (2003)		Hedberg and Staugard (1989), Van Koenen (2001)	Hedberg and Staugard (1989)			

Infrageneric taxon	Medicine sub-category[a]								
	Nervous	Nutrition	Pain	Poisoning	Pregnancy	Respiratory	Sensory	Skin	Undefined illness
Aloe affinis A. Berger			Smith et al. (2005)						
Aloe africana Mill.									
Aloe arborescens Mill.			Roberts (1990)		Watt and Breyer-Brandwijk (1962)				
Aloe aristata Haw.									
Aloe asperifolia A. Berger	Van den Eynden et al. (1992)			Van den Eynden et al. (1992)	Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000)	Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000)			
Aloe ballyi Reynolds								Riley and Brokensha (1988)	
Aloe barberae Dyer									
Aloe boylei Baker									
Aloe broomii Schönland							Reynolds (1950)		
Aloe buettneri A. Berger									
Aloe burgersfortensis Reynolds									
Aloe chabaudii Schönland									
Aloe ciliaris Haw.									
Aloe cooperi Baker					Hutchings et al. (1996)				Watt and Breyer-Brandwijk (1962), Hutchings et al. (1996)
Aloe cryptopoda Baker									
Aloe dewetii Reynolds									
Aloe dichotoma Masson						Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000)			
Aloe ecklonis Salm-Dyck					Johnson (1999)				
Aloe esculenta L.C. Leach					Rodin (1985), Van Koenen (2001)				
Aloe excelesa A. Berger									
Aloe ferox Mill.		Kleinschmidt (2004), Van Wyk and Wink (2004)	Crouch et al. (2006)				Smith (1888), Watt and Breyer-Brandwijk (1962), Githens (1979), Roberts (1990), Hutchings et al. (1996)	Roberts (1990), Van Wyk et al. (1997), Glen and Hardy (2000), Van Wyk and Wink (2004)	Robertson (1979)
Aloe fosteri Pillans								Watt and Breyer-Brandwijk (1962)	
Aloe globuligemma Pole-Evans								Van Wyk et al. (1997)	
Aloe greatheadii Schönland				Watt and Breyer-Brandwijk (1962), Roberts (1990), Glen and Hardy (2000)	Reynolds (1950), Watt and Breyer-Brandwijk (1962), Glen and Hardy (2000)			Roberts (1990), Van Wyk et al. (1997), Smith (2003)	

Aloe hereroensis Engl.	Van den Eynden et al. (1992), Van Damme and Van den Eynden (2000)			Van den Eynden et al. (1992), Van Koenen (2001)	Van Koenen (2001)		
Aloe kraussii Baker			Reynolds (1950)				Reynolds (1950)
Aloe littoralis Baker					Van Koenen (2001)		
Aloe marlothii A. Berger			Watt and Breyer-Brandwijk (1962), Bredenkamp and Van Vuuren (1987), Roberts (1990), Hutchings et al. (1996), Glen and Hardy (2000)				
Aloe maculata All.		Hutchings et al. (1996)		Hutchings et al. (1996)		Raina (1982), Maliehe (1997), Hutchings et al. (1996)	
Aloe parvibracteata Schönland							
Aloe pearsonii Schönland							
Aloe pendens Forssk.							
Aloe perryi Baker							
Aloe plicatilis (L.) Mill.							
Aloe rupestris Baker					Hutchings et al. (1996)		
Aloe spicata L.f.			Hutchings et al. (1996)				
Aloe thraskii Baker			Hutchings et al. (1996)				
Aloe variegata L.	Reynolds (1950), Glen and Hardy (2000)						
Aloe zebrina Baker			Van Wyk and Gericke (1999)		Leffers (2003)	Leffers (2003)	

[a] After Cook (1995).

3.1.5. Skin complaints

Sixteen use records describing the topical application of fresh leaves or sap of seven species were gathered; some of these referred to the use of *Aloe* spp. to treat dermatological ailments caused by infections (see Section 3.1.1). The leaves and roots of *Aloe ferox* are applied topically, sometimes mixed with animal fat, or taken internally to treat conditions such as eczema, dermatitis and acne (Hutchings et al., 1996; Maliehe, 1997; Van Wyk et al., 1997). An infusion of *Aloe maculata* is used in South Africa to promote hair growth (Raina, 1982) while the leaf mesophyll of *Aloe greatheadii* is placed inside shoes to prevent blisters (Hutchings et al., 1996). The wound healing effects of *Aloe vera* have been ascribed to β-sitosterol, increased collagen activity and suppression of contact hypersensitivity (Steenkamp and Stewart, 2007).

3.1.6. Sensory system

Six species were documented for their use to treat ailments of the eye, including opthalmia and conjunctivitis (see Section 3.1.7.). The sap of *Aloe ferox*, *Aloe hereroensis* and *Aloe littoralis* is administered as eye drops (Watt and Breyer-Brandwijk, 1962; Van Koenen, 2001), while preparations containing the leaves of other species of *Aloe* are also used. In the case of *Aloe zebrina*, the leaf mesophyll is applied to the eye (Leffers, 2003).

The liquid from boiled leaves of *Aloe broomii* Schönland was documented by Reynolds (1950) as a remedy for ear ailments in sheep.

3.1.7. Inflammation

Species documented for uses against inflammatory conditions included *Aloe esculenta* L.C. Leach, *Aloe ferox*, *Aloe maculata* and *Aloe littoralis*. These taxa have long been used throughout southern Africa to treat inflammation associated with injuries (Smith, 1888; Rodin, 1985), as well as ailments such as conjunctivitis and sinusitis (Van Wyk and Gericke, 1999; Crouch et al., 2006).

3.1.8. Pain

Seven references to the use of *Aloe* spp. for pain relief were recorded, including the use of *Aloe variegata* for toothache in the Cape (Reynolds, 1950), *Aloe aborescens* Mill. for stomach ache (Roberts, 1990) and *Aloe hereroensis* for chest, heart and stomach pains in Namibia (Van den Eynden et al., 1992; Van Damme and Van den Eynden, 2000).

3.1.9. Respiratory system

The use of *Aloe* spp. to treat respiratory ailments in southern Africa is infrequently recorded in the literature. *Aloe hereroensis* is taken for chest complaints in Namibia (Van Koenen, 2001) while an infusion of the powdered flowers of *Aloe maculata* is a Zulu traditional remedy for colds and fever in children (Hutchings et al., 1996).

3.1.10. Genito-urinary system

Six use records noted the use of *Aloe* spp. to treat disorders of the genito-urinary system. *Aloe ferox* and *Aloe rupestris* Baker were documented for use against infertility in women and impotence in men (Bryant, 1909). *Aloe zebrina* was recorded in Botswana as a treatment for sexual disorders (Hedberg and Staugard, 1989). *Aloe hereroensis* Engl. and *Aloe zebrina* were documented in Namibia for their used to treat urinary and kidney ailments (Van Koenen, 2001).

3.1.11. Muscular–skeletal system

Few species of *Aloe* are listed in the ethnographic literature for therapy of muscular–skeletal disorders. *Aloe excelsa* A. Berger was recorded for the treatment of depressed fontanel in infants (Gelfand et al., 1985) and *Aloe ferox* for arthritis (Van Wyk et al., 1997). Earlier references noted that leaves of *Aloe maculata* were placed beneath the broken limb of an animal to treat the fracture (Reynolds, 1950; Watt and Breyer-Brandwijk, 1962).

3.1.12. Poisoning

In contrast to species that may cause poisoning, *Aloe greatheadii* is documented to be used as an effective treatment for snake bite (Watt and Breyer-Brandwijk, 1962) while *Aloe asperifolia* is used in Namibia to treat donkeys after grazing on poisonous plants (Van den Eynden et al., 1992; Van Damme and Van den Eynden, 2000). An infusion of *Aloe maculata* was recorded as a Zulu traditional remedy for overindulgence in food and alcohol (Hutchings et al., 1996).

3.1.13. Circulation

The treatment of circulatory complaints was among the most infrequently recorded medicinal purposes for *Aloe* spp. in southern Africa. Examples include a mixture of *Aloe arborescens* and *Aloe maculata* reportedly taken to treat cardiac ailments (Amusan et al., 2002) and *Aloe asperifolia* taken for arteriosclerosis in Namibia (Van den Eynden et al., 1992).

3.1.14. Undefined illness

The use of *Aloe* spp. in therapy of ailments of an uncertain nature, categorised as 'undefined illnesses', included reference to the use of *Aloe rupestris* as a strengthening medicine for Zulu chiefs (Hutchings et al., 1996) and smoke from burning leaves of *Aloe cooperi* to protect cattle in kraals from the consequences of a poor diet (Watt and Breyer-Brandwijk, 1962).

3.1.15. Nutrition

Kleinschmidt (2004) described the health benefits of beverages and fortified food products containing the leaf parenchyma of *Aloe ferox*, a by-product of the Cape aloes processing industry in South Africa.

3.1.16. Endocrine system

A single reference described the use of *Aloe maculata* in Lesotho as an ingredient in a traditional remedy for diabetes (Maliehe, 1997).

3.1.17. Nervous system

A single use record in the literature referred to an illness of the nervous system: a leaf decoction of *Aloe asperifolia* is taken for epilepsy (Van den Eynden et al., 1992).

3.2. Social uses

Several species (*Aloe christianii* Reynolds, *Aloe gracilis* Haw. and *Aloe krausii* Baker) were documented only for purposes of wellbeing classified as Social Uses. These included magical and ritual applications, such as the use of plant preparations to protect people and property against harm from lightning or visiting strangers (Dold and Cocks, 2000). Thirteen species were recorded for spiritual purposes such as fertility and initiation rites, including *Aloe arborescens* (Arnold et al., 2002) and *Aloe thraskii* Baker (Pujol, 1990).

Other social uses included species taken as antifertility agents to induce abortion (*Aloe chabaudii* Schönland and *Aloe christianii*) (Van Wyk and Gericke, 1999), in contrast to accidental abortion caused by species taken medicinally, such as *Aloe cooperi* (Hutchings et al., 1996) and high doses of *Aloe ferox* (Roberts, 1990).

The leaves of four *Aloe* spp., notably *Aloe marlothii*, were cited as ingredients in snuff tobacco but this may be a conservative reflection of the number of species that have been used as smoking materials or drugs in southern Africa, owing to vague information in the literature. Smith (1888) reported that the sweet nectar of *Aloe* *ferox*, a snack favoured by children, caused intoxication and weakening of the joints. Other social uses indicated the cultural value of *Aloe* spp., such as the depiction on postal stamps of *Aloe aculeata* Pole-Evans, *Aloe angelica* Pole-Evans, *Aloe cryptopoda* Baker, *Aloe globuligemma*, *Aloe lutescens* Groenew. in the erstwhile Republic of Venda (Steffens, 1991) and of *Aloe aculeata* Pole-Evans on the original ten cent coin in South Africa (Smith and Glen, 1993).

3.3. *Vertebrate poisons*

Roberts (1990) noted that the sap of *Aloe ferox*, the source of Cape aloes, was regarded as an abortifacient and high doses should therefore be avoided. Cautions regarding the risk of poisoning associated with the medicinal use of *Aloe chabaudii*, *Aloe ortholopha* Christian & Milne-Redhead and *Aloe globuligemma* were noted by Gelfand et al. (1985). These southern African species are among a small number of *Aloe* spp. known to contain alkaloids (Dring et al., 1984) which may be the toxic agents. The social use of *Aloe marlothii* as snuff may be hazardous, as it was reported to contain carcinogens comparable to those in cigarette smoke (Watt and Breyer-Brandwijk, 1962).

4. Conclusions

As a surrogate for ethnobotanical field study, the ethnographic record is constrained by potential inaccuracies, preconception and interpretation in the literature and data repetition between sources. In this study, however, novel insight was gained into the species of *Aloe* used for health and wellbeing in southern Africa. Indeed, the diversity of species used (53% of species in the *FSA* region) illustrates the considerable biocultural significance of the genus. Taking into account this and the varied historical and contemporary therapeutic uses, the genus *Aloe* may yet hold promise as sources of commercial natural products. At least some of the phytochemical properties for which the commercially used species *Aloe vera*, *Aloe ferox* and *Aloe secundiflora* are valued, such as aloin and polysaccharide constituents, are known to be widely conserved in the genus (Reynolds, 2004). Frequently documented species such as *Aloe maculata* and *Aloe marlothii* warrant research for their potential as sources of natural products. Experiences from existing enterprises in Africa require consideration, however, such as concerns for the sustainable supply and quality of *Aloe ferox* for processing in South Africa (Sachedina and Bodeker, 1999) and vulnerability of value chains producing *Aloe vera* elsewhere in Africa. The rich ethnobotanical tradition and diversity of *Aloe* spp. in southern Africa highlight the prospects for their sustainable use and the need for their conservation.

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CHAPTER 4 PHYLOGENETICS

Introduction

The genus *Aloe* L. is the largest and arguably the most iconic of 15 genera in Asphodelaceae (Asparagales). With increasing appreciation of the diversity in *Aloe*, the genus has expanded over the past two centuries to include over 500 accepted specific and infraspecific names and almost as many synonyms (Newton 2001). The first comprehensive infrageneric classification of *Aloe* (Berger, 1908) was expanded and revised by Reynolds (1950, 1966) in a two volume work, but remained incomplete as the second volume was compiled shortly before the author's death. Berger's (1908) and Reynolds' (1950, 1966) infrageneric classifications of *Aloe* have been lauded for their intuitive arrangement, but the extent to which they remain artificial has limited their usefulness. For instance, the apparently natural group comprising fire tolerant, barely succulent species of *Aloe* occurring in grasslands is broadly circumscribed in two sections (*Leptaloe* A. Berger; *Graminaloe* Reynolds), while, in contrast, the relatively few taxa that are arborescent in form are recognised in no fewer than four sections (*Dracaloe* A. Berger, *Aloidendron* A. Berger, *Kumara* (Medik.) Baker and *Sabaealoe* Berger). The proliferation of names and incomplete infrageneric classification have contributed to considerable taxonomic confusion over generic boundaries and species demarcation in *Aloe*.

The classification of *Aloe* is further frustrated by the use of three family names in the literature. The original family circumscription of *Aloe* and other succulent-leaved alooid genera, in Aloaceae (Batsch 1802), continues to be recognised (e.g. Brummit 1992; Carter 1994; Glen and Hardy 2000). The more inclusive Asphodelaceae, comprising genera in Alooideae and Asphodeloideae (Cronquist 1981), was not widely recognised until it was convincingly shown to be monophyletic (Smith and Van Wyk 1998; Chase et al. 2000; Treutlein et al. 2003a, 2003b). Asphodelaceae is among the "bracketed" families considered to be "acceptable monophyletic alternatives to the broader circumscription favoured" by the Angiosperm Phylogeny Group (APG II 2003). The latter places Asphodelaceae and Hemerocallidaceae in the formerly monotypic Australian family Xanthorrhoeaceae. Due to the absence of morphological synapomorphies to support an expanded Xanthorrhoeaceae (Devey et al. 2006), and since Asphodelaceae is both a monophyletic and widely accepted taxonomic unit, we consider it the most practical classification for *Aloe* at the family rank.

Comparative data have accumulated in recent decades, contributing to emerging views of the systematics of *Aloe* not reflected by the infrageneric arrangement, which is largely based on floral characters (Berger 1908; Reynolds 1950, 1966). For instance, patterns in seed morphology (Kamstra 1971), leaf surface sculpturing (Cutler 1982), pollen morphology (Steyn et al. 1998) and the presence of secondary metabolites such as microdontin (Viljoen et al. 1999) are not congruent with existing infrageneric groups. However, similarities in gross morphology and certain phytochemical characters such as the presence of flavonoids (Viljoen et al. 1998) and the composition of waxes in the cuticle (Herbin and Robins 1968) do correspond with infrageneric groups recognised by the present classification. Treutlein et al. (2003a) found no agreement between traditional infrageneric groups and the relationships suggested by *matK*, *rbcL* and genomic fingerprinting in *Aloe*; these authors questioned (with unintended irony) the usefulness of cryptic characters that have highlighted, rather than resolved, taxonomic questions in Asphodelaceae. Nonetheless, the consensus of these studies is that considerable comparative data are required to inform a stable taxonomic classification of *Aloe* that not only reflects evolutionary relationships, but has practical value for assisting in plant identification and predicting plant properties.

This chapter focuses on the poorly resolved section *Pictae* Salm-Dyck of *Aloe*, the so-called maculate or spotted aloes. The name refers to their patterned leaf surfaces, which bear pale green to white markings, often described as “H-shaped” by Reynolds (1950, 1966) and arranged in transverse bands, on at least one leaf surface. Plants are usually robust with rosulate, succulent leaves that exude yellow, reddish or purple sap on wounding, the leaf margins armed with sharp teeth (prickles). Like other acaulescent or short-stemmed species of *Aloe*, the inflorescence is usually a tall, dichotomously branched panicle, bearing conical to capitate racemes of pale cream, but usually pink to bright orange or red flowers. However, the bulbous base of the perianth tube and constriction above the ovary are very distinctive of maculate species. The status of these floral and leaf morphological characters as synapomorphies for section *Pictae*, however, is uncertain, since all these characters are known in other infrageneric groups in *Aloe*. For example, a constricted perianth is typical of section *Paniculatae* Salm-Dyck ex Kunth which includes the glaucous-leaved *A. striata* Haw., while patterned leaf surfaces are typical of series *Hereroenses* Reynolds, including *A. hereroensis* Engl. In fact, Berger (1908) thought the latter species both belonged in the maculate group, his series *Saponariae* A. Berger.

Innovations in the infrageneric arrangement of *Aloe* introduced by Reynolds (1950, 1966) had little influence on the recognition of at least a core group within section *Pictae*, in which about forty species are currently accepted. Section *Pictae* has not, however, escaped the inconsistencies and nomenclatural confusion that affect the infrageneric classification of

Aloe; taxonomic irregularities have resulted in an arrangement of maculate species with very limited practical value. Indeed, among the most readily identifiable maculate species are atypical ones such as *A. suffulta* Reynolds, possessing an unusual inflorescence, and *A. simii* Pole-Evans, with channelled and often immaculate leaves. We have undertaken comparative studies of potentially informative taxonomic characters, including leaf surface morphology and phytochemistry (unpubl. data) in the maculate group to gain better understanding of its systematic relationships. Here, we evaluate for the first time phylogenetic evidence, from nuclear and plastid DNA data, for resolving the circumscription and assessing the monophyletic status of section *Pictae*.

Materials and methods

Taxonomic sampling

DNA sequence data were compiled for 29 species of *Aloe* from throughout continental Africa that have been classified at some time in sections *Pictae*, *Maculatae* or series *Saponariae*. Previous molecular studies of *Aloe* have included few maculate species, to which we have added 33 new sequences. Plant material was collected from natural populations in South Africa and plants of wild provenance kept in glasshouses at the Royal Botanic Gardens, Kew. Voucher specimens were deposited at Kew (K) and the National Herbarium (PRE) in South Africa. Additional published sequence data were obtained from GenBank for 17 ingroup taxa representing thirteen other infrageneric groups in *Aloe*. *Gasteria* was defined as outgroup in all analyses. Species voucher information and GenBank accession numbers are presented in Table 4.1

Table 4.1 Plant material and sequence data investigated in the phylogenetic analysis of *Aloe* section *Pictae*

Taxon	Accession(s)[1]
Aloe affinis A.Berger	Grace 87 (K, PRE), South Africa;
A. arborescens Mill.	Noguchi & De-yuan AB090942; Treutlein et al. 2003b AY323723; Adams et al. 2000a AF234333
A. aristata Haw.	—, Treutlein et al. 2003a AJ511407, Treutlein et al. 2003b AY323651
A. barbertoniae Pole-Evans	Grace 85 (K, PRE)
A. branddraaiensis Groenew.	RBG 1957-14502 (K), South Africa
A. burgersfortensis Reynolds	Grace 89 (K, PRE), South Africa
A. capitata var. gneisicola H.Perrier	—, Treutlein et al. 2003b AY323720, Treutlein et al. 2003b AY323677
A. compressa var. compressa H.Perrier	—, Treutlein et al. 2003b AY323721, Treutlein et al. 2003b AY323678
A. dewetii Reynolds Grace 83	(K, PRE), South Africa
A. doei Lavranos	—, Treutlein et al. 2003b AY323724, Treutlein et al. 2003b AY323682
A. ellenbeckii A.Berger	RBG 1977-2441 (K), Kenya;
A. ellenbeckii A.Berger	RBG 1973-2107 (K), Kenya
A. forbesii Balf.f.	—, Treutlein et al. 2003a AJ511389, Adams et al. 2000a AF234342
A. fosteri Pillans	RBG 2003-1796 (K), South Africa
A. glauca Mill.	—, Treutlein et al. 2003a AJ511396, Adams et al. 2000a AF234344
A. grandidentata Salm-Dyck	RBG 1972-2520 (K), South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S. Hardy	Grace 66 (K, PRE), South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy	Grace 67 (K, PRE), South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy	Grace 56 (K, PRE), South Africa
A. greatheadii Schönland	Grace 72 (K, PRE), South Africa
A. greenii Baker	Grace 74 (K, PRE), South Africa
A. humilis (L.) Mill.	—, Treutlein et al. 2003b AY323719, Treutlein et al. 2003b AY323675
A. immaculata Pillans	Grace 62 (K, PRE), South Africa
A. jucunda Reynolds	—, Treutlein et al. 2003b AY323718, Treutlein et al. 2003b AY323674

Table 4.1 *(continued)*

Taxon	Accession(s)
A. juvenna Brandham & S.Carter	—, Treutlein et al. 2003b AY323717, Treutlein et al. 2003b AY323673
A. lateritia var. *graminicola* (Reynolds) S.Carter	RBG 1973-2058 (K), Cult. Kenya
A. lettyae Reynolds	Grace 60 (K, PRE), South Africa
A. leptosiphon A.Berger	RBG 1967-16201 (K), Cult. Zambia
A. macrocarpa Tod.	RBG 1972-4103 (K), Cult. Ethiopia
A. maculata All.	Grace 82 (K, PRE), South Africa
A. maculata All.	RBG 1990-1902 (K), Cult. California, USA
A. monotropa I. Verd.	Grace 65 (K, PRE), South Africa
A. mudenensis Reynolds	RBG 1947-52506 (K), South Africa
A. prinslooi I. Verd. & D.S. Hardy	Grace 68 (K, PRE), South Africa
A. pruinosa Reynolds	Grace 69 (K, PRE), South Africa
A. scobinifolia Reynolds & P.R.O.Bally	—, Treutlein et al. 2003a AJ511388, Treutlein et al. 2003b AY323687
A. sinkatana Reynolds	—, Treutlein et al. 2003a AJ511386, Treutlein et al. 2003b AY323689
A. somaliensis var. *somaliensis* W.Watson	—, Treutlein et al. 2003b AY323716, Treutlein et al. 2003b AY323672
A. striata Haw.	—, Treutlein et al. 2003a AJ511392, Treutlein et al. 2003b AY323668
A. suffulta Reynolds	RBG 1961-56203 (K), Mozambique
A. suprafoliata Pole-Evans	—, Treutlein et al. 2003b AY323715, Treutlein et al. 2003b AY323676
A. swynnertonii Rendle	Grace 59 (K, PRE), South Africa
A. umfoloziensis Reynolds	Grace 73 (K, PRE), South Africa
A. vanbalenii Pillans	Grace 81 (K, PRE), South Africa
A. vanrooyenii G.F. Sm. & N.R. Crouch	Grace 70 (K, PRE), South Africa
A. vera L.	Chase et al. 2000 AJ290255 AJ290289, Treutlein et al. 2003b AY323726, Treutlein et al. 2003b AY323685
A. vogtsii Reynolds	Grace 57 (K, PRE), South Africa
A. zebrina Baker	Grace 63 (K, PRE), South Africa
Gasteria Duval	Chase et al. 2000 AJ290264 AJ290298, Treutlein et al. 2003b AJ511401, Treutlein et al. 2003b AY323655

[1]Listed in this order: *trnL–F* intron and spacer, *matK*, and ITS; — = sequence not obtained.

DNA sequencing

Total genomic DNA was extracted from silica-gel dried flowers or leaves (ca 0.3 g) or fresh leaf material (ca. 1.0 g) according to a protocol modified from those described by Doyle and Doyle (1987) and Saghai-Maroof et al. (1984). Aliquots of DNA were purified with the Nucleospin® Extract II minicolumn kit (Macherey-Nagel, Düren) using the binding buffer from Qiagen (Crawley). The remaining DNA was purified by caesium chloride-ethidium bromide density gradient (1.55 $g\mu l^{-1}$) followed by a dialysis procedure, and accessioned to the DNA bank at Kew (data.kew.org/dnabank).

The *matK* region was amplified using the XF and 5R primers (kew.org/barcoding/). Polymerase chain reactions (PCRs) were prepared in 20 µl volumes containing 5× GoTaq FlexiBuffer (supplied by the manufacturer), 2 µl of 0.04% bovine serum albumin (BSA), 1.25 mM $MgCl_2$, 0.4 µl dNTPs, 2 U GoTaq polymerase and 1 µl of each primer. The *trnL* intron and *trnL-F* spacer were amplified using the primer pairs c-d and e-f, respectively (Taberlet et al., 1991). PCRs in 25 µl volumes were prepared with 22.5 µl ReddyMix PCR Master Mix (Thermo Scientific) containing 2.5 mM $MgCl_2$, 0.5 µl of 0.04% BSA,0.5 µl of each primer and 1 µl template DNA. The internal transcribed spacers (ITS) ITS1 and ITS2 were amplified with the ITS4 and ITS5 primers of White et al. (1990). The same PCR protocol described for the *trnL-F* region was used, but using 1.5 mg $MgCl_2$ ReddyMix PCR Master Mix (Thermo Scientific) and 4% DMSO.

Thermal cycling was conducted with a GeneAmp PCR System 9700 (Applied Biosystems) using the following procedures. For *matK*, we used an initial denaturation at 94 °C for 2 min followed by 33 cycles of denaturation at 94 °C for 1 min, annealing at 53 °C for 1 min and extension at 72 °C for 1.5 min, and a final extension of 4 min at 72 °C. For the *trnL-F* region, the initial denaturation at 94 °C for 2 min was followed by 28 cycles comprising denaturation at 94 °C for 1 min, annealing at 50 °C for 1 min and extension at 72 °C for 1.5 min, and a final extension of 7 min at 72 °C. For the ITS region, the initial denaturation at 94 °C for 3 min was followed by 33 cycles of denaturation at 94 °C for 1 min, annealing at 50 °C for 30 sec and extension at 72 °C for 1.5 min, and a final extension of 4 min at 72 °C. PCR products were purified with the Nucleospin® Extract II minicolumn kit (Macherey-Nagel, Düren) using the binding buffer from Qiagen (Crawley).

Cycle sequencing of the PCR products was performed with the same primer pairs used for amplification and the BigDye Terminator Cycle Sequencing kit (version 3.1; Applied Biosystems) in 10 µl reaction volumes. The products were purified on a Biomek NX S8 (Beckman Coulter) automated workstation according to the manufacturer's protocol. Sequences from the complementary strands of the amplified templates were recorded on a 3730 DNA Analyzer (Applied Biosystems/Hitachi). Electropherograms were edited and assembled using Sequencher 4.5 (Gene Codes Corporation) and aligned by eye in PAUP* 4.0b10 (Swofford, 2002).

Phylogenetic analyses

Phylogenetic reconstructions were obtained using maximum parsimony and Bayesian inference with *Gasteria* defined as outgroup. Maximum parsimony analyses were conducted in PAUP* 4.0b10 (Swofford 2002). All characters were treated as independent, unordered and equally weighted (Fitch parsimony; Fitch 1971). An analysis was performed using the heuristic search option with 1000 replicates of random taxon addition, tree bisection and reconnection (TBR) branch swapping, and no more than 10 trees were saved per replicate. The trees obtained from the first analysis were used as starting trees in a second analysis using the same parameters, and saving a maximum of 10000 trees. Support for the internal nodes was evaluated with bootstrap percentages (Felsenstein 1985) calculated by performing 1000 replicates with simple taxon addition, TBR branch swapping and saving no more than 10 trees per replicate. Clades with bootstrap percentages (BP) of 50–74% were described as weakly supported, 75–89% moderately supported and 90–100% strongly supported.

Trees determined by Bayesian inference were obtained in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit model of DNA substitution for each partition using the Akaike and Bayesian Information Criterion. Two parallel runs of four simultaneous chains of the Markov Chain Monte Carlo (MCMC) were executed for 5,000,000 generations, sampled every 1000 generations. All parameters were stationary after 500 000 generations; the 500 initial suboptimal trees were removed (burn-in) from the compilation of posterior probabilities (PP). A majority rule consensus tree was calculated from the remaining trees in PAUP* 4.0b10. Clades with posterior probabilities above 0.95 were considered strongly supported.

Results

The resulting aligned sequence matrix comprised 2267 characters, of which 13.6% were variable and potentially parsimony informative. The ITS region comprises 51 (7.5%) potentially parsimony informative characters, while the *trnL* intron, *trnL-F* spacer and *matK* have 8.4%, 4.4% and 3.4%, respectively (Table 4.2). Trees generated from parsimony analyses of each partition were congruent but lacked internal support (trees not shown), prompting us to conduct further analyses on the combined plastid and nuclear data partitions. Heuristic searches identified 4660 trees of 525 steps with a consistency index (CI) of 0.42 and retention index (RI) of 0.59 (excluding uninformative characters), and good bootstrap support for deeper nodes. A majority rule consensus tree calculated from trees generated by Bayesian inference produced a very similar topology (Fig. 4.1), with high posterior probabilities shown for the spine of the tree.

Representatives of *Aloe* were recovered in a strongly supported clade (PP 1.00; 100 BP) sister to *Gasteria* and a *Haworthia*-like species, *A. aristata* Haw. (Fig. 4.1). A well supported (PP 1.00; 99 BP) yet morphologically diverse southern African clade (*A. arborescens* Mill., *A. glauca* Mill., *A. humilis* (L.) Mill.) was sister to *A. suprafoliata* Pole-Evans, a southern African species bearing distinctive glaucous leaves with toothed margins. A large group (PP 0.94; 80 BP) comprising the remainder of the genus was sister to this. The first diverging lineages in this large clade comprised two short-stemmed species endemic to Madagascar (*A. capitata* Baker and *A. compressa* H. Perrier; PP 1.00, 86 BP), together sister to a polytomy (in the parsimony analysis) consisting of four lineages: (1) a clade comprising East African and Arabian species (PP 1.00; 59 BP); (2) a Horn of Africa clade, (PP 1.00; 73 BP), (3) a maculate group, which is convincingly supported by a high posterior probability (PP 1.00) and moderate bootstrap value (87 BP); (4) species of marginal status in section *Pictae*, *A. suffulta* Reynolds and *A. leptosiphon* A. Berger (PP 0.98; 56 BP). A southern African stemless species, *A. vanbalenii* Pillans, was unplaced in the strict consensus tree, but was associated, although not supported (PP 0.35), with the Horn of Africa group by Bayesian inference. The East Africa/Arabia clade comprised a group of three East African species (*A. forbesii* Balf. f., *A. scobinifolia* Reynolds & P. R. O. Bally, *A. sinkatana* Reynolds; 74 BP) sister to two Arabian species (*A. doei* Lavranos, *A. vera* L.) and the Horn of Africa clade (*A. jucunda* Reynolds, *A. juvenna* Brandham & S. Carter, and *A. somaliensis* W. Watson). The crown node of the maculate clade was a large polytomy comprising most species in this group with a few weakly to moderately supported species assemblages.

Table 4.2. Characteristics of the four partitions used in the phylogenetic analyses of *Aloe* section *Pictae*.

	ITS	*trnL* intron	*trnL-F* spacer	*matK*	Combined
Aligned length (characters)	736	600	406	818	2560
Included characters	680	406	363	818	2267
Parsimony informative characters	7.5%	8.4%	4.4%	3.4%	5.7%
Variable characters	15.0%	23.2%	16.5%	11.2%	13.6%
Constant characters	85%	76.8%	83.5%	88.8%	84.6%

Discussion

Closely comparable trees generated by parsimony and Bayesian inference analyses yielded the first molecular evidence for the monophyletic status of section *Pictae* (Fig. 4.1). *Aloe* is a heterogeneous and possibly polyphyletic taxonomic entity; its boundaries with *Gasteria* and *Haworthia* are particularly unclear (Treutlein et al. 2003a). The original broad concept of *Aloe* circumscribed by Linneaus (1753) in *Species Plantarum* has since been segregated into seven morphologically recognisable and widely accepted genera (Smith and Van Wyk 1991), yet natural classifications of these genera and constituent species have remained unresolved. The suspected polyphyletic status of segregate genera such as *Haworthia* has even led to the Linnean concept of *Aloe* being reconsidered (Treutlein et al. 2003b). Morphologically, *Aloe* differs from *Gasteria* and *Haworthia* in its usually straight, tubular flowers, often spiny leaves, and species with tree-like woody growth. *Gasteria* has characteristic gasteriform (curved) flowers that are pendulous at anthesis, whereas flowers in *Haworthia* are bilabiate and whitish; prominent spines are absent from the leaves of species in both genera (Smith and Van Wyk 1998, Smith and Steyn 2004). We used published sequence data for *A. aristata* which was consistently resolved within *Haworthia* in studies by Treutlein et al. (2003b). While it was beyond the scope of the present study to test generic boundaries among alooid taxa, in this case the *Haworthia*-like *A. aristata* was shown to be more closely related to *Gasteria* (defined as outgroup in our analyses), and is a doubtful member of *Aloe.*

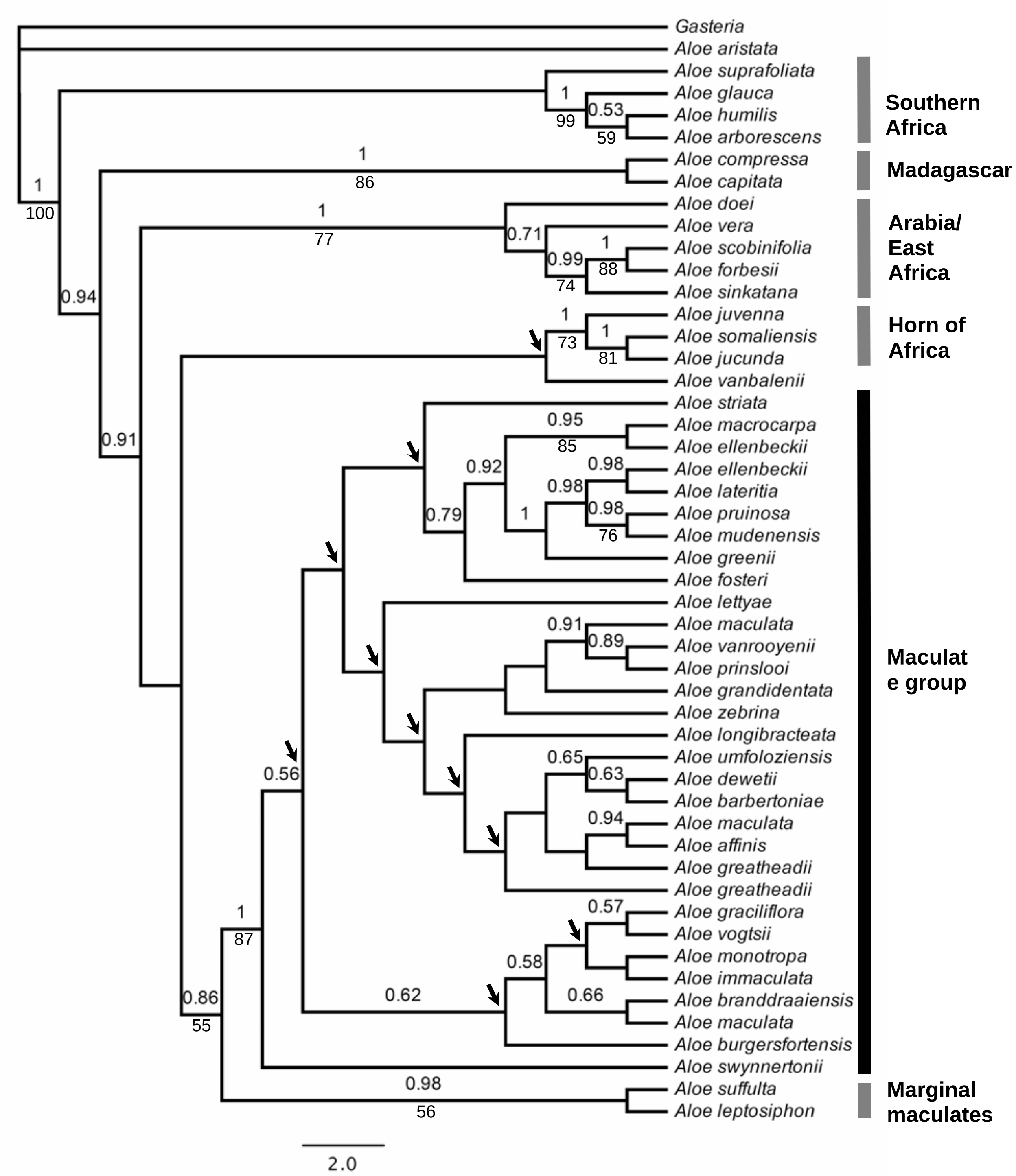

Figure 4.1 Topology from Bayesian analysis of nuclear and plastid data, with *Gasteria* as outgroup. Posterior probabilities >0.5 are shown above branches and bootstrap percentages >50 are shown below branches. Branches that collapsed in a strict consensus tree of 4660 equally parsimonious trees from the same data are indicated by arrows.

Aloe section *Pictae* is generally regarded as a natural group, comprising an assemblage of poorly defined, closely related species with spotted leaf surfaces, and a perianth that is basally inflated and constricted above the level of the ovary (Groenewald 1941, Glen and Hardy 2000). Despite the questionable validity of these morphological apomorphies at the infrageneric rank, the traditionally core maculate group was recovered (PP 1.00) with moderate support (87 BP) in our phylogenetic reconstructions.

Evolutionary interpretation of these data would require a revised hypothesis for section *Pictae* to accommodate descendants from a common ancestor, in which *A. striata* and related species are included, and which excludes the marginal species *A. leptosiphon* and *A. suffulta.* Significantly, *A. leptosiphon* and *A. striata* are among only four accepted species that Reynolds (1950, 1966) excluded in his revision of Berger's (1908) classification of maculate species. In a parsimony tree inferred from ITS data, *A. striata* was sister to the well supported maculate group (98 BP), but the position lacked support (57 BP) (results not shown); cladistic analyses of additional genomic characters and species may add clarity. Morphologically, *A. striata* and close relatives in section *Paniculatae* Salm-Dyck ex Kunth (*A. buhrii* Lavranos, *A. karasbergensis* Pillans, *A. komaggasensis* Kritzinger & Van Jaarsv., *A. kouebokkeveldensis* van Jaarsv. & A. B. Low, and *A. reynoldsii* Letty) share the basal swelling and perianth constriction typical of section *Pictae.* Leaves of some members of the group (*A. buhrii*, *A. reynoldsii*) also have irregular white spots typical of maculate species. Phytochemical affinities have been noted between *A. striata* and southern African representatives of section *Pictae* (unpubl. data). However, the glaucous and conspicuously striate, sometimes leathery (e.g. *A. reynoldsii*) leaves with entire or minutely dentate leaf margins of *Paniculatae* differ markedly to the sharply toothed, robust leaves of section *Pictae.* Berger (1908) was the single author to adopt a broad circumscription of maculate species in *Aloe* that included section *Paniculatae.* Subsequent authors (e.g. Groenewald 1941; Reynolds 1950, 1966; Glen and Hardy 2000) followed the narrow concept of sections *Pictae* and *Paniculatae* originally circumscribed by Salm-Reifferscheid-Dyck (1837). Further molecular data are necessary to resolve the relationships between these two sections.

The status in section *Pictae* of the unusual species *A. leptosiphon* and *A. suffulta* may also be clarified on the basis of molecular evidence. In addition to convincing posterior probability value (PP 0.98), the two species comprise a well supported group sister to the maculate group in parsimony trees based on ITS data (79 BP) (results not shown), although confidence is notably lower (56 BP) in trees generated from combined plastid and nuclear data. Berger (1908) included *A. leptosiphon* in his broad concept of the maculate section, presumably on account of the pale leaf surface markings, and in spite of its atypical floral morphology. The tenuous affiliation of *A. leptosiphon* with section *Pictae* is further illustrated by Reynolds' (1966) failure to associate *A. greenwayi* Reynolds, a species subsequently reduced to synonymy under *A. leptosiphon*, with the maculate section when he named it. In a similar case, the copiously spotted leaf surfaces of *A. suffulta* led Berger (1908) and Groenewald (1941) to include this species with southern African representatives of the maculate section. However, *A. suffulta* has since been classified, on the basis of floral characters, with other species of *Aloe* characterised by diagnostic trigonous indentations in the perianth above the ovary (series *Aethiopicae* A. Berger; section *Chabaudia* Glen and Hardy) (Reynolds 1950; Glen and Hardy 2000). It is clear that perianth characters have greater significance as synapomorphies for section *Pictae* than leaf markings.

The natural boundaries of section *Pictae* identified from phylogenetic reconstructions include maculate species from throughout southern and tropical Africa. With the exception of Berger's (1908) infrageneric treatment of *Aloe*, tropical and southern African maculate species have been dealt with separately, adding to taxonomic inconsistency evident in section *Pictae.* Seventy-two species names have been proposed for 39 species taxa currently accepted as representing valid taxa (Newton 2001) in section *Pictae*. Infraspecific ranks have been more conservatively used in the classification of maculate species than in other infrageneric groups in *Aloe* (varieties are recognised only in the southern African *A. greatheadii* Schönland and East African *A. lateritia* Engl.). However, it is likely that there are still more species names than good species in section *Pictae*, due to the treatment of variable, widespread taxa as poorly defined species, as well as the challenge of defining species undergoing hybridisation and active speciation (Reynolds 1966, Glen and Hardy 2000). Evidence for active speciation in *Aloe* has been recovered from chromosome termini, and in ITS variation (Adams et al. 2000a, 2000b). These factors may also explain low levels of support for terminal branches in the maculate clade, which pre-empt detailed analysis of relationships among species reduced to a polytomy in the clade.

Unambiguous phylogenetic signals were recovered for relationships among very few species in the maculate group, the remainder reduced to polytomies. *Aloe ellenbeckii* A. Berger collected near Marsabit in northern Kenya was convincingly associated (PP 0.95; 85 BP) with *A. macrocarpa* Tod., a maculate species occurring from the Horn of Africa region into West Africa, while a second accession of *A. ellenbeckii* collected near Nairobi in Kenya was associated with *A. lateritia*, a species that Wabuyele (2006) reduced to synonymy under *A. macrocarpa* on the basis of morphometric, phytochemical and isozyme data. The KwaZulu-Natal endemics *A. mudenensis* Reynolds and *A. pruinosa* Reynolds were well resolved (PP 0.98; 76 BP) together. In a majority rule consensus tree, the closely related *A. greenii* Baker was sister to the KwaZulu-Natal assemblage in all of the most parsimonious trees, while the East African *A. lateritia* was associated with *A. ellenbeckii* in 70% of the most parsimonious trees. Other terminal groups recovered in the majority rule consensus included *A. affinis* A. Berger and *A. maculata* All. (100%), two southern African species which bear capitate or sub-capitate racemes; the morphologically distinct but geographically overlapping *A. dewetii* Reynolds and *A. umfoloziensis* Reynolds (100%); and the very restricted southern African *A. branddraaiensis* Groenew. and another accession of *A. maculata* (97%). The appearance of *A. maculata* and *A. greatheadii* at different positions in the topology of the parsimony trees may be explained by the heterogeneity of these species. Despite major phylogenetic patterns being recognised in this analysis, we anticipate that considerable additional data will be necessary to resolve the apparently complex species relationships in this section.

Ingroup species included in our study were recovered in geographically congruent groups representing southern Africa, Madagascar, southern Arabia, East Africa and the Horn of Africa. The absence of any species of *Aloe* with maculate leaves on Madagascar could indicate that *Aloe* species with leaf markings diversified in Africa after the dispersal event that lead to the diversification of Madagascan species (Holland 1978).

The absence of groups comprising species alike in habit or gross morphology is striking, and may be explained by convergent evolution. For instance, maculate leaves in *Aloe* may have arisen independently in section *Pictae* and other infrageneric groups of *Aloe*, presumably as an adaptive advantage to regulate photosynthetic capacity and for camouflage. On the other hand, it is not clear if the floral morphology restricted to section *Pictae* (and the segregate section *Paniculatae*) is associated with a primitive or derived pollination syndrome, or indeed a reversal. Insect pollination is speculated to be ancestral in *Aloe*, and is less common than bird pollination (Hargreaves et al. 2008). In section *Pictae*, the bulbous base and constricted perianth of flowers may constrain nectar thieving by birds (although in several maculate species we have observed external damage to the base of flowers caused by birds). In *A. greatheadii* var. *davyana* (Schönland) Glen and D.S. Hardy, the nectar is considerably more concentrated (approximately 20% w/w) than in other species of *Aloe* (Human and Nicolson 2008). Nectar accumulates in the bulbous base of the perianth and moves by capillarity along a nectar duct in the corolla tube, to be presented as droplets at the mouth of the flower where it is foraged by bees (Nepi et al. 2006). *Aloe greatheadii* var. *davyana* is visited by bees for nectar and pollen during the winter flowering period and is greatly valued for apiculture in South Africa (Human and Nicolson 2008). Although among the most common visitors to the flowers of *Aloe*, however, bees are seldom the pollinators (Hargreaves et al. 2008); neither bees nor other insects and sunbirds known to visit *A. greatheadii* var. *davyana* have been positively identified as the pollinating agents. The significance of the distinctive floral morphology of section *Pictae*, and the direction of pollination syndromes in *Aloe*, require systematic study.

Phylogenetic reconstructions based on nuclear and plastid sequence data provided novel insights into the infrageneric status, and interspecific relationships, of *Aloe* section *Pictae.* We anticipate that further phylogenetic evidence will add considerable understanding of evolutionary relationships and taxonomic stability to help propose a revised infrageneric classification of *Aloe.* This evolutionary framework will also be essential to examine the biogeographical patterns and causes of speciation in this important genus of succulents.

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CHAPTER 5 CHEMOSYSTEMATICS

[1] Supplementary spectral data are provided in Appendix C on the enclosed CD.

Introduction

The succulent-leaved genus *Aloe* L. (Asphodelaceae) is an Old World monocot group of over 500 species occurring throughout Africa, the Arabian Peninsula and western Indian Ocean Islands (Newton, 2001). At least a quarter of *Aloe* species are valued for traditional medicine (Grace et al., 2009) while a small number are wild harvested or cultivated for natural products prepared from the bitter leaf exudate or gel-like leaf mesophyll; *A. vera* is particularly common in cultivation and supports a global natural products industry. The genus has been the subject of considerable phytochemical research during the past century, intended to characterise and authenticate natural products from species in trade and identify their bioactive properties. The purgative effects of *Aloe* leaf exudate ('drug aloes') have been attributed to anthraquinone *C*-glycosides, notably barbaloin and aloins A and B (Reynolds, 1985; Chauser-Volfson and Gutterman, 2004; Steenkamp and Stewart, 2007). The mucilaginous leaf mesophyll ('aloe gel') is rich in acylated polysaccharides possessing anti-inflammatory properties (Steenkamp and Stewart, 2007).

Besides bioactivity, compounds in the leaves and roots of *Aloe* spp. are of potential taxonomic value (Viljoen et al., 1999). Phytochemical characters have been useful in the discussion of a natural (evolutionary) infrageneric classification of *Aloe*, since several groups in the existing classification are seemingly highly artificial, their taxonomy lacking predictive strength. For instance, the presence of bitter phenolic compounds in the brown floral nectar of *A. spicata* L.f., *A. castanea* Schönland and *A. vryheidensis* Groenewald (Johnson et al., 2006) supports their circumscription in the same infrageneric group. At the generic rank, nectar sugar composition has assisted to clarify relationships among *Aloe* and related genera (Van Wyk et al., 1993). Over 200 species of *Aloe* have been chemically characterised (Reynolds, 1985; Dagne et al., 2000; Reynolds, 2004), yet a number of taxonomically problematic groups of species are among those for which chemical data are lacking. One such example is section *Pictae* Salm-Dyck (= section *Maculatae* Baker; series *Saponariae* Berger), a distinctive yet poorly resolved taxonomic entity loosely referred to as the "maculate species complex". In the broadest sense, the section comprises about 40 infraspecific taxa characterised by the shape of the perianth (tubular with a pronounced constriction above a bulbous basal swelling) and patterned leaf surfaces. The adaxial, and sometimes abaxial, leaf surface is densely adorned with conspicuous or obscure white or pale yellow-green spots, which may converge in transverse bands or longitudinal striae. Whilst these morphological characters make representatives of section *Pictae* distinctive, species relationships within the group are puzzling. To date, chemical characters shared by representatives of section *Pictae* have been evaluated at the supraspecific level only. The presence of isoeleutherol in the roots of maculate taxa has been interpreted as a taxonomic marker for them (Yenesew and Dagne, 1993; Van Wyk et al., 1995), while an anthrone *C*-glycoside was similarly interpreted for East African maculate taxa (Wabuyele, 2006). Here, we report on the first comprehensive comparative study of UV-absorbing leaf constituents in section *Pictae*, and the systematic significance of selected chemical characters in resolving inter- and infraspecific relationships in the group and its sectional circumscription.

Materials and methods

Plant material for chemical analyses was collected from wild populations in South Africa and plants of wild provenance kept in glasshouses at the Royal Botanic Gardens, Kew. Voucher specimens were deposited in the herbarium at Kew (K) and the National Herbarium (PRE) in South Africa (Table 5.1). Mature leaves were removed close to the stem axis and sliced thinly; where possible, the mucilaginous mesophyll was removed. Material was extracted for 24–48h in MeOH, filtered through filter paper (Whatman No. 1) and the filtrate air-dried. Residues were dissolved in MeOH; aliquots were centrifuged for 5–10 min at 100 rpm and the supernatant analysed.

UV-absorbing components in methanolic leaf extracts (50mg ml^{-1} in 50% MeOH) were separated and detected by analytical HPLC (Grace et al., 2008). Chromatograms were extracted at 254 nm and 335 nm; data were recorded with Waters Empower software. UV spectra, retention times (R_t) and the surface areas of peaks showing at least half the UV absorbance of the most-absorbing peak (100%) were recorded from each chromatogram. Peak area, calculated from integrals measured in uV sec^{-1}, was used to quantify the presence of these major components. The relative molecular mass (*M*r) of compounds of interest in leaf extracts was determined by LC-MS (Grace et al., 2008). A Thermo Finnigan Surveyor LC system coupled to a quadrupole ion trap mass spectrometer (Thermo Finnigan LCQ Classic) was used to acquire mass spectral data for compounds of interest. Samples were separated on a column (Phenomenex Ltd., Luna C_{18}, dp 5µm, 4.6 × 150 mm) at 30 ^{o}C with a mobile phase comprising a linear gradient of MeOH: water:5 % methanolic acetic acid (t=0, 0:80:20; t=20, 80:0:20; t=27, 0:80:20; t=37, 0:80:20). The eluate was monitored at 200–500nm prior to the positive APCI mode and scanned in the range 125–1200 *m/z*. The most prevalent ions in each scan were isolated and collision induced dissociation (CID) spectra obtained of their ions.

Data were recorded with Thermo Scientific Xcalibur software, and compounds were identified by comparison of UV- and mass spectral data to reference samples and the literature (Viljoen et al., 1998; Viljoen et al., 1999).

Results and discussion

Spectral data indicated that UV-absorbing constituents in 34 representatives of section *Pictae* are of systematic interest (Table 5.2). The present discussion is focused on compounds which may be particularly relevant, the flavones isoorientin and isovitexin and the anthrone *C*-glycoside 6′-malonylnataloin.

Isoorientin (luteolin-6-*C*-glucoside) was the major constituent in leaf extracts of 13 of the 20 species in which it was detected, including the type species for section *Pictae*, *A. maculata* (Table 5.2). It was present in highest concentrations ($\log_{10}$ peak area 6.12–6.96 uVsec^{-1}) in individuals of *A. umfoloziensis* collected from four populations over an area of approximately 100 km^2 (Table 5.1). Isoorientin was detected in species occurring throughout the pan-African range of the representatives of the maculate species complex. These included the widespread *A. greatheadii* var. *greatheadii*, *A. macrocarpa* and *A. zebrina*, as well as species found only within local regions of high species richness in southern and East Africa.

Isovitexin (apigenin 6-*C*-glucoside) was less prevalent among representatives of the maculate species complex. It was the major constituent in leaf extracts of four southern African taxa (*A. greenii*, *A. parvibracteata*, *A. pruinosa* and *A. striata*), but was absent in the East African species surveyed. The highest concentrations of isovitexin were identified in *A. parvibracteata* ($\log_{10}$ peak area 6.1–6.8 uVsec^{-1}). Significantly, isoorientin was observed in similarly high concentrations in two populations of *A. parvibracteata* sampled over approximately 120 km^2. Similar concentrations of isoorientin were observed in the closely related and co-occurring *A. umfoloziensis*, but the absence of isovitexin in the latter supports the retention of two separate species. The absence of isovitexin in *A. maculata* also contests the hypothesis that *A. umfoloziensis* is conspecific with the type species of section *Pictae.* The single other taxon in which both isovitexin and isoorientin were recorded was *A. macrocarpa*, a geographically disjunct representative of section *Pictae.*

Table 5.1 Plant material used for phytochemical analysis of *Aloe* section *Pictae*

Taxon (names reduced to synonymy in parentheses)	Voucher number	Origin
Aloe affinis A.Berger	Grace 87	Mac Mac Falls, South Africa
A. amudatensis Reynolds	RBG 1977-6734	Weiwei, Kenya
A. barbertoniae Pole-Evans	Grace 85	Barberton, South Africa
A. branddraaiensis Groenew.	RBG 1957-14502	South Africa
A. burgersfortensis Reynolds	Grace 89	Burgersfort, South Africa
A. burgersfortensis Reynolds	RBG 1965-72105	Lydenburg, South Africa
A. chabaudii Schönland	RBG 1996-1526	Buffel's Drift, Zimbabwe
A. dewetii Reynolds	Grace 83	Alpha, South Africa
A. ellenbeckii A.Berger	RBG 1973-2107	Nairobi, Kenya
A. ellenbeckii A.Berger	RBG 1977-2441	Marsabit, Kenya
A. ellenbeckii A.Berger (*A. dumetorum*)	RBG 1977-3962	Marsabit, Kenya
A. fosteri Pillans	Grace 88	Ohrigstad, South Africa
A. fosteri Pillans	RBG 2003-1796	South Africa
A. grandidentata Salm-Dyck	RBG 1973-2520	Orange Free State, South Africa
A. greatheadii Schönland	RBG 1996-1525	Harare, Zimbabwe
A. greatheadii var. *davyana* (Schönland) Glen & D.S. Hardy (*A. graciliflora* Groenew.)	Grace 67	Tonteldoos, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S. Hardy (*A. longibracteata* Pole-Evans)	Grace 66	Lydenburg, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy	RBG 1965-12201	Pretoria, South Africa
A. greatheadii var. *davyana* (Schönland) Glen & D.S.Hardy (*A. davyana*)	RBG 1973-2542	Pretoria, South Africa
A. greatheadii var. *greatheadii*	Grace 58	Louis Trichardt, South Africa
A. greatheadii var. *greatheadii*	Grace 61	Boyne, South Africa
A. greenii Baker	Grace 74	eShowe, South Africa
A. immaculata Pillans	Grace 62	Chuniespoort, South Africa

Table 5.1 *(continued)*

Taxon (names reduced to synonymy in parentheses)	Voucher number	Origin
A. immaculata Pillans	Grace 64	Chuniespoort, South Africa
A. lateritia var. *graminicola* (Reynolds) S.Carter	RBG 1973-2058	Thompson's Falls, Kenya
A. lateritia var. *graminicola* (Reynolds) S.Carter (*A. lateritia* var. *solaiana*)	RBG 1973-2070	Nanyuki, Kenya
A. leptosiphon A.Berger (*A. greenwayi)*	RBG 1967-16201	Abercorn, Zambia
A. lettyae Reynolds	Grace 60	Haenertsburg, South Africa
A. macrocarpa Tod.	RBG 1972-4103	Adamitulla, Ethiopia
A. maculata All.	Grace 82	Ngome, South Africa
A. maculata All.	Grace 84	Carolina, South Africa
A. maculata All. (*A. saponaria* var. *ficksburgensis*)	RBG 1982-268	Ficksburg, South Africa
A. maculata All. (*A. saponaria*)	RBG 1990-1902	Cape Province, South Africa
A. monotropa I.Verd.	Grace 65	Mmafefe, South Africa
A. mudenensis Reynolds	RBG 1947-52506	Natal, South Africa
A. parvibracteata Schönland	Grace 77	Jozini, South Africa
A. parvibracteata Schönland	Grace 78	iNgwavuma, South Africa
A. parvibracteata Schönland	Grace 79	Pongola, South Africa
A. parvibracteata Schönland	Grace 80	Pongola, South Africa
A. petrophila Pillans	RBG 1973-2501	Transvaal, South Africa
A. prinslooi I.Verd. & D.S.Hardy	Grace 68	Colenso , South Africa
A. pruinosa Reynolds	Grace 69	Ashburton, South Africa
A. simii Pole-Evans	Grace 86	White River, South Africa
A. striata Haw.	RBG 1985-4082	Karoo, South Africa
A. suffulta Reynolds	RBG 1961-56203	Mozambique
A. swynnertonii Rendle	Grace 59	Thohoyandou, South Africa
A. swynnertonii Rendle	RBG 1970-2395	Livingstone Falls, Malawi

Table 5.1 *(continued)*

Taxon (names reduced to synonymy in parentheses)	Voucher number	Origin
A. umfoloziensis Reynolds	Grace 71	eShowe, South Africa
A. umfoloziensis Reynolds	Grace 72	eShowe, South Africa
A. umfoloziensis Reynolds	Grace 73	eShowe, South Africa
A. umfoloziensis Reynolds	Grace 75	eShowe, South Africa
A. umfoloziensis Reynolds	Grace 76	eShowe, South Africa
A. vanbalenii Pillans	Grace 81	Nongoma, South Africa
A. vanrooyenii G.F.Sm. & N.R.Crouch	Grace 70	Muden, South Africa
A. vogtsii Reynolds	Grace 57	Louis Trichardt, South Africa
A. wollastonii Rendle (*A. lateritia* var. *kitaliensis*)	RBG 1973-1982	Kitale, Kenya
A. zebrina Baker (*A. ammophila* Reynolds)	Grace 63	Chuniespoort, South Africa
A. zebrina Baker (*A. ammophila* Reynolds)	RBG 1973-2574	Potgietersrus, South Africa

Chemosystematic similarities among *A. greenii*, *A. parvibracteata* and *A. pruinosa* may have biogeographical significance, since these species occur in the eastern sub-tropical savanna regions of South Africa. Indeed, the similarity between *A. greenii* and *A. pruinosa* is unsurprising, as they are remarkably alike in features of gross morphology (leaf shape, flower colour, pruinose flowers). However, these species can be separated by plant size, stem length, surculose growth habit, and the restricted distribution of *A. pruinosa* to the vicinity of Pietermaritzburg in KwaZulu-Natal.

The presence of isovitexin as a major constituent of *A. striata* is noteworthy. Berger (1908) included this species in his concept of the maculate group (series *Saponariae* Berger) on account of its floral morphology, but, due to its striking glaucous leaves with entire, red margins, *A. striata* and its close relatives (*A. buhrii*, *A. karasbergensis*, *A. komaggasensis* and *A. reynoldsii*) have since been recognised in section *Paniculatae* (Reynolds, 1950; Glen and Hardy, 2000). *A. striata* hybridises readily with *A. maculata*, with which it shares a similar range and flowering period (Smith 2003). Future taxonomic assessment may confirm the relationship between *A. striata*, or indeed *Paniculatae* in its entirety, and section *Pictae.* Isovitexin has, however, been detected in several basal infrageneric groups related distantly to section *Pictae*; it is a major constituent of grass-like species of *Aloe* in sections *Leptaloe* A.Berger and *Graminaloe* Reynolds, species with a rambling habit in series *Macrifoliae* A.Berger, as well as species with berried fruits in the segregate genus *Lomatophyllum* (Viljoen et al., 1998).

These are, to our knowledge, the first records of isoorientin and isovitexin in the maculate species complex of *Aloe*. Flavonoids were absent from the few maculate taxa included in a previous screening for this compound class in *Aloe* (Viljoen et al. 1998), while uncharacterised luteolin and apigenin derivatives have been reported in East African maculate taxa (Wabuyele, 2006).

In addition to flavonoids, plicataloside, a naphthalene derivative widespread in *Aloe*, was detected for the first time as a minor constituent of *A. greatheadii*. The co-occurrence of a naphthalene derivative and a flavone (isoorientin, the major constituent detected in *A. greatheadii*) is unusual (Viljoen et al., 1999).

A malonylated anthrone *C*-glycoside of systematic interest was detected in five species included in our survey. The compound, 6′-malonylnataloin (7-hydroxychrysaloin 6′-O-malonate), was characterised from *A. ellenbeckii* (Grace et al., 2008) after it was proposed as a marker for maculate species occurring in East Africa (Wabuyele, 2006). It was the major constituent detected in *A. ellenbeckii*, and was also present in another East African species, *A. lateritia* var. *graminicola*. However, the detection of 6′-malonylnataloin in southern African representatives of section *Pictae*, *A. mudenensis* and *A. vogtsii*, as well as non-maculate species *A. ciliaris* and *A. vanbalenii*, diminished the value of this compound as an informative taxonomic character at the infrageneric level. Indeed, due to the instability of *C*-glycosylanthrones and likelihood of the malonyl moiety being lost during extraction, we surmise that malonylated anthrone *C*-glycosides may be more common in *Aloe* than presently appreciated.

Table 5.2 Isoorientin, isovitexin and 6′-malonylnataloin in *Aloe* section *Pictae* and related species

Infrageneric taxon[a]	Major constituents (++), presence (+) and absence (–)		
	Isoorientin	Isovitexin	6′-Malonylnataloin
Aloe affinis	+	–	–
A. amudatensis	++	–	–
A. barbertoniae	+	–	–
A. branddraaiensis	–	–	–
A. burgersfortensis	–	–	–
A. burgersfortensis	–	+	–
A. dewetii	–	–	–
A. ellenbeckii (*A. dumetorum*)	–	–	+
A. ellenbeckii	–	–	++
A. fosteri	+	–	–
A. fosteri	++	–	–
A. grandidentata	++	–	–
A. greatheadii	–	–	–
A. greatheadii var. *davyana* (*A. davyana*)	–	–	–
A. greatheadii var. *davyana* (*A. verdoorniae*)	–	–	–
A. greatheadii var. *davyana* (*A. graciliflora*)	+	–	–
A. greatheadii var. *davyana*	++	–	–
A. greatheadii var. *davyana* (*A. longibracteata*)	+	–	–
A. greatheadii var. *greatheadii*	++	–	–
A. greatheadii var. *greatheadii*	++	–	–

Table 5.2 *(continued)*

Infrageneric taxon[a]	Major constituents (++), presence (+) and absence (–)		
	Isoorientin	Isovitexin	6′-Malonylnataloin
A. greatheadii var. *greatheadii*	++	–	–
A. greatheadii var. *greatheadii*	–	–	–
A. greenii	–	++	–
A. immaculata	++	–	–
A. lateritia var. *graminicola*	+	–	+
A. lateritia var. *graminicola* (*A. lateritia* var. *solaiana*)	+	–	–
A. leptosiphon	–	–	–
A. lettyae	+	–	–
A. macrocarpa	+	+	–
A. maculata	++	–	–
A. maculata	++	–	–
A. maculata	++	–	–
A. monotropa	–	–	–
A. mudenensis	–	–	++
A. parvibracteata	+	++	–
A. parvibracteata	–	++	–
A. parvibracteata	–	++	–
A. parvibracteata	+	++	–
A. petrophila	–	–	+
A. prinslooi	++	–	–
A. pruinosa	–	++	–
A. simii	++	–	–
A. striata	–	++	–
A. suffulta	–	–	–
A. swynnertonii	–	–	–
A. umfoloziensis	++	–	–
A. umfoloziensis	++	–	–
A. umfoloziensis	++	–	–
A. umfoloziensis	++	–	–
A. umfoloziensis	++	–	–
A. vanrooyenii	+	–	–
A. vogtsii	++	–	+
A. wollastonii (*A. lateritia* var. *kitaliensis*)	++	–	–
A. zebrina (*A. ammophila*)	++	–	–
A. zebrina (*A. ammophila*)	+	–	–

Conclusions

Aloe section *Pictae* is widely considered to be a natural or monophyletic assemblage (Groenewald, 1941) defined by a combination of synapomorphies, including distinctive perianth and leaf characters. While none of the chemical constituents identified in the present study was typical of all representatives of section *Pictae*, the detection for the first time of flavonoids in maculate members of *Aloe* is of systematic interest. The presence of flavonoids have been postulated to be a pleisiomorphic character state, restricted in *Aloe* to basal taxa in which leaf succulence and armature are not pronounced (Viljoen et al., 1998). The presence of flavonoids as the major constituents in maculate species possessing conspicuously succulent and spiny leaves, and apparently still undergoing active speciation (Glen and Hardy, 2000) introduces a new perspective to this discussion. Due to the strong selective pressures exserted on adaptive characters such as secondary metabolites, their sometimes erratic occurrence in a plant group can be accounted for not only by convergence, but also by the loss or silencing of genes coding for a biosynthetic pathway (Wink, 2003). Since a molecular phylogeny has yet to be resolved for *Aloe*, however, these possibilities are equally plausible: maculate species may be derived from basal flavonoid-containing groups in *Aloe*, or the gene encoding flavonoid biosynthesis is differentially expressed in species throughout the genus.

Within section *Pictae*, comparative data suggest that the capacity for isoorientin biosynthesis is common among tropical and sub-tropical representatives of section *Pictae*, while isovitexin is restricted to southern African maculate species. Flavonoid profiles are relevant to the problematic taxonomy, at the species and sectional levels, of this section. The presence of isoorientin in *A. striata* corresponds with the original, broad circumscription of the maculate group (Berger, 1908). It would be informative to test for the presence of isoorientin in the other members of section *Paniculatae*. Whereas 6′-malonylnataloin is typical of East African maculate species, it is not a convincing chemical synapomorphy for section *Pictae* as a whole. From a chemosystematic perspective, the distribution of flavonoids and other UV-absorbing constituents in maculate species of *Aloe* may prove useful in resolving the uncertain classification of section *Pictae*, in particular when assessed against an anticipated molecular phylogeny for the group.

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Short communication

Characterisation of a nataloin derivative from *Aloe ellenbeckii*, a maculate species from east Africa

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Abstract

6′-Malonylnataloin, a malonylated derivative of the rare anthrone nataloin, is characterised for the first time from *Aloe ellenbeckii* A. Berger. Anthrone *C*-glycosides are among a suite of chemical constituents of systematic importance in *Aloe*. The compound is of interest as a putative phytochemical marker for the east African taxa in the maculate species complex.

Keywords: *Aloe ellenbeckii*; 6′-Malonylnataloin; *C*-glycosylanthrone; Maculate aloes

1. Introduction

The genus *Aloe* L. (Aloaceae) is an exclusively Old World group comprising ca. 400 species, with centres of diversity in southern and east Africa, the Arabian Peninsula and Madagascar (Newton, 2004). The phytochemical constituents and bioactivity of *Aloe* spp. have attracted research interest since the trade in 'drug aloes', prepared from the leaf exudate, expanded rapidly in the nineteenth century (Yeats, 1870). Today, the principle sources of these natural products are wild populations of *A. ferox* Mill. in South Africa, and *A. scabrifolia* L.E. Newton & Lavranos, *A. secundiflora* Engl. and *A. turkanensis* Christian in east Africa (Oldfield, 2004). In contrast, *A. vera* (L.) Burm.f., the source of the leaf parenchyma known as 'aloe gel', is widely cultivated. Harvesting for the natural products industry is a significant threat which has resulted in all species of *Aloe*, with the exception of *A. vera*, being protected by national as well as international conventions such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Besides being of pharmacological importance, the leaf chemistry of *Aloe* spp. bears systematic significance, particularly at the infrageneric rank. Secondary metabolite profiles have been used in the evaluation of infrageneric groups such as series *Longistylae* Berger (Van Heerden et al., 1996), section *Pachydendron* Haw. (Reynolds, 1997), section *Anguialoe* Reynolds and series *Purpurascentes* Salm-Dyck (Viljoen and Van Wyk, 2001). Phytochemical data may offer insights into the maculate species complex, an assemblage of about 40 species so-named for their conspicuous leaf markings. Although it is widely regarded as a well-supported group, infrageneric boundaries and species delimitation in the maculate complex are problematic.

The present investigation yielded a malonylated nataloin derivative, 6′-malonylnataloin (**1**), from *Aloe ellenbeckii* A. Berger (Fig. 1). This compound had previously been detected in *A. ellenbeckii* and several related east African species by high performance liquid chromatography-photodiode array (HPLC-PDA) analysis (Wabuyele, 2006), but remained uncharacterised. Anthrones, particularly *C*-glycosylanthrones, have been recognised for their systematic significance in *Aloe* (Chauser-Volfson and Gutterman, 1998; Viljoen et al., 1998). In addition to the relevance of **1** as a putative marker for east African taxa in the maculate species complex, it may prove informative regarding affinities with other infrageneric groups in *Aloe*.

2. Materials and methods

Whole fresh leaves (992 g) of *A. ellenbeckii* from the Living Collections of the Royal Botanic Gardens, Kew (accession

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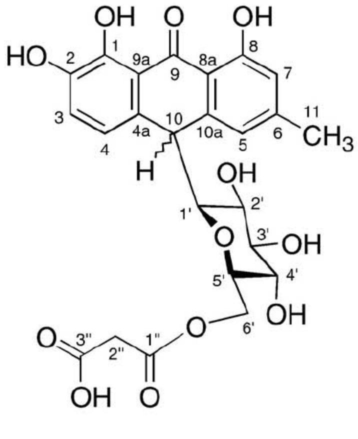

1

Fig. 1. 6′-Malonylnataloin from *Aloe ellenbeckii* (anthrone core numbered according to IUPAC).

1973–2107), were thinly sliced and extracted with 2.2 L ethyl acetate for 48 h on an orbital shaker. The extract was filtered through filter paper (Whatman No 1) before and after treatment with sodium sulphate anhydrate, and the solvent evaporated under reduced pressure at 40 °C. The residue (2 g) was dissolved in 20 mL methanol (MeOH), of which an aliquot was subjected to HPLC-PDA and subsequently on-line mass spectrometric analysis (LC-UV-MS).

Analytical HPLC was carried out with a Waters system (600 pump, 717plus autosampler and 2996 PDA detector) and a reversed phase column (Jones Chromatography, Genesis C_{18}, dp 4 µm, 4.6 mm i.d.×250 mm) at 30 °C. The solvent system comprised a linear gradient of 24–99% MeOH in water, containing 1% formic acid (HCOOH) throughout, over 30 min, followed by isocratic elution for 10 min until re-equilibration of the column, at a flow rate of 1 mL/min. The eluate was monitored between 200 and 500 nm at 1.2 nm resolution. A prominent component eluting at 19.0 min with UV absorption maxima (λ_{max}) 273, 307 and 355 nm was observed. These UV spectral data compared well to those reported by Wabuyele (2006), and those of nataloin ($C_{21}H_{22}O_9$, M_r 418), previously isolated from the leaf exudate of the non-maculate Kenyan species *A. kedongensis* Reynolds [=*A. nyeriensis* var. *kedongensis* (Reynolds) S. Carter] (Conner et al., 1987).

The relative molecular mass of the compound corresponding to the component eluting at 19.0 min was deduced from mass spectrometric data, acquired with a Waters Alliance HPLC system coupled with a PDA detector (Waters 2996) and a Micromass ZQ mass detector. A Phenomenex Luna C_{18} column (dp 5 µm, 3 mm i.d.× 150 mm) was used at 30 °C. The mobile phase comprised a gradient of aqueous acetonitrile, 10–100% containing 0.1% HCOOH throughout, over 20 min, followed by isocratic elution for 5 min, at a flow rate of 0.5 mL/min. The eluate was monitored at 200–500 nm, followed by electrospray (ES) and atmospheric pressure chemical (APC) ionisation using an ESCi multiprobe in positive and negative modes. The *m/z* values at 505 $[M+H]^+$ and 527 $[M+Na]^+$ in the positive mode, and 503 $[M-H]^-$ in the negative mode, indicated a relative molecular mass of 504. The presence of a free carboxylic acid was indicated by a fragment with *m/z* 459 detected in the negative mode $[M-H-CO_2]^-$, as well as marked sharpening of the peak and prolonged retention in the presence of acid (1% HCOOH) during HPLC analysis.

The crude ethyl acetate extract was applied to a polyamide column (30×340 mm), packed and eluted with MeOH. Fractions containing a high proportion of **1** were identified by HPLC-PDA analysis, combined and the solvent evaporated under reduced pressure. The residue was re-dissolved in 2 mL MeOH and applied to a column of Sephadex LH-20 equilibrated in MeOH. Nuclear magnetic resonance (NMR) spectral data (1D ^1H, 1D ^{13}C, 1D selective NOE, COSY, HSQC and HMBC experiments) of the combined fractions containing **1** were acquired in deuterated methanol (CD_3OD) at 30 °C on a Bruker Avance 400 MHz spectrometer.

3. Results and discussion

Chemical shift values were referenced from the residual solvent resonances of CD_3OD at 3.31 ppm (^1H) and 49.1 ppm (^{13}C), with respect to TMS. The ^{13}C NMR spectral data and correlations observed in the 2D spectra (Table 1) indicated that **1** contained twelve aromatic carbons including three oxygen-bearing ones, two carbonyl functions (keto and ester groups)

Table 1
NMR spectral data for 6′-malonylnataloin (**1**) (CD_3OD, 30 °C, δ in ppm, J in Hz)

Position	δ (^1H)	δ (^{13}C)	HMBC (H→C)	sel. NOE (H→H)
1		145.9		
2		151.2		
3	7.01 (1H; d; 8.1)	121.2	C–1, 2, 4a	
4	6.89 (1H; d; 8.1)	120.8	C–1[a], 2, 9[a], 9a, 10	
4a		132.2		
5	6.82 (1H; s)	120.8	C–7, 8a, 10, 11	H–10, 11, 1′
6		149.2		
7	6.68 (1H; s)	117.0	C–5, 8, 8a, 11	H–11
8		162.9		
8a		117.1		
9		195.9		
9a		119.3		
10	4.43 (1H; br d; 2.1)	45.0	C–4, 4a, 5, 8a, 9a, 10a, 1′	H–4, 5, 1′
10a		147.8		
11	2.37 (3H; s)	22.2	C–5, 6, 7	
1′	3.26 (1H; dd; 9.5, 2.0)	86.2	C–4a, 10a	
2′	3.07 (1H; m)	71.7	C–10, 1′, 3′	
3′	3.27 (1H; m)	79.7	C–1′, 2′, 4′, 5′	
4′	2.85 (1H; m)	71.9	C–2′, 3′, 5′, 6′	
5′	3.03 (1H; m)	78.8		
6′	4.19 (1H; m)	65.6	C–4′, 1″	
	3.85 (1H; m)		C–4′, 5′, 1″	
1″		168.5		
2″	nd[b]	nd		
3″		nd		

[a] Weak ^4J correlations.
[b] Not detected.

and six *O*-substituted sp^3 hybridised carbons, the latter suggesting the presence of a glycosidic residue. Only four protons could be observed in the aromatic region of the 1D ^{1}H NMR spectrum, comprising two *ortho*-coupled doublets at δ 6.89 and 7.01 ppm and two singlets at δ 6.68 and 6.82 ppm, indicating a highly substituted and/or fused ring system. The methine resonance of C–10 (δ_H 4.43; δ_C), however, showed correlations with two sets of aromatic resonances in the HMBC and selective NOE spectra. Interpretation of long-range correlations, including a weak ^4J coupling from H–4 (δ 6.89) to the C–9 carbonyl carbon (δ_C 195.9), a coupling between H–10 and H–1′ in the COSY spectrum, and NOE connectivities from H–10 to H–4, H–5 and H–1′ led to the 1,2,8-trihydroxy-6-methylanthrone core. The glycosyl residue was identified as a *C*-linked β-glucopyranose from 2D spectra. A further substitution at glucose CH_2–6′, suggested by its downfield-shifted resonances (δ_H 3.85, 4.19; δ_C 65.6), was confirmed by long-range correlations between the methylene protons to an ester carbonyl carbon C–1″ (δ 168.5). Taking into consideration the molecular mass and the presence of a free carboxylic acid, malonic acid was identified as the acylating group. The resonances for protons CH_2–2″ and carbons C–2″ and C–3″ could not be observed in the respective 1D NMR spectra, due to their exchangeable and acidic properties causing resonance broadening (Hirakura et al., 1997; Schliemann et al., 2006). DMSO-d_6 and pyridine-d_5 caused a rapid colour change of the sample from bright yellow to reddish brown. Attempts to work-up the compound of interest from polyamide column fractions using preparative HPLC were precluded by sample deterioration.

In spite of these shortcomings, the available evidence indicates that the compound is a new malonylated *C*-glycosylanthrone, 6′-malonylnataloin (=7-hydroxychrysaloin 6′-*O*-malonate, $C_{24}H_{24}O_{12}$, **1**). This is, to our knowledge, the first report of a malonylated derivative of an anthrone *C*-glycoside in *Aloe*. The known instability of *C*-glycosylanthrones may account for the perceived rarity of nataloin (Conner et al., 1987; Chauser-Volfson and Gutterman, 1998; Zonta et al., 1995) and malonylated derivatives in the genus to date.

The distribution of **1** in *Aloe* is of systematic interest. Within the maculate species complex, the compound is restricted to *A. ellenbeckii* and related east African species and may, therefore, serve as a phytochemical marker for them (Wabuyele, 2006). The compound has been detected in few maculate species occurring outside this region but has been observed in non-maculate species as diverse in form and infrageneric position as *A. ciliaris* Haw. (subsection *Macrifoliae*) and *A. vanbalenii* Pillans (subsection *Arborescentes*) from South Africa. The findings will be considered with additional characters in a systematic evaluation of the maculate species complex.

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CHAPTER 6 MICROMORPHOLOGY

6.1 Taxonomic significance of leaf surface morphology in *Aloe* section *Pictae* (Xanthorrhoeaceae)

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Taxonomic significance of leaf surface morphology in *Aloe* section *Pictae* (Xanthorrhoeaceae)

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Running title: Leaf surface morphology in *Aloe.*

ABSTRACT

Leaf surface morphology is analysed in 32 species representing the maculate species complex (the poorly resolved section *Pictae*) in the genus *Aloe* (Xanthorrhoeaceae). Few comparative morphological data are available for the complex. Leaf surface and stomatal characters observed by SEM show taxonomically significant interspecific variation. Most species are characterised by irregularly-outlined, 4–6-sided epidermal cells, of which the periclinal walls are flat and embellished with micropapillae and the anticlinal walls are indicated by channels on the leaf surface. The outer stomatal pore is typically sunken or plane and surrounded by four lobes on the leaf surface that may overarch the epistomatal chamber. The guard cells have distinct outer and inner stomatal ledges. Two geographical groups, comprising southern and east African species, are distinguishable by their leaf surface morphology. These characters are diagnostic in *A. ellenbeckii*, *A. prinslooi* and *A. suffulta* and support changes in the delimitation of *A. greatheadii*, *A. macrocarpa* and *A. swynnertonii*.

ADDITIONAL KEYWORDS: Asphodelaceae – maculate – classification – leaf surface – stomata – guard cell – epidermis.

INTRODUCTION

Aloe L. is a leaf-succulent genus found throughout Africa, the Arabian Peninsula and islands in the western Indian Ocean, and includes numerous endemic species from Madagascar. The genus is traditionally included in Asphodelaceae, a 'bracketed family' within the expanded family Xanthorrhoeaceae according to APG II (2003). Besides pharmaceutical and cultural significance, *Aloe* spp. have considerable appeal to succulent collectors and in the horticultural trade. Ever-increasing diversity recognised in the genus necessitated Berger's original (1908) infrageneric classification in *Das Pflanzenreich* and a subsequent, expanded revision in two volumes (Reynolds, 1950; 1966). The most recent inventory of *Aloe* listed 548 accepted species and infraspecific names and 428 synonyms (Newton, 2001), reflecting new perspectives on diversity and relationships in the genus, increased collecting activity and possible taxonomic exaggeration, a pattern also observed in other popular groups such as Orchidaceae (Pillon & Chase, 2007).

Comparative studies of morphology, anatomy and phytochemistry in several infrageneric groups have led to a revised view of species relationships, including the *A. somaliensis* W.Watson complex (Carter *et al.*, 1984) and section *Anguialoe* Reynolds (Van Heerden, Viljoen & Van Wyk, 2000). The present study focused on leaf surface morphology in the maculate species complex, a group of ca. 40 species in the poorly resolved section *Pictae* Salm-Dyck (= *Maculatae* Baker; *Saponariae* Berger). The maculate complex is among the most well-defined groups in *Aloe* (Groenewald, 1941). However, distinguishing characters for the group (prominent leaf markings, perianth constricted above the ovary and short stem) are shared with related groups and are likely symplesiomorphic. Species delimitation in the maculate complex is problematic (see Glen & Hardy, 2000; Wabuyele, 2006).

The value of leaf surface morphology in the systematics of alooid genera has been shown in *Aloe*, *Chortolirion* Berger, *Gasteria* Duval, *Haworthia* Duval and *Poellnitzia* Uitewaal (Cutler, 1969, 1972, 1979, 1982; Cutler *et al*., 1980; Lubbinge, 1971; Newton, 1972; Smith & Van Wyk, 1992). In these genera, leaf surface features are remarkably constant within species and show little geographical variation and environmentally induced plasticity (Cutler & Brandham, 1976; Brandham & Cutler, 1978). Variability has been reported in an unusual species (*A. bowiea* Schult. & J.H.Schult. (Smith & Van Wyk, 1992) and in widely distributed species, in which changes in leaf surface morphology were consistent with observed clinal variation (Cutler *et al*., 1980). The stomatal arrangement in *Aloe* is of adaptive importance in regulating gas exchange and water loss in habitats experiencing alternating periods of drought and humidity, whereas superficial stomata in *Aloe* have been correlated with humid habitats (Cutler, 1982). Similar stomatal arrangements occur in xeromorphic members of Asparagaceae, such as *Agave* L. (Blunden & Jewers, 1973) and *Dracaena* Vand. ex L. (Klimko & Wiland-Szymańska, 2008). Wax has possible taxonomic significance in *Aloe* (Cutler, 1979) and protects the leaf surface against microbial infection and herbivory. The cuticular membrane extends throughout the stomatal complex and delimits a series of air-filled chambers (Evert & Eichhorn, 2006). Ledges between the chambers are formed by the tearing of a continuous cutinised layer covering adjacent guard cells (Cutler, 1979). Cuticular lobes on the leaf surface coincide with the position of subsidiary cells, with which they are associated (Cutler, 1979). The lobes and cuticular ledges of the stomatal complex in *Aloe* have received little attention in subsequent studies of the leaf surface.

Leaf markings and surface morphology are of value in the identification of closely related *Aloe* spp. (Cutler, 1972), in particular for sterile specimens. Indeed, the similarity of juvenile plants (Smith, Klopper & Crouch, 2008) and morphology of mature leaves of many species substantiate the regulation of the trade in *Aloe* spp. (with the exception of the intensively farmed *A. vera* L.) by the Convention on International Trade in Endangered Species of Fauna and Flora (CITES). Kenya and South Africa are export hubs for excised leaves, leaf exudate and living plants gathered in the wild and exported mainly to Asia, Europe and the United States (Sachedina & Bodeker, 1999; Oldfield, 2004; Knapp, 2006). Representatives of the maculate complex that have been recorded in trade include *A. ellenbeckii* A.Berger (Oldfield, 2004) and *A. maculata* All. (Pole-Evans, 1919). Many species in the maculate complex are used locally for traditional medicine, dyes and ornamentals (Grace *et al*., 2009).

In this paper we present an analysis of leaf surface and stomatal characters in the maculate complex in *Aloe*. This is the first systematic survey of leaf surface morphology in the complex and includes new observations for 25 species and further observations for seven species described in previous studies (Newton, 1972; Cutler, 1982). Terminology largely follows that of Cutler (1972; 1979). The taxonomic significance of leaf surface morphology in the maculate complex is discussed.

MATERIALS AND METHODS

PLANT MATERIAL

Leaf surfaces and stomata were examined in 32 species representing the maculate species complex and three other groups in the genus *Aloe* (Table 1). Species of problematic taxonomic position in the maculate complex (*A. suffulta* Reynolds and *A. wollastonii* Rendle) and outgroups *A. chabaudii* Schönland (section *Aethiopicae* Berger, a stemless shrub) and *A. vanbalenii* Pillans (section *Arborescentes* Berger, a multi-stemmed shrub) were included in the analysis. Plant material was collected from wild populations in South Africa and plants of field provenance grown in glasshouses at the Royal Botanic Gardens, Kew. Voucher specimens were deposited in the National Herbarium of South Africa (PRE) and the herbarium at Kew (K) (Table 1). Living material was fixed in formalin-acetic acid-alcohol (FAA: 70% ethanol, formaldehyde and glacial acetic acid, 85: 10: 5) for at least 48 hours, washed twice in distilled water and transferred to 70% ethanol prior to examination.

ELECTRON MICROSCOPY

Specimens were prepared for examination with a scanning electron microscope (SEM) using a method adapted from Cutler (1972). Leaves were split longitudinally with a sharp blade and mesophyll tissue scraped from the inside of the adaxial leaf surface until only a few cell layers remained attached to the epidermis. A piece (ca. 2 cm^2) from the leaf mid-region was dehydrated through an ethanol dilution series (70–100%) over 2.5 hours. Specimens were critical-point dried (Tousimis® Autosamdri® 815B–Series A unit), mounted on aluminium stubs with double-sided tape and coated with gold/palladium alloy in a sputter coater (Emitech K550). Specimens were examined using a Hitachi cold-field emission SEM S4700 at 2 kV over a range of magnifications. Micrographs were recorded digitally.

RESULTS

Observations of leaf surface morphology in representatives of the maculate complex in *Aloe* are presented in Tables 2 and 3. Micrographs are shown in Figs. 1–37.

Leaf surface characters in *Aloe* are organised at three levels; the following description refers to maculate species (Tables 2 and 3). Primary sculpturing comprises the outline of epidermal cells in surface view. In the maculate complex, these are usually 4–6-sided and irregular (e.g. *A. affinis* A.Berger; Fig. 2) or, rarely, uniform (e.g. *A. branddraaiensis* Groenew.; Fig. 6). Cell shape is discernible by a depression (e.g. *A. dewetii* Reynolds; Fig. 9) over the anticlinal walls, which may be flanked by ridges on the periclinal walls of one or both neighbouring epidermal cells (e.g. *A. pruinosa* Reynolds; Fig. 28). Secondary sculpturing refers to the curvature of the periclinal wall in leaf epidermal cells; these are flat (e.g. *A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy; Fig. 14), convex (e.g. *A. swynnertonii* Rendle; Fig. 31) or even domed, as in *A. vogtsii* Reynolds (Fig. 35). Tertiary sculpturing of the periclinal walls comprises micropapillae variably arranged in a fine, low relief (e.g. *A. pruinosa*;

Fig. 28) or a coarse and dense arrangement (e.g. *A. greatheadii* Schönland var. *greatheadii*; Fig. 15). In addition to ridges associated with anticlinal walls, micropapillae may aggregate to form ridges on the periclinal walls, particularly near stomata (e.g. *A. petrophila* Pillans; Fig. 26). Occasionally, dense tertiary sculpturing obscures the primary features (e.g. *A. fosteri* Pillans; Fig. 11). The epidermal surface is further covered by a thick cuticle and a layer of wax, which is usually continuous but sometimes deposited as flakes on the leaf surface (e.g. *A. wollastonii*; Fig. 36).

Stomatal frequency is similar on both leaf surfaces in the maculate species complex. The guard cells are always positioned well below the leaf surface and surrounded by four subsidiary cells (Fig. 1). The well-developed cuticle on the leaf surface forms four more or less distinct lobes that surround and partially cover the outer pore of the epistomatal chamber (Fig. 1). In most maculate species, two opposing lobes surrounding this opening are aligned parallel to the longitudinal axis of the leaf and are here termed the 'L-lobe pair', whereas the 'T-lobes' are aligned parallel to the transverse axis of the leaf (e.g. Fig. 24). The difference in their length, described by a ratio, is of taxonomic significance (Table 3); length refers to the dimension parallel to the respective leaf axis (not to be confused with the length of the lobe projecting over the outer pore of the epistomatal chamber, which is not considered here). The cuticle associated with the guard cell forms an inner and outer cuticular ledge, protruding into the epistomatal and substomatal chambers; the outer cuticular ledge is visible in Fig. 37.

Leaf surface morphology was similar among 88% of maculate species examined (Fig. 2–37), but was conspicuously different in the outgroups *A. chabaudii* (Fig. 8) and *A. vanbalenii* (Fig. 33). In these outgroup species, leaf surface morphology was characterised by dense, rugulose tertiary sculpturing, indistinct anticlinal cell walls, and the outer pore of the epistomatal chamber sunken and surrounded by poorly developed lobes. Limited infraspecific variation was observed in *A. greatheadii* var. *greatheadii* (Fig. 15), *A. immaculata* Pillans (Fig. 17), *A. maculata* (Fig. 22), *A. parvibracteata* Schönland (Fig. 25) and *A. umfoloziensis* Reynolds (Fig. 32), whereas in *A. amudatensis* Reynolds (Fig. 4) there was little variation in the surface features of different leaves from the same individual.

DISCUSSION

Patterns in leaf surface morphology support the recognition of maculate species as section *Pictae.* A phytogeographical link is evident between the centres of diversity in the maculate complex. Species from east Africa (*A. lateritia* Engl. var. *graminicola* (Reynolds) S.Carter, Fig. 18; *A. macrocarpa* Tod., Fig. 21; *A. wollastonii*, Figs 36 and 37) are characterised by epidermal cells that are more or less circular in outline, with the periclinal walls convex and micropapillae aggregated into ridges. These characters also occur in *A. maculata* (Fig. 22), *A. swynnertonii* (Fig. 31) and *A. vogtsii* Reynolds (Fig. 35) in southern Africa, and they support the recognition of *A. vogtsii* as a southern form of the widespread *A. swynnertonii* (Glen & Hardy, 2000). Leaf surface features typical of southern African maculate species include epidermal cells that are irregular in outline, with the periclinal walls flat and tertiary sculpturing comprising micropapillae ranging from the distinctly papillate (e.g. *A. burgersfortensis* Reynolds, Fig. 7; *A. parvibracteata*, Fig. 25) to a coarse, dense arrangement (e.g. *A. greatheadii* var. *greatheadii*, Fig. 15; *A. lettyae* Reynolds, Fig. 19).

Our results indicate that leaf surface morphology assists in resolving species concepts among maculate species. In the *A. greatheadii* complex, the present survey found marked similarities in the leaf surface morphology of the closely related species *A. barbertoniae* Pole-Evans (Fig. 5), *A. graciliflora* Groenew. (Fig. 12) and *A. greatheadii* var. *davyana* (Fig. 14), but not *A. longibracteata* Pole-Evans (Fig. 20). The latter shares the distinctive sunken outer pore and dense tertiary sculpturing typical of *A. greatheadii* var. *greatheadii* (Fig. 15). This pattern is also present in *A. immaculata* (Fig. 17), a species considered by Van Wyk & Smith (2005) to be conspecific with *A. greatheadii*. Similarities in leaf surface morphology supports Wabuyele's (2006) hypothesis for *A. lateritia*. Convex outer periclinal walls, reticulated tertiary sculpturing and poorly developed lobes surrounding the outer pore are common to *A. lateritia* var. *graminicola* (length ratio = 1.2; Fig. 18), *A. wollastonii* (1.2; Figs 36 and 37) and *A. macrocarpa* (1.1; Fig. 21). Leaf surface characters do not, however, support *A. amudatensis* (Fig. 4) as a synonym of *A. ellenbeckii* (Fig. 10). *Aloe ellenbeckii* is morphologically distinct from all other maculate species: the leaf surfaces bear discontinuous elevated ridges, reticulated tertiary sculpturing and poorly developed lobes (length ratio = 1.1). The second maculate taxon with very distinctive leaf surface morphology is *A. prinslooi* I.Verd. & D.S.Hardy (Fig. 27), in which deep folds are present along the periclinal cell walls, the tertiary sculpturing is densely papillate, and the convex L- and T-lobe pairs enclose a small and almost circular outer pore. The noticeable difference between the papillate tertiary sculpturing of *A. parvibracteata* (Fig. 25) and the reticulate tertiary sculpturing of *A. umfoloziensis* (Fig. 32) supports the recognition of these taxa as distinct species.

Noteworthy differences in leaf surface characters were observed in certain atypical members of the maculate complex. *Aloe monotropa* I.Verd. (Fig. 23), the only maculate taxon consistently found in deep shade and bearing secund flowers, is characterised by copious wax deposits. In *A. suffulta* (Fig. 30), a species of doubtful status in the maculate group due to a peculiarly lax inflorescence and flowers lacking a swollen base and constricted perianth, the anticlinal walls of the epidermal cells are indicated by a prominent ridge in place of the depression present in other species, the outer cuticular ledge is plane, and lobes do not overarch the outer pore of the epistomatal chamber (length ratio = 2.3).

Evidence from the present study indicates that the *A. greatheadii* complex has yet to be resolved, whereas resolution may have been reached for the *A. lateritia* complex. Leaf surface characters are sufficiently distinctive to be diagnostic in *A. ellenbeckii* and *A. prinslooi.* Morphological similarities in leaf surface characters support the circumscription of the maculate species at the sectional level, add insights into contentious taxonomic hypotheses and highlight the systematic relationships between tropical and subtropical species of *Aloe.*

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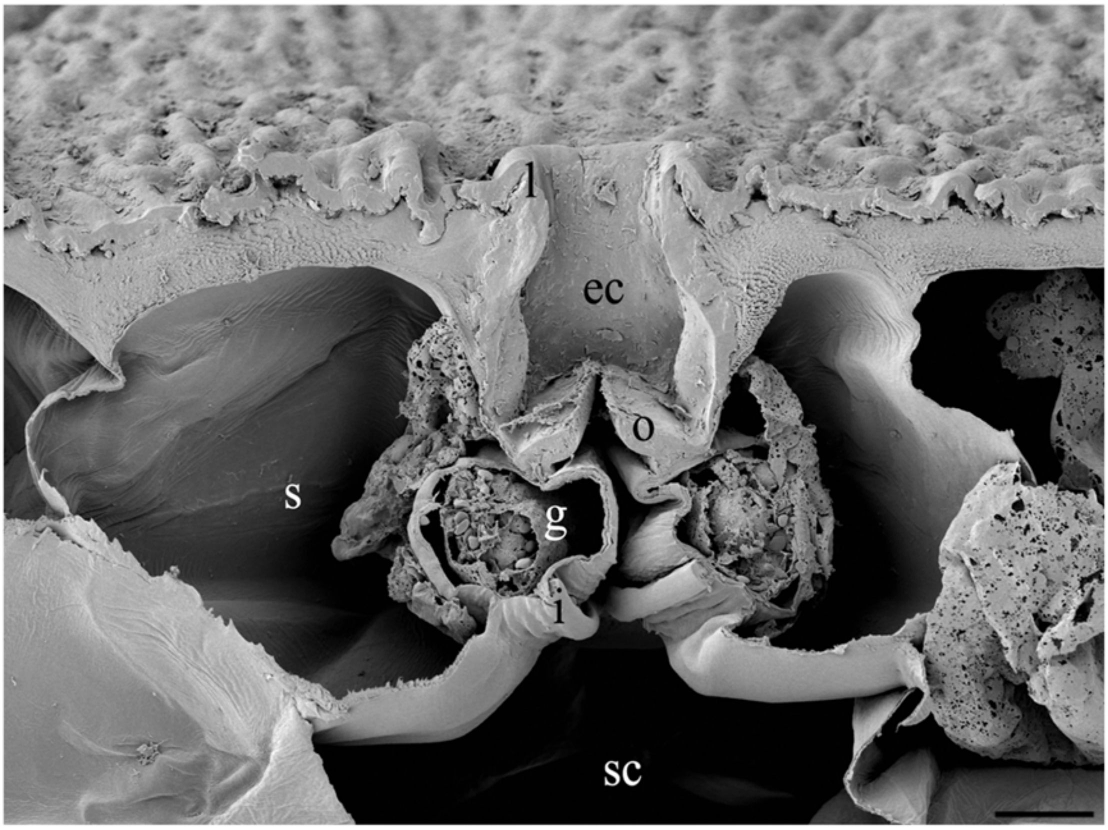
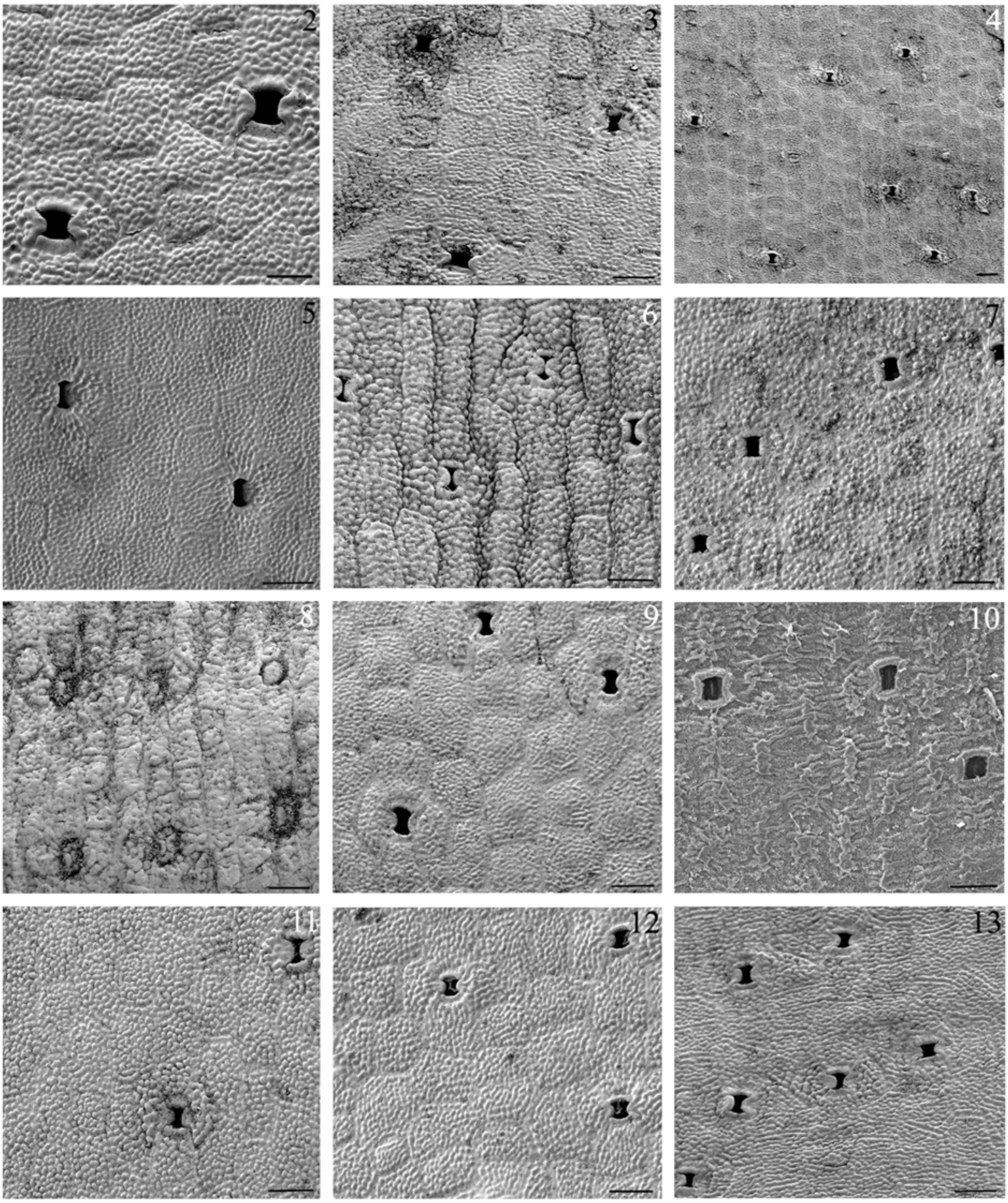
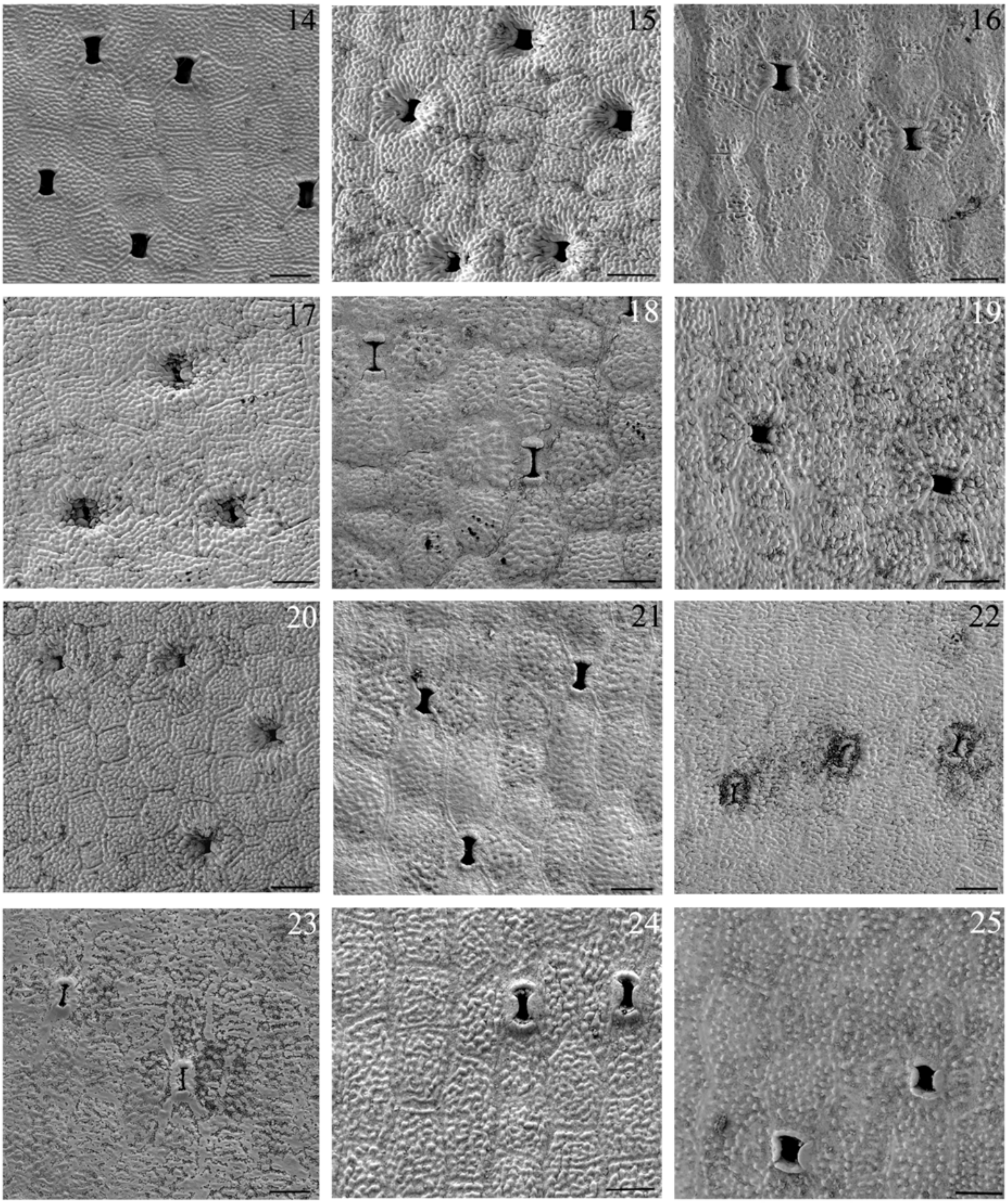


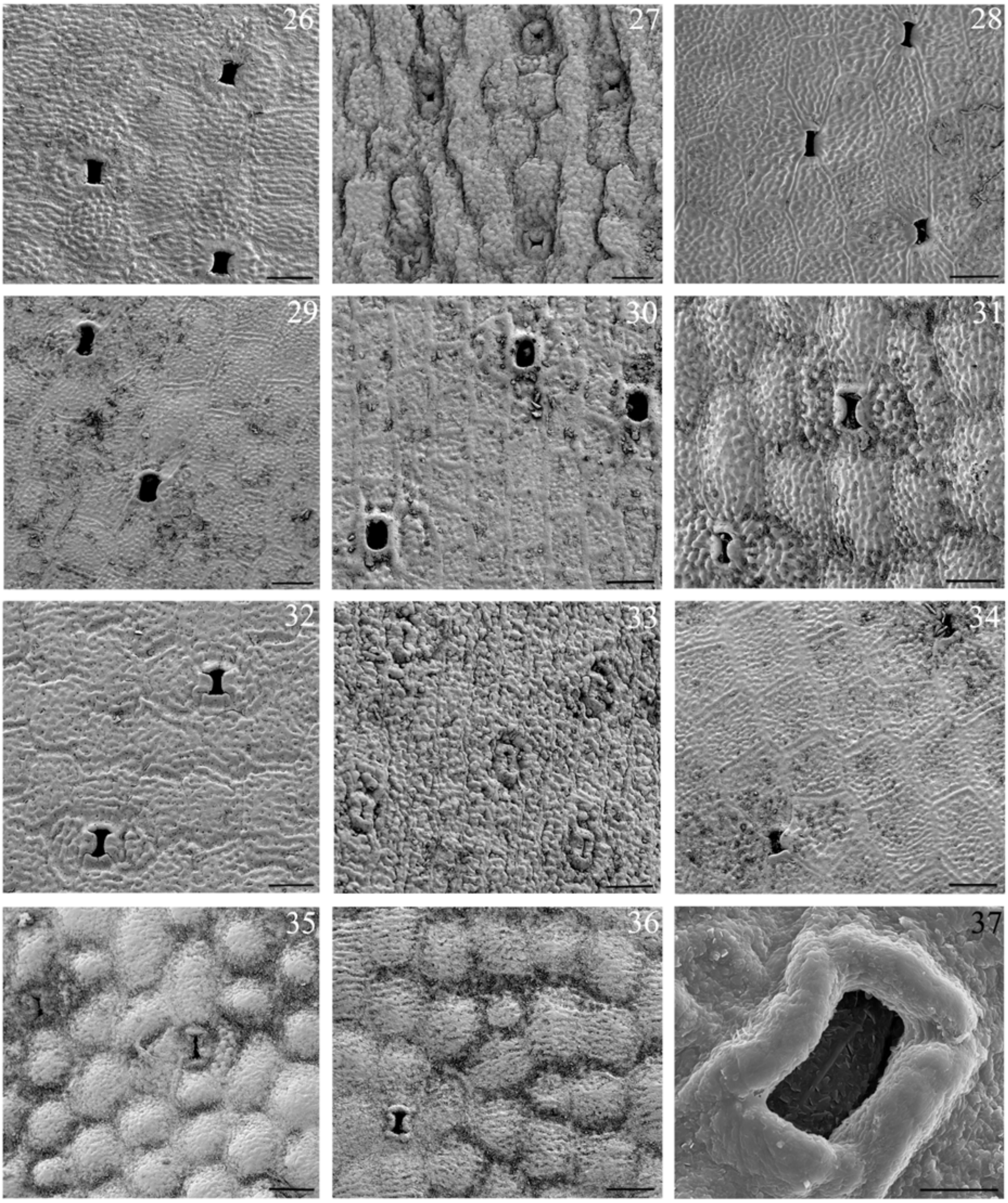
Figure 1. Scanning electron micrograph of stomatal complex on adaxial leaf surface of *Aloe umfoloziensis* in transverse section. l, lobe; ec, epistomatal chamber; sc, sub-stomatal chamber; g, guard cell; s, subsidiary cell; o, outer cuticular ledge; i, inner cuticular ledge. Scale bar 10 μm.



Figures 2–13. Leaf surfaces in *Aloe*; longitudinal axis of leaves orientated ± vertically. Fig 2, *A. affinis*. Fig 3, *A. ammophila*. Fig. 4, *A. amudatensis*. Fig 5, *A. barbertoniae*. Fig 6, *A. branddraaiensis.* Fig 7, *A. burgersfortensis*. Fig 8, *A. chabaudii*. Fig 9, *A. dewetii*. Fig 10, *A. ellenbeckii.* Fig 11, *A. fosteri*. Fig 12, *A. grandidentata*. Fig 13, *A. graciliflora.* Scale bars 50 µm.



Figures 14–25. Leaf surfaces in *Aloe*; longitudinal axis of leaves orientated ± vertically. Fig 14, *A. greatheadii* var. *davyana*. Fig 15, *A. greatheadii* var. *greatheadii*. Fig 16, *A. greenii*. Fig 17, *A. immaculata*. Fig 18, *A. lateritia* var. *graminicola*. Fig 19, *A. lettyae*. Fig 20, *A. longibracteata*. Fig 21, *A. macrocarpa*. Fig 22, *A. maculata*. Fig 23, *A. monotropa*. Fig 24, *A. mudenensis*. Fig 25, *A. parvibracteata*. Scale bars 50 µm.



Figures 26–37. Leaf surfaces in *Aloe*; longitudinal axis of leaves orientated ± vertically. Fig 26, *A. petrophila*. Fig 27, *A. prinslooi*. Fig 28, *A. pruinosa*. Fig 29, *A. simii*. Fig 30, *A. suffulta*. Fig 31, *A. swynnertonii*. Fig 32, *A. umfoloziensis*. Fig 33, *A. vanbalenii*. Fig 34, *A. vanrooyenii*. Fig 35, *A. vogtsii*. Figs 36, *A. wollastonii*. Scale bars 50 µm. Fig 37, *A. amudatensis*. Scale bar 20 µm.

CHAPTER 7 DISCUSSION AND CONCLUSIONS

7.1 Discussion

The history of *Aloe* L. as a group of considerable ethnomedicinal and horticultural value is inextricably linked with its complex taxonomy and, more recently, concerns for its conservation. The pursuit of novel subjects for succulent collections and natural products from *Aloe* spp. (the quest for the "new *A. vera* L.") undoubtedly contributed to the proliferation of *species nova.* The unwieldy size and inconsistencies in the delineation of taxonomic units in *Aloe* have impacted on the predictive power of the present classification, limiting the taxonomic information available to prospective users, who may include conservation practitioners and natural product developers. Their needs will require careful consideration in a future revision of *Aloe* since a classification with practical field value, that reflects putative evolutionary relationships, is needed to support the conservation and sustainable use of *Aloe*.

The utility value of *Aloe* is indicated by a large volume of literature describing the modern uses of approximately one third of accepted species of *Aloe.* They are reportedly used for an exceptional variety of purposes, notably traditional medicine and natural products. Quantifiable measures of utility indicate that the genus is also frequently documented for social and environmental uses, but is most highly valued by people for medicine and pest control (Grace et al. 2009a). Species such as *A. perryi* Baker and *A. ferox* Mill., known in trade for centuries, continue to be of considerable economic importance today. A snapshot of utility in the *Flora of Southern Africa* region revealed that, for extensively documented plant groups such as *Aloe*, the literature is a reliable surrogate for anecdotal ethnobotanical information (Chapter 5). A comparison of these data with those collected by interview would be informative. Earlier papers evaluated the authentication and trade in natural products from *Aloe* (Hodge 1953; Morton 1961) but the present research was seemingly the first attempt to review all uses of *Aloe*, assess their contemporary value, and test the literature as a proxy for ethnobotanical field data.

There are almost as many synonyms as there are accepted names for *Aloe* (Newton 2001); this presented certain difficulties during the collection of utility data from the literature. The high degree of synonymy also affected systematic studies of the maculate group, section *Pictae* Salm-Dyck, in which there are 30 synonyms for 37 accepted species names (Newton 2001). Geographical range is an important aid in the identification of maculate species, since numerous species represent local forms of a larger taxonomic unit.

For instance, the restricted distribution of *A. pruinosa* Reynolds helps to distinguish it from the closely related *A. greenii* Baker. Glen and Hardy (2000) and Wabuyele (2006) recently proposed changes to the number of maculate species recognised in southern and East Africa, respectively. However, the lumping of taxa into heterogeneous entities has not resolved the delineation of maculate species. The case of *A. greatheadii*, in which Glen and Hardy (2000) placed 11 taxa formerly recognised at the species level, has attracted controversy among fellow taxonomists, horticulturalists and succulent enthusiasts. In the present study, heterogeneous species were sampled as thoroughly as possible to include conspecific taxa. For example, representatives of *A. graciliflora* Groenew., *A. longibracteata* and *A. verdoorniae* Reynolds, sunk by Glen and Hardy (2000), were treated as segregates in studies of *A. greatheadii.* Although the present investigation added many new data to the original assessment of the maculate species complex by Groenewald (1941), gaps have remained as a consequence of a lack of material or poor data, and it would be desirable to fill these in future.

Insights were gained during the present research into relationships among certain maculate species. The present circumscription of section *Pictae* does not reflect proposed evolutionary relationships among species in the maculate complex. Representatives of sections *Pictae* and *Paniculatae* possessing flowers with a bulbous base and constricted perianth, but not necessarily patterned leaf surfaces, comprise a convincing group. Species lacking such floral morphology but with patterned leaf surfaces (the unusual species *A. leptosiphon* and *A. suffulta*) comprise a sister group (Figure 7.1). A revised hypothesis of section *Pictae* exclude the unusual marginal sister group and possibly include section *Paniculatae*; the holophyletic group would also meet the phylogenetic principle of monophyly (the discussion on evolutionary versus phylogenetic approaches to classification has generated a substantial body of literature; see, for example, Mayr and Ashlock (1991), Brummitt (2002, 2003), Van Wyk (2007)). The grouping of representatives of *Paniculatae* with the maculate species is not novel; Berger (1908) included *A. striata* Haw. in his series *Saponariae* a little over a century ago. However, *Paniculatae* differ from core maculate species in their diminutive stature, many-branched inflorescences, minimal leaf succulence, and entire or barely toothed and glaucous leaves. The two groups are geographically distinct; section *Paniculatae* is restricted to the south-western remit of southern Africa, from the Albany Centre to the Succulent Karoo Region. With the exception of *A. maculata*, the southern-most limit of the largely tropical section *Pictae* is in the eastern parts of southern Africa. To avoid perpetuating inconsistencies in the classification of *Aloe*, however, the decision to uphold or include species presently recognised in *Paniculatae* in section *Pictae* will ultimately need to be made in the context of a taxonomic revision.

Phytochemical (Chapter 5) and micromorphological (Grace et al. 2009b) evidence support the hypothesis that floral characters are of greater significance as synapomorphies for section *Pictae* than patterned leaf surfaces (Figures 7.1 and 7.2). The present study included the first characterisation of flavonoids in maculate species and noteworthy biogeographical patterns were shown in the occurrence of two flavonoids in particular (isoorientin and isovitexin) (Chapter 5). Flavonoids have been widely used in plant chemosystematics, since they are ubiquitous, readily detected, variable, and under genetic control (Crawford & Giannasi 1982). Due to their supposed ecological or functional role, secondary metabolites in plants (and indeed other organisms) are subject to acute selective pressure and may be indicators of evolutionary relationships. Flavonoids can be treated in a strict cladistic context but, as adaptive traits in which a small physiological difference may result in significant character shift, their taxonomic value lies in careful interpretation (Wink 2003; Steussy 2009). The same principle applies to the relevance of leaf surface and stomatal morphology among maculate species. Indeed, epidermal cell area and guard cell size have been shown to be undergoing correlated evolution with genome size in angiosperms (Beaulieu et al. 2008). At the species level, leaf surface features may be indicators of relatedness in *Aloe* as they, too, are under tight genetic regulation (Brandham & Cutler 1978).

It would be premature to assign character states to these data for cladistic analysis because the direction of evolution is uncertain for many of them. For instance, it is unclear whether the preponderance of flavonoids in basal groups of *Aloe* indicate that the presence of this compound group in the actively evolving maculate group is primitive or derived (Chapter 5). Indeed, the assignment of evolutionary direction to flavonoid structures is often dependant on their distribution on a phylogenetic tree (Crawford & Giannasi 1982). Similarly, the main pollinating agent in maculate species is unknown and therefore prevents a score being allocated to the "constricted perianth" character. However, presence\absence evaluations of characters considered in the present study were informative regarding species relationships in section *Pictae* and the sectional circumscription.

An evolutionary hypothesis for section *Pictae* is proposed on the basis of the present findings. A core section *Pictae* is supported, representatives of which possess maculate-typical floral morphology, succulent, toothed and often patterned leaves, and commonly contain isoorientin. Within the section, an East African species assemblage is additionally broadly characterised by 6′-malonylnataloin in the leaves, leaf epidermal cells more or less circular in outline, convex periclinal cell walls and micropapillae aggregated into ridges on the leaf surface. In southern African maculate species, the leaves are more likely to contain isovitexin, and leaf epidermal cells are generally irregular in outline, the periclinal wall flat, and the tertiary sculpturing sparsely or densely papillate. Species occurring in subtropical and tropical regions may display intermediates of certain character states, such as *A. maculata*, *A. swynnertonii* and *A. vogtsii* (Grace et al. 2009b). At the species level, the present research substantiates the pragmatic (yet controversial) proposal by Glen and Hardy (2000) to include *A. barberoniae*, *A. graciliflora*, *A. immaculata* and *A. longibracteata* in *A. greatheadii*, and the inclusion of *A. lateritia* and *A. wollastonii* in the widespread *A. macrocarpa* (Wabuyele 2006). Conversely, the status of *A. amudatensis*, *A. parvibracteata* and *A. umfoloziensis* at the species rank is maintained. Section *Pictae* is most speciose and complex near its southern limit, particularly in the Mpumalanga-KwaZulu-Natal interior in South Africa neighbouring Swaziland.

Comments on the systematics of species in section *Pictae* and the segregate section *Paniculatae* are presented later in this Chapter.

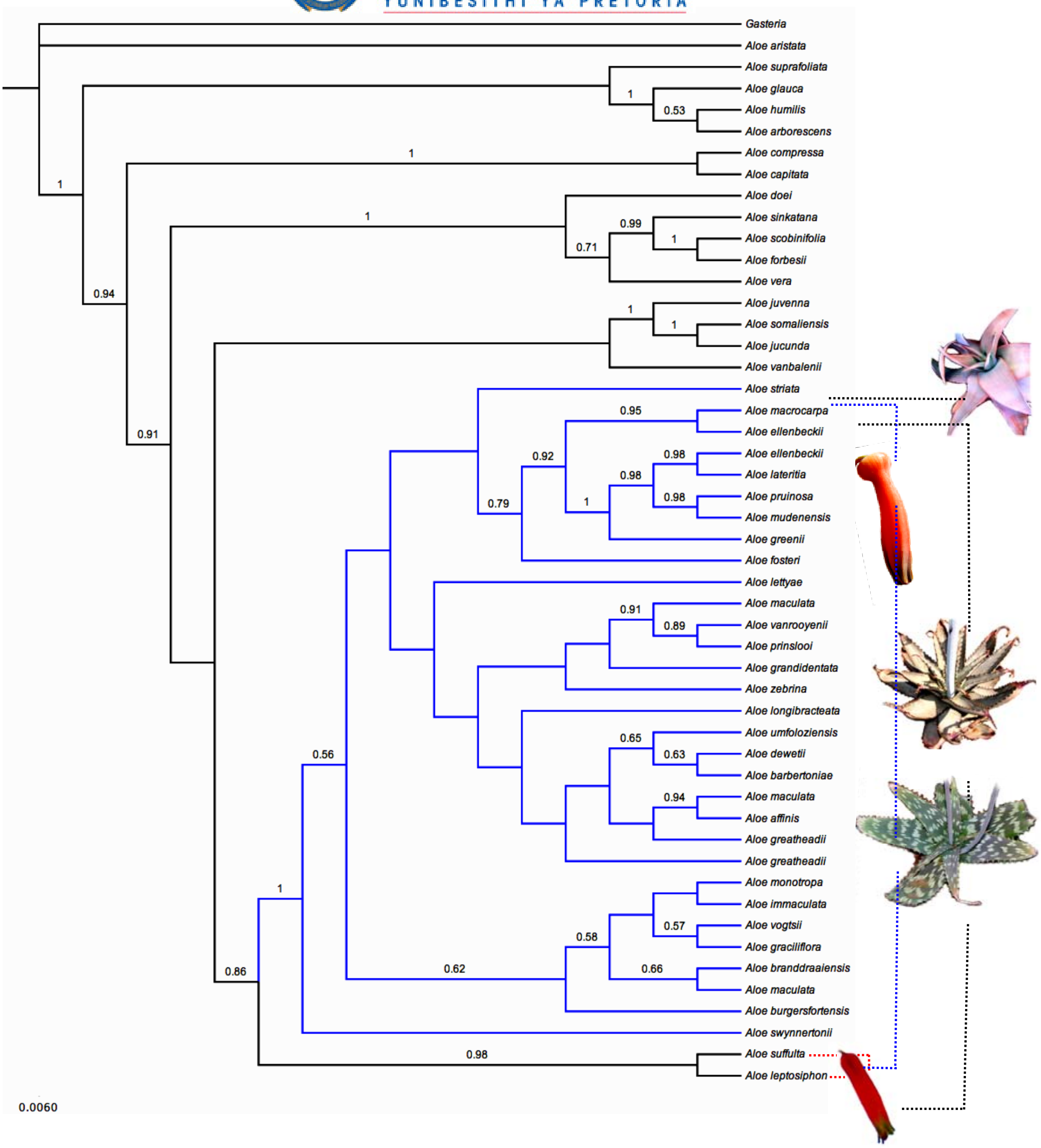


Figure 7.1 Gross morphological features of systematic importance in the maculate species complex. Features are mapped on a maximum likelihood tree based on ITS, *trnL–F* and *matK* with posterior probabilities above branches (see Chapter 4).

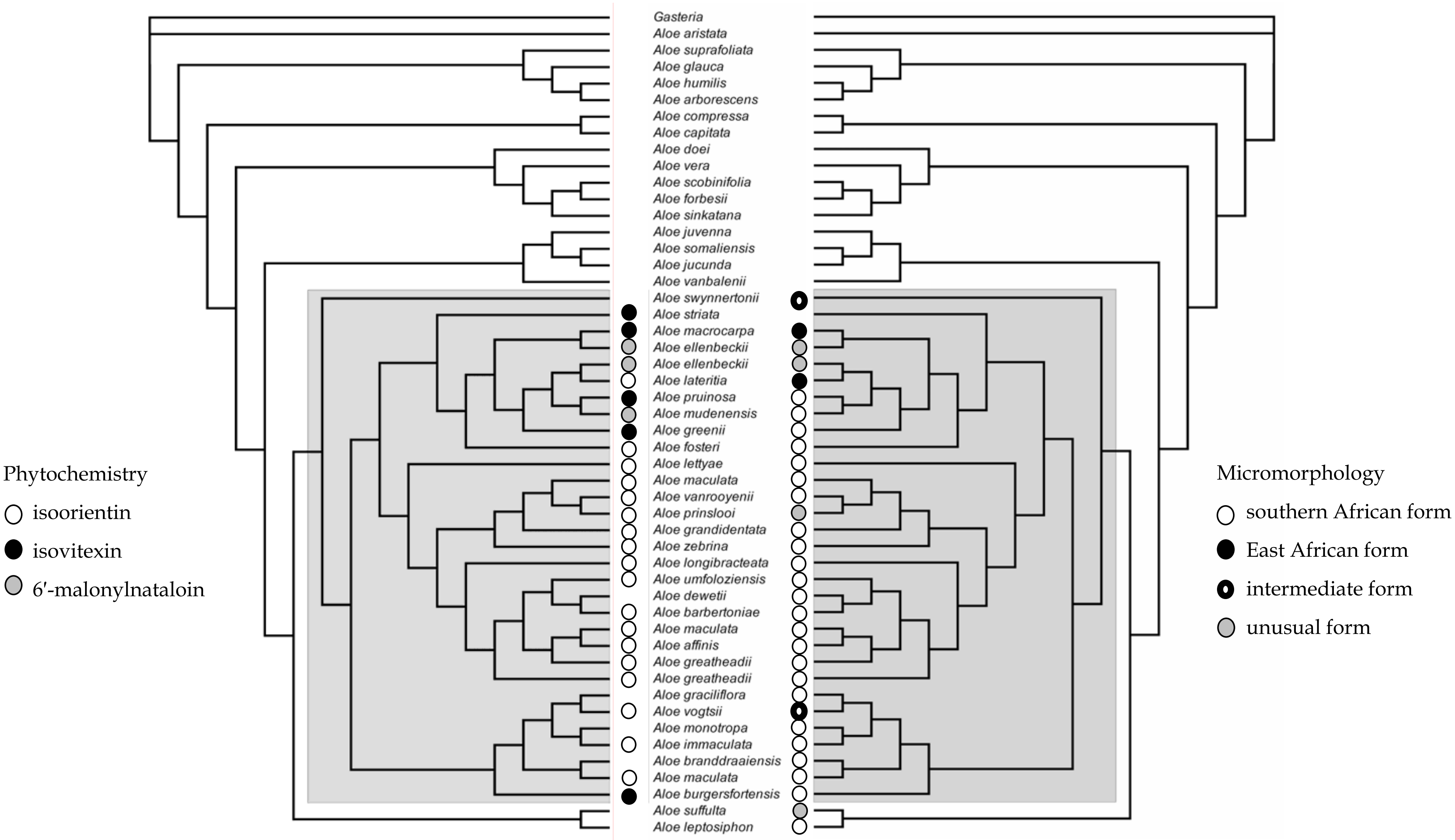


Figure 7.2 Phytochemical (left) and morphological (right) features of systematic significance in the maculate species complex, mapped on a maximum likelihood tree reconstructed from ITS, *trnL–F* and *matK* data. The core maculate group is highlighted (see Chapters 4, 5 and 6).

Recommendations

- Current ethnobotanical data are required for *Aloe* to enable further evaluation of the literature as a proxy for anecdotal information acquired directly by interview methods (Grace et al. 2008a, 2009a).

- Accurate trade data for *Aloe* spp. are required. This is a persistent obstacle to identifying sustainable rates of wild harvesting and effective management (Newton & Vaughan 1996; Oldfield 2004).

- The economic value (in addition to the biocultural value) of *Aloe* spp. for different user groups, notably those dependant on *Aloe* products for their livelihoods, needs to be quantified and advocated to secure support for community conservation efforts.

- A comprehensive taxonomic revision of *Aloe* is necessary. A classification of practical value to those who use *Aloe* species is anticipated to impact positively on the conservation of the genus and opportunities for its use.

- Investigations to identify the most taxonomically informative genome regions in *Aloe* and related genera are needed to reconstruct a robust and well-resolved phylogenetic tree for the genus.

- The inclusion of section *Paniculatae* in section *Pictae* should be considered when other infrageneric groups in the genus are revised.

- Comparative data are needed for nine species in the maculate species complex (*A. angolensis*, *A. duckeri*, *A. dyeri*, *A. hereroensis*, *A. keithii*, *A. kilifensis*, *A. menyharthii*, *A. petrophila* and *A. vandermerwei*).

- Further research is recommended to resolve the delineation of species from the complex relationships among maculate species.

Conspectus of section *Pictae* Salm-Dyck and section *Paniculatae* Salm-Dyck ex Kunth

Summary notes are given on the systematics, taxonomic status and distribution of maculate taxa classified by various authors in the maculate species complex. Species recognised in section *Pictae* by the present author are indicated in **bold** type, recognised species of doubtful status in the section are indicated by ?, and species not recognised are indicated by ■. Distribution data according to Newton (2001).

Aloe affinis **A.Berger**

1908, Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 206.

A maculate species endemic to Mpumalanga (South Africa). Leaf markings within populations are variable or absent (Glen & Hardy 2000).

A. amudatensis **Reynolds**

1956, J. South Afr. Bot. 22(3): 136–137.

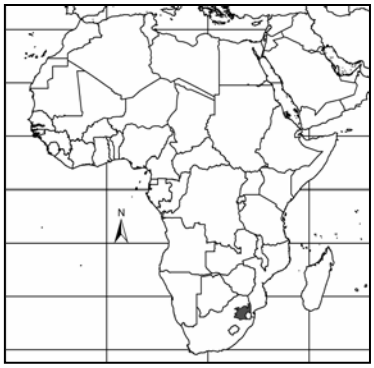
An East African maculate species, included in *A. ellenbeckii* by Wabuyele (2006). However, this species differs in leaf surface sculpturing and in a flavonoid being the major UV-absorbing compound in its leaves (Chapter 5, Grace et al. 2009b).

A. angolensis **Baker**

1878, Trans. Linn. Soc. London, Bot. 1: 236.

A putative natural hybrid between the maculate species *A. zebrina* Baker and *A. littoralis* Baker (section *Pachydendron* Haw.) (Glen & Hardy 2000). Data were not acquired during the present study due to a lack of material.

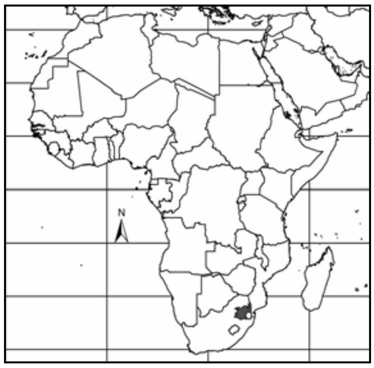
A. barbertoniae Pole-Evans ■



1917, Trans. Roy. Soc. South Afr. 5: 705.

A maculate species endemic to Mpumalanga (South Africa). Gross morphology, leaf surfaces and chemical constituents support the inclusion of this species in *A. greatheadii* var. *davyana* (Glen & Hardy 2000).

***A. branddraaiensis* Groenew.**



1940, Flow. Pl. South Afr. 20: t. 761.

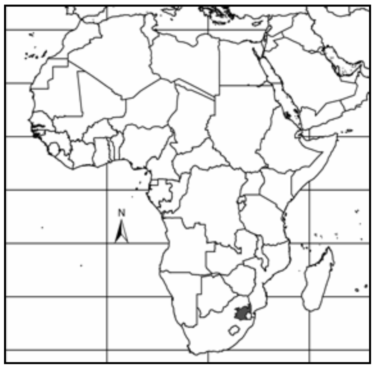
A maculate species with densely sculptured leaf surfaces (Grace et al. 2009b) and in which flavonoids were not detected (Chapter 5). It is distinctively different from the geographically overlapping *A. fosteri*, a species also endemic to Mpumalanga (South Africa).

***A. buhrii* Lavranos**

1971, J. South Afr. Bot. 37(1): 37–40.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata.*

A. burgersfortensis Reynolds ■



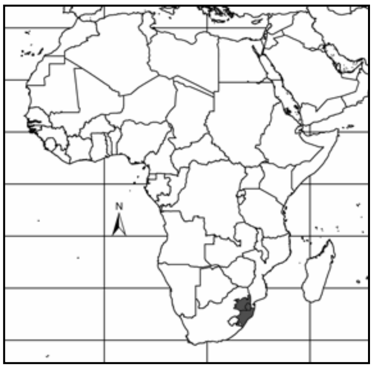
1936, J. South Afr. Bot. 2(1): 31–34.

A maculate species included in *A. parvibracteata* by Glen & Hardy (2000). Gross morphology, similarities in leaf surface morphology and chemistry (Chapter 5, Grace et al. 2009b) support this hypothesis. See *A. parvibracteata.*

***A. dewetii* Reynolds**

1937, J. South Afr. Bot. 3(3): 139–141.

A large maculate species, with inflorescences up to 2m tall and glossy leaves. Flavonoids were not detected in the leaves (Chapter 5).



***A. duckeri* Christian**

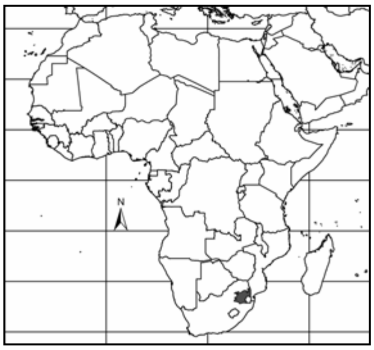
1940, J. South Afr. Bot. 6(4): 179–180.

A robust species occurring in south tropical and East Africa. Data were not acquired during the present study due to a lack of material.

***A. dyeri* Schönland**

1905, Rec. Albany Mus. 1: 289.

A large maculate species endemic to Mpumalanga (South Africa). Data were not acquired during the present study due to a lack of material.



***A. ellenbeckii* A.Berger**

1905, Bot. Jahrb. Syst. 36: 39.

Includes *Aloe dumetorum* B.Mathew & Brandham.

A distinctive East African representative of section *Pictae* with unusual leaf chemistry (Grace et al. 2008a) and leaf surface features (Chapter 5, Grace et al. 2009b). Related to the East African maculate species *A. lateritia* and the West African maculate species *A. macrocarpa.*

A. fosteri **Pillans**

1933, South Afr. Gard. 23: 140.

A maculate species endemic to Mpumalanga (South Africa) characterised by variable floral colour and pruinose leaves (Glen & Hardy 2000). A flavonoid is one of the major UV-absorbing constituents of its leaves (Chapter 5).

A. grandidentata **Salm-Dyck**

1822, Observ. Bot. Hort. Dyck. 3.

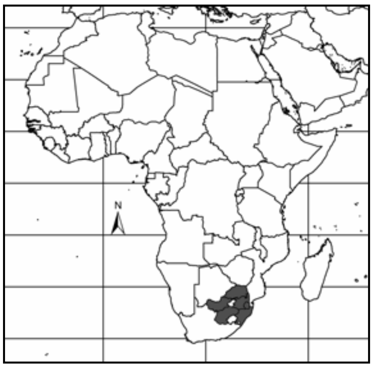
A widespread maculate species distinguished by clavate flowers. A flavonoid is one of the major UV-absorbing constituents of its leaves (Chapter 5).

A. greatheadii **Schönland**

1904, Rec. Albany Mus. 1: 121.

A heterogeneous and problematic taxonomic entity.

A. greatheadii var**. _davyana_ (Schönland) Glen & D.S.Hardy**



1987, South Afr. J. Bot. 53(6); 490–491.

≡ *Aloe davyana* Schönland; includes *Aloe barbertoniae* Pole-Evans, *Aloe davyana* var. *subolifera*, *Aloe longibracteata* Pole-Evans, *Aloe comosibracteata* Reynolds, *Aloe graciliflora* Groenew., *Aloe labiaflava* Groenew., *Aloe mutans* Reynolds. Individuals of this and segregate species included in this variety (*A. barbertoniae*, *A. graciliflora* and *A. longibracteata*) by Glen and Hardy (2000) were all recovered in the maculate group (Chapter 4). Similarities in leaf surface and phytochemical characters support the inclusion of *A. barbertoniae* and *A. graciliflora*, but not *A. longibracteata*, in this variety (Chapter 5, Grace et al. 2009b). See *A. barbertoniae* and *A. longibracteata.*

A. greatheadii var. **_greatheadii_**

Includes *Aloe immaculata* Pillans, *Aloe pallidiflora* A.Berger, *Aloe termetophila* De Wild.

The differences between this variety and the heterogeneous *A. greatheadii* var. *davyana* are unclear, particularly where they co-occur. However, they can be separated by leaf surface morphology (Grace et al. 2009b).

A. greenii Baker

1880, J. Linn. Soc. Bot. 18: 165.

A maculate species endemic to KwaZulu-Natal (South Africa) and closely related to other KwaZulu-Natal endemic maculates *A. mudenensis* and *A. pruinosa* (Chapter 4). It is very similar to the latter, in gross morphology, leaf surface features and phytochemistry (Chapter 5, Grace et al. 2009b) but the two species are separable and upheld. See *A. pruinosa.*

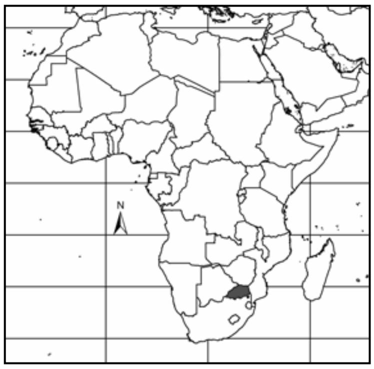
***A. hereroensis* Engl.** ?

1888, Bot. Jahrb. Syst. 10: 2.

Includes *Aloe hereroensis* var. *hereroensis*

Patterned leaf surfaces of this species led Berger (1908) to group it with the maculate species. Reynolds (1950) erected a new group, series *Hereroenses* Reynolds, to accommodate it. He believed it to be an intermediate of series *Saponariae* (the maculate group) and series *Asperifoliae*. Glen and Hardy (2000) recognised affiliations with the latter and placed it in their section *Asperifoliae* (A.Berger) Glen & D.S.Hardy. This species lacks the floral characters synapomorphic for section *Pictae* and is of doubtful status in the group. Data were not acquired during the present study due to a lack of material.

A. immaculata Pillans ■



1934, South Afr. Gard. 24: 25.

A maculate species of unresolved status in section *Pictae*; it was included in *A. affinis* by Glen and Hardy (2000) and *A. greatheadii* by Van Wyk and Smith (2005). Similarities in leaf surface morphology and phytochemistry support the latter (Chapter 5, Grace et al. 2009b).

***A. karasbergensis* Pillans**

1928, Journ. Bot. 66: 233.

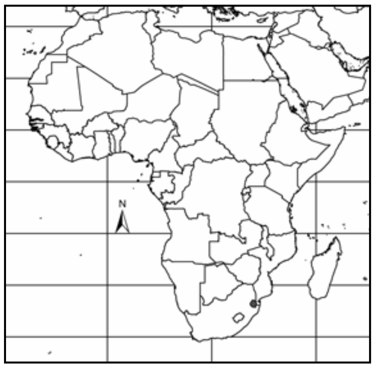
≡ *Aloe striata* subsp. *karasbergensis* (Pillans) Glen & D.S.Hardy.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata*.

A. keithii Reynolds ■

1937, J. South Afr. Bot. 391: 47–49, t. 5.

A maculate species considered to be conspecific with *A. parvibracteata* (Glen & Hardy 2000), the differences highlighted by Reynolds (1950) are accommodated by infraspecific variability. Data for *A. keithii* were not acquired during the present study due to a lack of material.

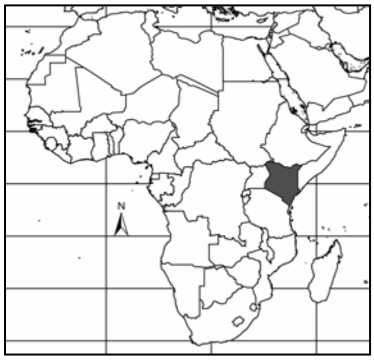


***A. kilifiensis* Christian**

1942, J. South Afr. Bot. 8(2): 169–170.

A species typical of East African representatives of section *Pictae.*

Data were not acquired during the present study due to a lack of material.



***A. komaggasensis* Kritzinger & van Jaarsv.**

1985, S. Afr. J. Bot. 51: 287–289.

≡ *Aloe striata* subsp. *komaggasensis* (Kritzinger & van Jaarsv.) Glen & D.S.Hardy.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata.*

***A. kouebokkeveldensis* van Jaarsv. & A.B.Low**

2004, Aloe 41: 36.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata.*

A. lateritia Engl. ■

1895, Pfl.-welt Ost-Afr., Teil C, 140.

A maculate species recovered with other East African species in a phylogenetic study (Chapter 4). Contains an anthrone *C*-glycoside typical of *A. ellenbeckii*, and a flavonoid common to many maculate species (Chapter 5). Similarities in leaf surface morphology (Grace et al. 2009b) support the inclusion of this species in *A. macrocarpa* (Wabuyele 2006). See *A. macrocarpa.*

A. lateritia Engl. var. *graminicola* (Reynolds) S.Carter ■

1994, Fl. Trop. East Afr., Aloaceae, 17.

≡ *Aloe graminicola* Reynolds; includes *Aloe solaiana* Christian. Differs from the other variety by persistently capitate inflorescences (Carter 1994). Wabuyele (2006) proposed this variety is conspecific with *A. macrocarpa.* See *A. lateritia.*

A. lateritia var. *lateritia* ■

Includes *Aloe boehmii* Engl., *Aloe campyosiphon* A.Berger, *Aloe amanensis* A.Berger.

Form with capitate inflorescences becoming elongated on fruiting (Carter 1994). Wabuyele (2006) proposed this variety to be conspecific with *A. macrocarpa.* See *A. lateritia.*

***A. leptosiphon* A.Berger** ?

1905, Bot. Jahrb. Syst. 36: 66.

Includes *Aloe greenwayi* Reynolds.

A species recovered in the maculate sister group, comprising marginal maculate species with patterned leaf surfaces but lacking floral characters typical of section *Pictae* (Chapter 4). Leaf constituents typical of maculate species were not detected (Chapter 5). It is of doubtful status in the section.

A. lettyae **Reynolds**

1937, J. South Afr. Bot. 3: 137.

Glen and Hardy (2000) included this species in *A. zebrina*, but it is tentatively upheld here on the basis of its restricted distribution and rounded peduncles, which are peculiar to this species (Van Wyk & Smith 2005).

A. longibracteata **Pole-Evans**

1915, Trans. Roy. Soc. South Afr. 5: 25.

A maculate species included in the heterogeneous *A. greatheadii* var. *davyana* by Glen and Hardy (2000). It seems to be more closely related to *A. greatheadii* var. *greatheadii* on the basis of leaf surface morphology (Grace et al. 2009b). It is upheld here on the basis of its distinctively elongated racemes.

A. macrocarpa **Tod.**

1875, Hort. Bot. Panorm. 1: 36, t. 9.

Includes *Aloe barteri* Schnell (nom. illeg.), *Aloe commutata* A.Engl., *Aloe edulis* A.Chev., *A. lateritia* Engl., *Aloe macrocarpa* var. *major* A.Berger.

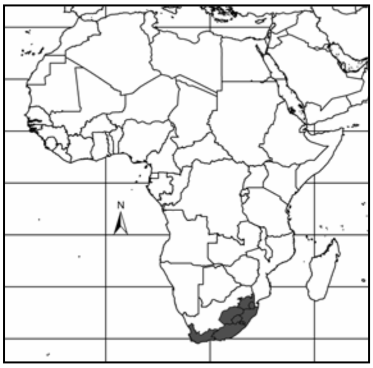
A widespread species found widely in the tropics, and the single maculate species occurring in West Africa. It is unclear whether the widespread occurrence of this species is due to radiation, or the relic of a previously widespread maculate distribution.

The species was resolved on a long terminal branch in the maculate group and is related to the East African species *A. ellenbeckii* and *A. lateritia* (Chapter 4) Wabuyele (2006) proposed the latter should be included in this species. It is one of few maculate species in which two flavonoids have been detected (Chapter 5).

***A. maculata* All.**

1773, Auct. Syn. 13.

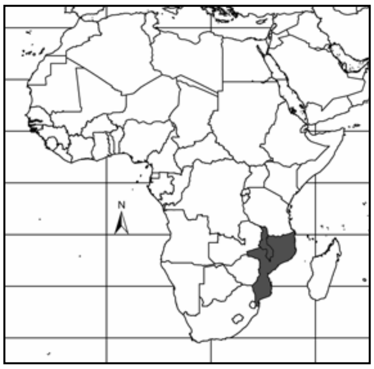
The type species for section *Pictae*. A common flavonoid is the major UV-absorbing constituent of the leaves (Chapter 5), which possess distinctive micromorphological surface features (Grace et al. 2009b).



***A. menyharthii* Baker**

1898, Fl. Trop. Afr. 7: 459.

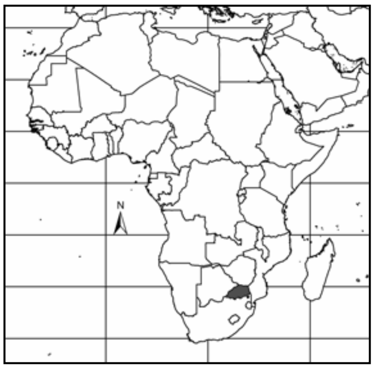
A maculate species occurring in south Tropical Africa. Data were not acquired during the present study due to a lack of material.



***A. monotropa* I.Verd.**

1961, Flow. Pl. Afr. 34, t. 1342.

A distinctive maculate species endemic to the Northern Province (Limpopo; South Africa). It occurs in deep shade and is the only maculate species with secund racemes. However, the flowers are typical of section *Pictae* and it was recovered in the maculate group in a phylogenetic study (Chapter 4). The leaves bear copious wax deposits and lack flavonoids found in other maculate species (Chapter 5, Grace et al. 2009b).



***A. mudenensis* Reynolds**

1937, J. South Afr. Bot. 3: 39–42, t. 1.

A maculate species endemic to KwaZulu-Natal (South Africa), and closely related to the other KwaZulu-Natal endemics *A. pruinosa* and *A. greenii*. Flavonoids were not detected in this species (Chapter 5).

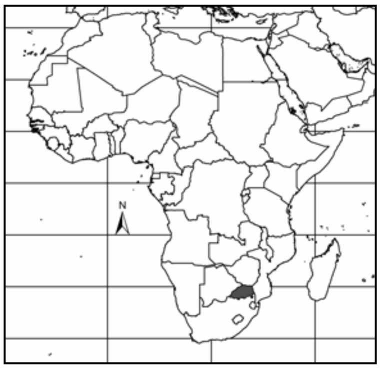
A. parvibracteata **Schönland**

1907, Rec. Albany Mus. 2: 139.

Includes *Aloe burgersfortensis* Reynolds, *Aloe komatiensis* Reynolds, *Aloe pongolensis* Reynolds, *Aloe decurvidens* Groenew., *Aloe keithii* Reynolds, *Aloe lusitanica* Groenew., *Aloe pongolensis* var. *zuluensis* Reynolds ≡ *Aloe parvibracteata* var. *zuluensis* (Reynolds) Reynolds.

A south-east African maculate species associated with other species in the region. The major UV-absorbing constituent of the leaves is a flavonoid typical of maculate species in southern Africa (Chapter 5).

A. petrophila **Pillans**



1933, S. Afr. Gard. 23: 213.

A diminutive maculate species endemic to the Northern Province (Limpopo, South Africa). Glen and Hardy (2000) included it in *A. swynnertonii*, but it has been upheld by Van Wyk and Smith (2005) and Newton (2001). Data were not acquired during the present study due to a lack of material.

A. pruinosa **Reynolds**

1936, J. South Afr. Bot. 2: 122–124, t. 17.

A maculate species endemic to KwaZulu-Natal (South Africa). It is closely related to other KwaZulu-Natal endemics *A. mudenensis* and particularly to *A. greenii*. This species is upheld largely on the basis of its restricted distribution and pruinosity. The flavonoid typical of southern African maculate species is the principal UV-absorbing constituent of the leaves (Chapter 5).

***A. prinslooi* I.Verd & D.S.Hardy**

1965, Fl. Pl. Afr. 37, t. 1453.

A diminutive maculate species readily distinguished by its stature, dense racemes of pale flowers, and leaf surface morphology (Grace et al. 2009b). Phylogenetic evidence and similarities in leaf chemistry suggest it is closely related to another KwaZulu-Natal endemic, *A. vanrooyenii* (Chapter 5, Grace et al. 2009b).

***A. reynoldsii* Letty**

1934, Flow. Pl. South Afr. 14 t. 558.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata.*

***A. striata* Haw.**

1804, Trans. Linn. Soc. London 7: 18.

A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). Representatives of section *Paniculatae* possess floral characters typical of maculate species and, often, patterned leaf surfaces. However, they differ in the somewhat leathery, glaucous distinctly striate and sometimes entire leaves. This species is chemically similar to southern African species of section *Pictae* (Chapter 5). The close relationship between sections *Paniculatae* and *Pictae* should be reflected in a revised taxonomy of *Aloe.*

***A. simii* Pole-Evans**

1917, Trans. Roy. Soc. South Afr. 5: 504.

A large maculate species endemic to Mpumalanga (South Africa), with scarcely patterned leaf surfaces and deeply channelled leaves. The leaf chemistry and micromorphology are typical of maculate species (Chapter 5, Grace et al. 2009b).

***A. suffulta* Reynolds** ?

1937, South Afr. J. Bot. 3: 151.

A species recovered in the maculate sister group, comprising marginal maculate species with patterned leaf surfaces but lacking floral characters typical of section *Pictae* (Chapter 4). Glen and Hardy (2000) included this species in section *Chabaudia* Glen & D.S.Hardy on account of the distinct trigonous indentation in the perianth above the level of the ovary.

Leaf constituents typical of maculate species were not detected, and leaf surface micromorphology does not resemble other maculate species (Chapter 5, Grace et al. 2009b). It is of doubtful status in the section.

***A. swynnertonii* Rendle**

1911, J. Linn. Soc. Bot. 40: 215.

Includes *Aloe chimanimaniensis* Christian, *Aloe melsetterensis* Christian.

A maculate species in which flavonoids were not detected, but the leaf surfaces are similar to other maculate species (Chapter 5, Grace et al. 2009b).

***A. umfoloziensis* Reynolds**

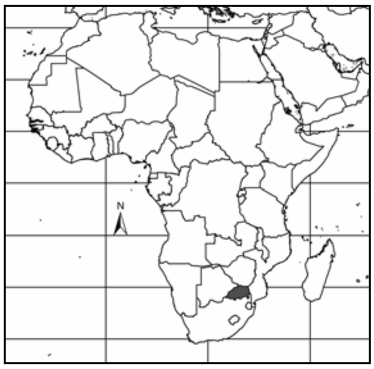
1937, J. South Afr. Bot. 3: 42–45, t. 2.

A maculate species endemic to KwaZulu-Natal and related to geographically overlapping species such as *A. dewetii*. Glen and Hardy (2000) included it in their hypothesis of *A. maculata* but differences in leaf micromorphology contest this (Grace et al. 2009b).

A. vandermerwei Reynolds ■

1950, Aloes South Afr.: 267–270.

A maculate species considered an Mpumalanga variant of *A. zebrina* (Glen & Hardy 2000; Van Wyk & Smith 2005). Data were not acquired during the present study due to a lack of material.



***A. vanrooyenii* G.F.Sm. & N.R.Crouch**

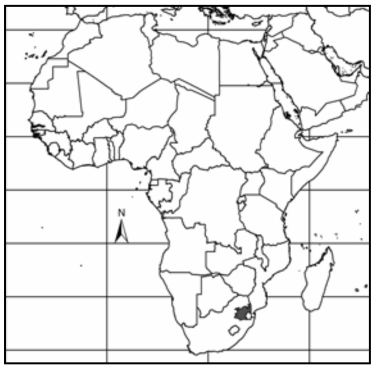
2006, Bothalia 36: 73–80.

The most recently named maculate species, endemic to KwaZulu-Natal. Phylogenetic evidence and similarities in leaf chemistry suggest it is related to another KwaZulu-Natal endemic, *A. prinslooi* (Chapter 5, Grace et al. 2009b).

***A. verdoorniae* Reynolds**

1936, J. South Afr. Bot. 5: 173.

A maculate species included in *A. greatheadii* var. *davyana* by Glen and Hardy (2000) but also affiliated with *A. zebrina* (Van Wyk & Smith 2005). Constituents typical of maculate species were not found in the leaves (Chapter 5). The status of this species remains unclear.



A. vogtsii Reynolds ■

1936, J. South Afr. Bot. 2: 118–120, t. 15.

A maculate species containing a flavonoid common to many maculate species (Chapter 5). Similarities in leaf surface micromorphology, but not chemistry (Chapter 5, Grace et al. 2009b), support the hypothesis that this species is a southern form of *A. swynnertonii* (Glen & Hardy 2000).

***A. zebrina* Baker**

1878, Trans. Linn. Soc. London. Bot. 1: 264.

Includes *Aloe platyphylla* Baker, *Aloe transvaalensis* Kuntze, *Aloe lugardiana* Baker, *Aloe bamangwatensis* Schönland, *Aloe ammophila* Reynolds, *Aloe laxissima* Reynolds, *Aloe angustifolia* Groenew. (nom. illeg.), *Aloe transvaalensis* var. *stenacantha* F.S.Mull., *Aloe vandermerwei* Reynolds

A maculate species representing a heterogeneous and problematic species complex including *A. greatheadii* and *A. parvibracteata.* The leaves contain a flavonoid common to the maculate species (Chapter 5). The delineation of this species remains unclear.

7.2 Conclusions

Ethnobotany

- A large volume of literature (excluding *A. vera* L.) recounts an extraordinary number of species and varied uses in *Aloe.*

- Documented use records of *Aloe* can serve as an approximate surrogate for ethnobotanical field study.

- Consensus analysis may be used to quantify the relative biocultural importance of the uses of *Aloe*.

- *Aloe* is most widely valued for medicine and poisons against invertebrate pests.

- While *Aloe* is an exceptionally popular collector's group, particularly in the Northern Hemisphere, this is not reflected in literature which focuses on the traditional uses of *Aloe* in its natural range.

- The majority of *Aloe* spp. occurring in southern Africa are used for medicine, most commonly to treat infections and internal parasites.

- The rich ethnobotanical history and contemporary value of *Aloe* substantiates the need for conservation to mitigate the risks of exploitation and habitat loss.

Phylogenetics

- Phylogenetic reconstructions based on new DNA sequences of nuclear ribosomal (ITS) and chloroplast (*mat*K, *trnL* intron, *trnL–F* spacer) regions generated for 29 (mostly maculate) species of *Aloe* offer insights into putative evolutionary relationships for the maculate group.

- Core maculate species in section *Pictae* and representatives of section *Paniculatae* comprise a convincing holophyletic (monophyletic in a phylogenetic sense) group.

- Geographical rather than morphological clades among ingroups suggest convergence has occurred among spatially isolated groups in *Aloe*.

- In agreement with Treutlein et al. (2003), *Aloe aristata* Haw. is a *Haworthia*-like species with a tenuous affiliation to *Aloe.*

Chemosystematics

- Flavonoids, including the common compounds isoorientin and isovitexin, are among the major UV-absorbing constituents in the leaves of maculate species.

- Flavonoids have previously been detected almost exclusively in primitive sections of *Aloe*; the presence of flavonoids in section *Pictae*, an actively diverging group, could indicate selective gene expression or loss in other infrageneric groups lacking them.

- The flavonoid biosynthesis pathway in East African and southern African species in section *Pictae* may differ, as isoorientin is common to many species but isovitexin appears to be restricted to southern African species.

- Isoorientin and isovitexin are present in the southern African *A. parvibracteata* and *A. macrocarpa*, the single West African representative of section *Pictae.*

- Infraspecific variation in UV-absorbing leaf constituents was limited in species assessed.

- A novel anthrone *C*-glycoside, 6′-malonylnataloin, characterised in *A. ellenbeckii* occurs in certain maculate species of *Aloe*.

- 6′-Malonylnataloin is common among East African species in section *Pictae* but is not a convincing "chemotaxonomic marker" for them.

- The co-occurrence of plicataloside, a naphthalene derivative, and isoorientin, a flavone, were detected for the first time in *A. greatheadii*, is unusual (Viljoen & van Wyk 1999).

Micromorphology

- Leaf surface morphology and stomatal anatomy are of potential taxonomic significance, particularly at the species level, among 36 maculate species of *Aloe* examined.

- There is minimal infraspecific variation in leaf surface features among maculate species.

- The leaf surface features typical of section *Pictae* comprise irregularly-outlined, 4–6-sided epidermal cells, the periclinal walls flat and embellished with micropapillae, the anticlinal walls indicated by channels on the leaf surface. The outer stomatal pore is typically sunken or plane and surrounded by four lobes on the leaf surface that may overarch the epistomatal chamber. The guard cells have distinct outer and inner stomatal ledges.

- The ratio describing the difference in lengths of the lobe pairs surrounding the epistomatal chamber, termed 'L-lobes' (parallel to the long side of the leaf) and 'T-lobes' (perpendicular to the long side of the leaf), may be of taxonomic significance in section *Pictae.*

- Leaf surface micromorphology differs between East African and southern African species in section *Pictae.*

- Leaf surface micromorphology is unusual in *A. ellenbeckii*, *A. prinslooi* and the marginal species *A. suffulta.*

General

- Relationships among East African species in section *Pictae* are more clearly defined than among the numerous, poorly defined southern African species.

- *A. leptosiphon* and *A. suffulta*, recovered as sister to the maculate group in phylogenetic analyses, are doubtful members of section *Pictae* due to their atypical floral morphology.

- The present circumscription of section *Pictae* does not reflect putative evolutionary relationships indicated by molecular, phytochemical and micromorphological characters in *Aloe.*

- A revised, evolutionary hypothesis for section *Pictae* excludes the marginal maculate species *A. leptosiphon* and *A. suffulta*, and may include species presently recognised in section *Paniculatae.*

- Floral characters (basally inflated corolla, constricted perianth) are of greater significance than maculate leaves as synapomorphies for section *Pictae.*

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SUMMARY

Contributions to the systematics and biocultural value of *Aloe* L. (Asphodelaceae)

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Co-Supervisor: Prof. Dr. G. F. Smith

This thesis focuses on the biocultural value of Aloe L. (Asphodelaceae), the influence of utility on taxonomic complexity and conservation concern, and the systematics and phylogeny of section *Pictae*, the spotted or maculate group.

The first comprehensive ethnobotanical study of *Aloe* (excluding the cultivated *A. vera*) was undertaken using the literature as a surrogate for data gathered by interview methods. Over 1400 use records representing 173 species were gathered, the majority (74%) of which described medicinal uses, including species used for natural products such as *A. ferox* Mill. and *A. perryi* Baker. In southern Africa, 53% of approximately 120 *Aloe* species in the region are used for health and wellbeing. Homogeneity in the literature was quantified using consensus analysis; consensus ratios showed that, overall, uses of *Aloe* spp. for medicine and invertebrate pest control are of the greatest biocultural importance. The rich ethnobotanical history and contemporary value of *Aloe* substantiate the need for conservation to mitigate the risks of exploitation and habitat loss.

A systematic evaluation of the problematic maculate species complex, section *Pictae* Salm-Dyck, was undertaken. In a phylogenetic study, new sequences were acquired of the nuclear ribosomal internal transcribed spacer (ITS), chloroplast *trnL* intron, *trnL–F* spacer

and *matK* gene in 29 maculate species of *Aloe*. Parsimony analysis and Bayesian inference (maximum likelihood) were used to generate trees of comparable topology from these and augmented sequence data. A well supported holophyletic (monophyletic) maculate group was recovered. A representative of the related section *Paniculatae*, *A. striata*, was recovered in the maculate group, whereas doubtful maculate species with unusual floral morphology (*A. leptosiphon* and *A. suffulta*) comprised a sister group. East African maculate species were associated with the single West African maculate species, *A. macrocarpa.* Further geographical trends were evident among ingroup clades.

Analogous patterns were identified in chemosystematic and comparative morphological studies of maculate species, respectively, and insights were gained into interspecific relationships. The flavonoids isoorientin and isovitexin, and a new C-glycosylanthrone, 6′-malonylnataloin, were characterised in *Aloe* for the first time using hyphenated chromatographic techniques and nuclear magnetic resonance (NMR) spectroscopy. 6′-Malonylnataloin is common among East African species in section *Pictae* but is not a convincing "chemotaxonomic marker" for them. Leaf surface features typical of section *Pictae* were identified from scanning electron micrographs of 36 maculate species. Leaf surface sculpturing, stomata and lobes surrounding the epistomatal pore are of potential taxonomic significance, particularly at species level.

Evidence presented here indicates that the current circumscription of section *Pictae* does not reflect evolutionary relationships among maculate species. Importantly, floral characters, namely a basally swollen perianth with constriction above the ovary, are of greater significance than maculate leaves as synapomorphies for section *Pictae*. An evolutionary hypothesis for section *Pictae* excludes the marginal maculates species with unusual flowers.

CURRICULUM VITAE

Olwen Megan Grace was born in Durban, South Africa in 1977. Her interest in natural history was established during her childhood in the rural outskirts of Hillcrest in KwaZulu-Natal. She matriculated from Hillcrest High School in 1995 and enrolled at the University of Natal in Pietermaritzburg, where she completed her BSc in 1998 and BSc (Hons) *cum laude* in 1999, in the Department of Botany. During a sojourn from her studies in 2000, she joined the Centre for Economic Botany at the Royal Botanic Gardens, Kew to research documented uses of African plants. She returned to the University of Natal and was awarded her MSc *cum laude* in 2002. Her dissertation on the use of bark in traditional healthcare was awarded the Junior Captain Scott Medal from the Suid-Afrikaanse Akademie vir Wetenskap en Kuns, and earned the S_2A_3 Bronze Medal from the Southern African Association for the Advancement of Science. In 2003, she was appointed by the National Botanical Institute at Natal Herbarium to work on medicinal plants and systematics. She returned to the Royal Botanic Gardens, Kew, in 2004, where her work has focused on the sustainable use and conservation of the African flora. Olwen is the author or co-author of about 25 scientific papers, book chapters and popular articles.

APPENDIX A

APPENDIX A

References to the uses of *Aloe* spp.

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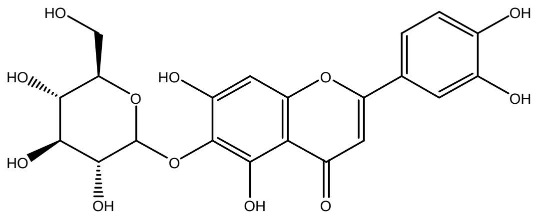
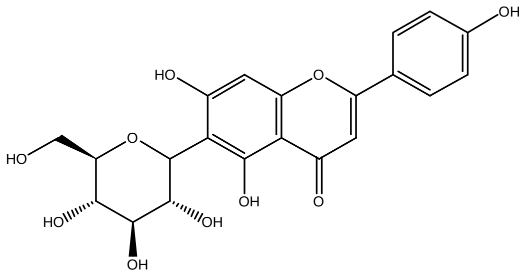
APPENDIX B

Compounds of chemosystematic interest in *Aloe* section *Pictae*: structural data

Flavonoids

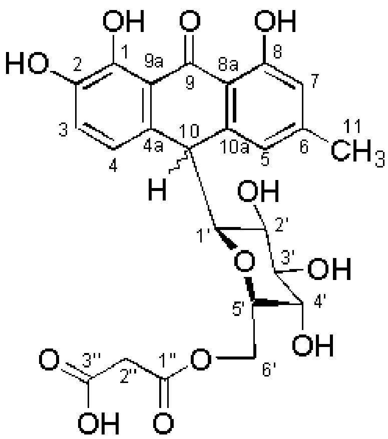


isoorientin (luteolin-6-glucoside)



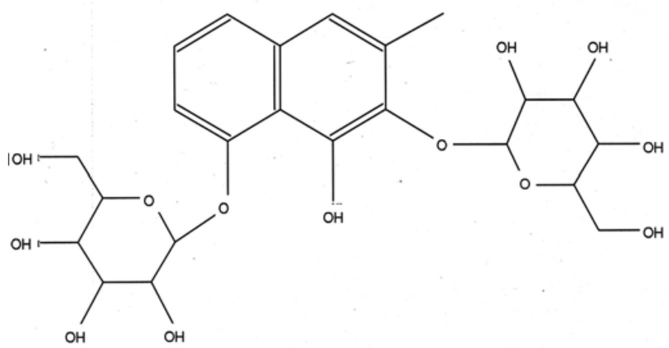
isovitexin (6-*C*-glucosylapigenin)

Anthrone *C*-glycoside



6′-malonylnataloin (anthrone *C*-glycoside)

Napthalene derivative



plicataloside (2,8-Di-*O*-β-D-glucopyranoside)