

CHAPTER 7 DISCUSSION AND CONCLUSIONS

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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 Wabuye (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 (isorientin 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* (Wabuye 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.

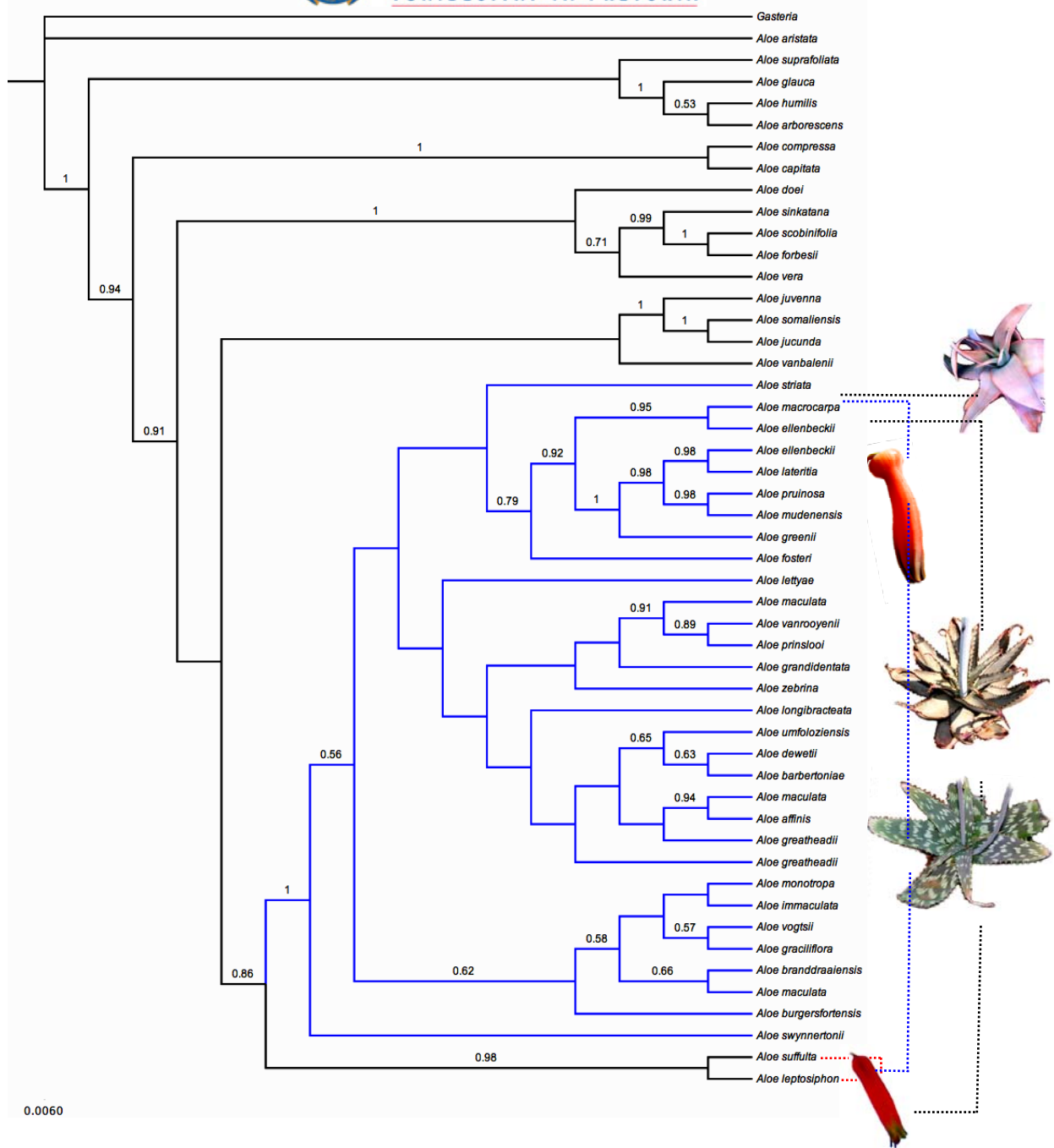


Figure 7.1 Gross morphological features of systematic importance in the maculate species complex. Features are mapped on a maximum likelihood tree based on ITS, *trnL-F* and *matK* with posterior probabilities above branches (see Chapter 4).

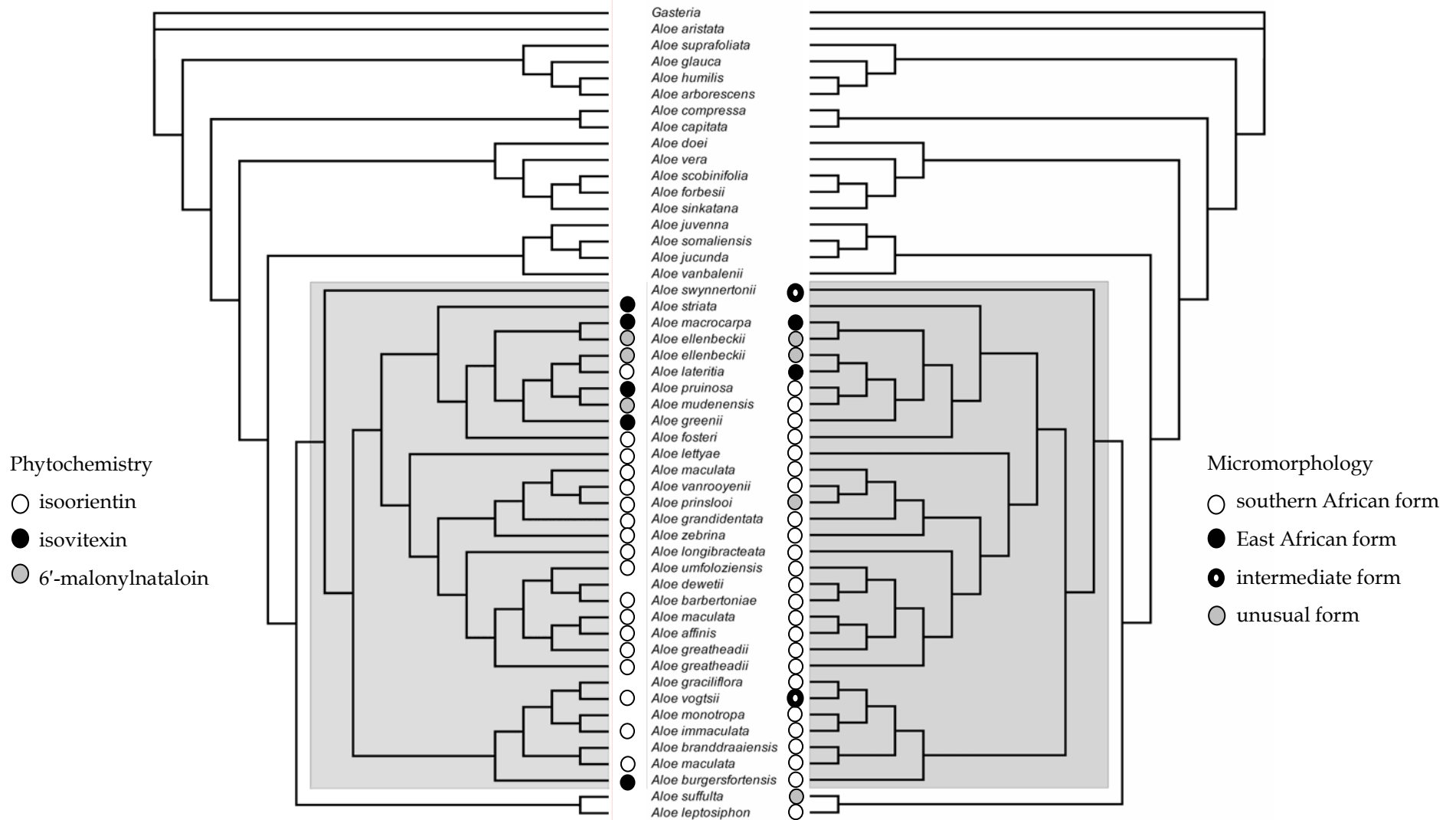


Figure 7.2 Phytochemical (left) and morphological (right) features of systematic significance in the maculate species complex, mapped on a maximum likelihood tree reconstructed from ITS, *trnL-F* and *matK* data. The core maculate group is highlighted (see Chapters 4, 5 and 6).

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.

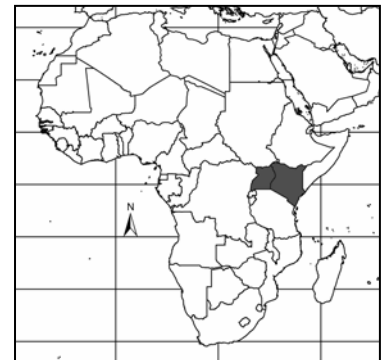
A maculate species endemic to Mpumalanga (South Africa). Leaf markings within populations are variable or absent (Glen & Hardy 2000).



***A. amudatensis* Reynolds**

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

An East African maculate species, included in *A. ellenbeckii* by Wabuye (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.





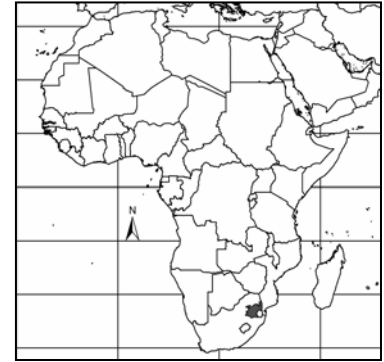
***A. barbertoniae* Pole-Evans ■**

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.**

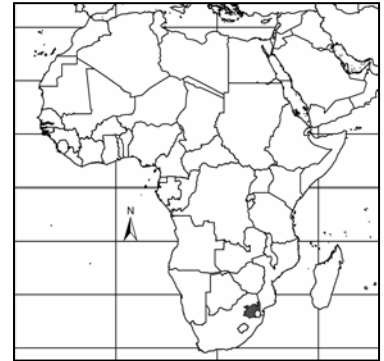
1940, Flow. Pl. South Afr. 20: t. 761.

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).



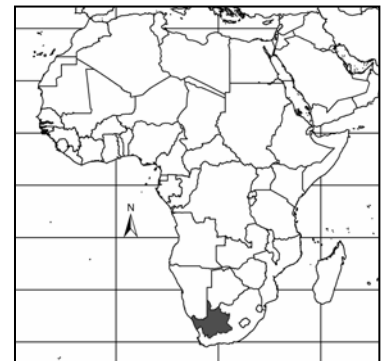
***A. buhrii* Lavranos**

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*.



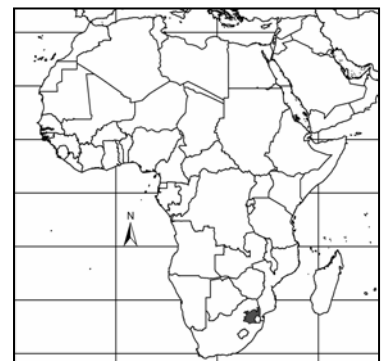
***A. burgersfortensis* Reynolds ■**

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)

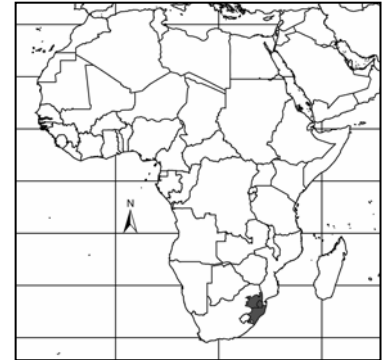
support this hypothesis. See *A. parvibracteata*.



***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.

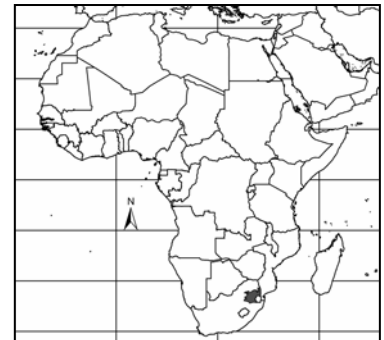
A robust species occurring in south tropical and East Africa. Data were not acquired during the present study due to a lack of material.



***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.

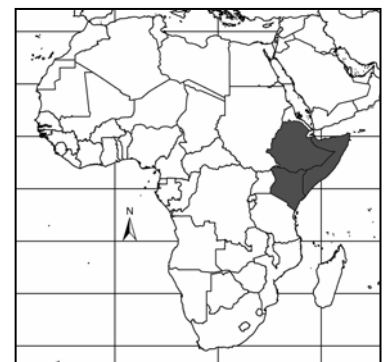


***A. ellenbeckii* A.Berger**

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

Includes *Aloe dumetorum* B.Mathew & Brandham.

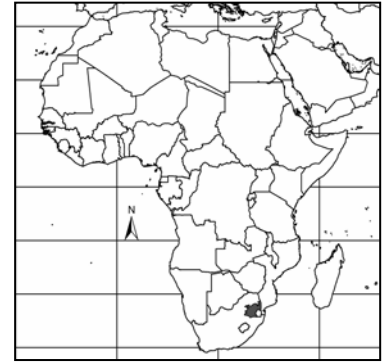
A distinctive East African representative of section *Pictae* with unusual leaf chemistry (Grace et al. 2008a) and leaf surface features (Chapter 5, Grace et al. 2009b). Related to the East African maculate species *A. lateritia* and the West African maculate species *A. macrocarpa*.



***A. fosteri* Pillans**

1933, South Afr. Gard. 23: 140.

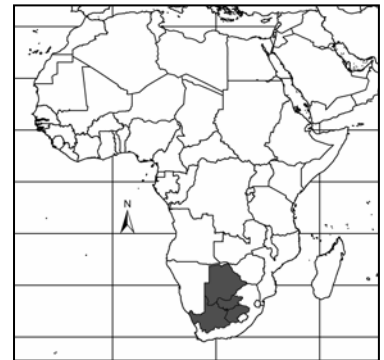
A maculate species endemic to Mpumalanga (South Africa) characterised by variable floral colour and pruinose leaves (Glen & Hardy 2000). A flavonoid is one of the major UV-absorbing constituents of its leaves (Chapter 5).



***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. greathedii* Schönland**

1904, Rec. Albany Mus. 1: 121.

A heterogeneous and problematic taxonomic entity.

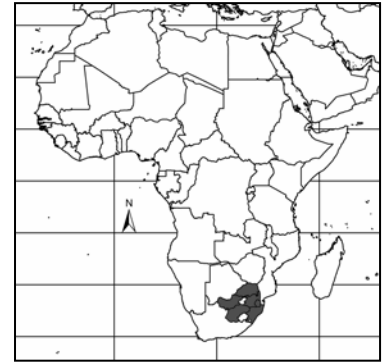


***A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy**

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.

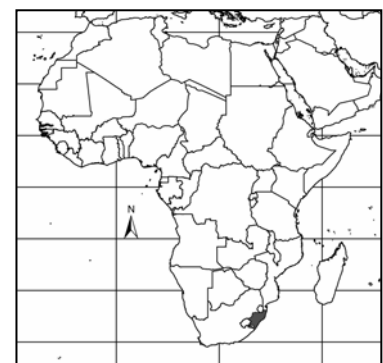
The differences between this variety and the heterogeneous *A. greatheadii* var. *davyana* are unclear, particularly where they co-occur. However, they can be separated by leaf surface morphology (Grace et al. 2009b).



***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*.

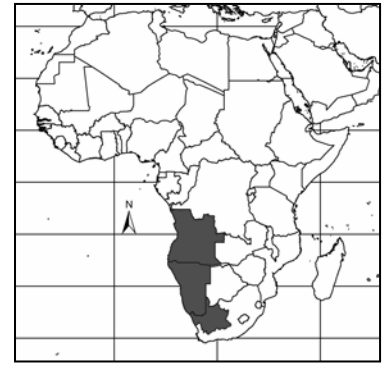


***A. hereroensis* Engl. ?**

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

Includes *Aloe hereroensis* var. *hereroensis*

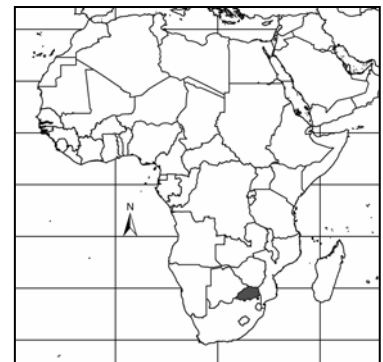
Patterned leaf surfaces of this species led Berger (1908) to group it with the maculate species. Reynolds (1950) erected a new group, series *Hereroenses* Reynolds, to accommodate it. He believed it to be an intermediate of series *Saponariae* (the maculate group) and series *Asperifoliae*. Glen and 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).

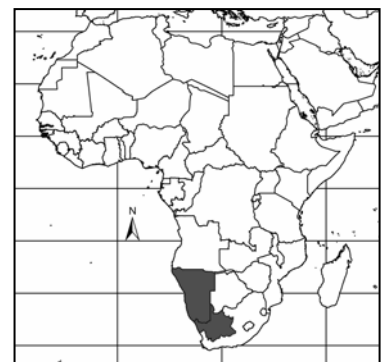


***A. karasbergensis* Pillans**

1928, Journ. Bot. 66: 233.

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

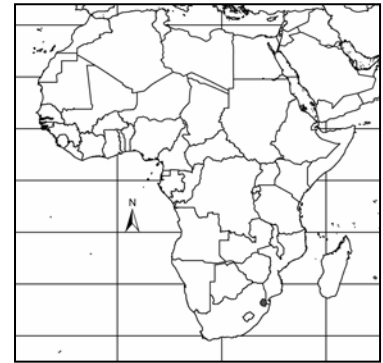
A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata*.



***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.

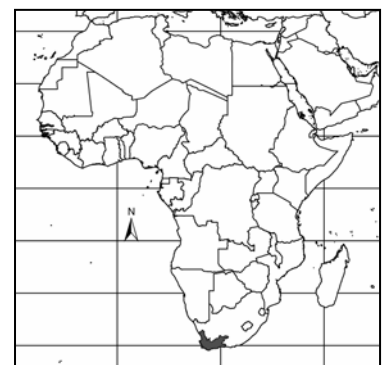
A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata*.



***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*.

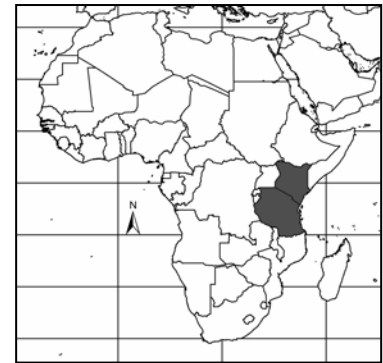


A. lateritia Engl. var. *graminicola* (Reynolds) S.Carter ■

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

≡ *Aloe graminicola* Reynolds; includes *Aloe solaiana* Christian.

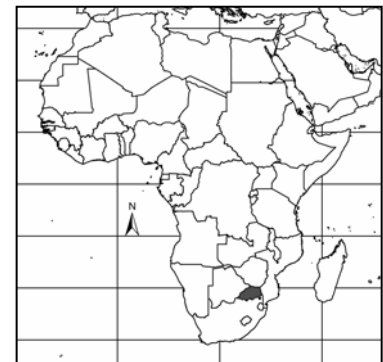
Differs from the other variety by persistently capitate inflorescences (Carter 1994). Wabuyele (2006) proposed this variety is conspecific with *A. macrocarpa*. See *A. lateritia*.



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*.

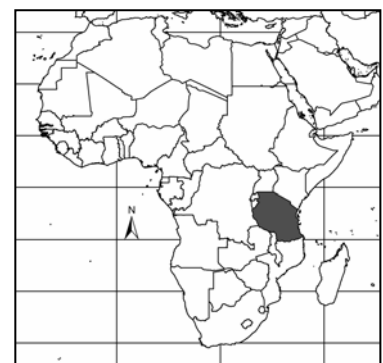


A. leptosiphon A.Berger ?

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.

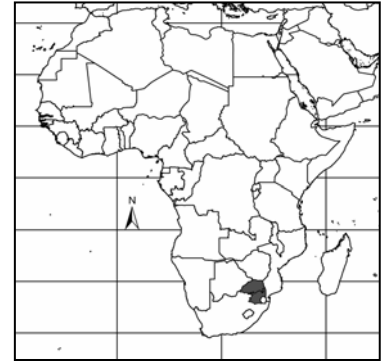




***A. lettyae* Reynolds**

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

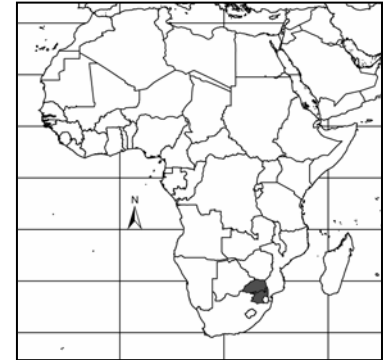
Glen and Hardy (2000) included this species in *A. zebrina*, but it is tentatively upheld here on the basis of its restricted distribution and rounded peduncles, which are peculiar to this species (Van Wyk & Smith 2005).



***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.



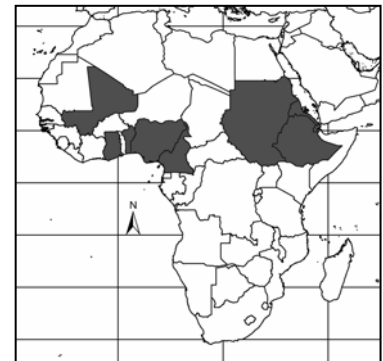
***A. macrocarpa* Tod.**

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.

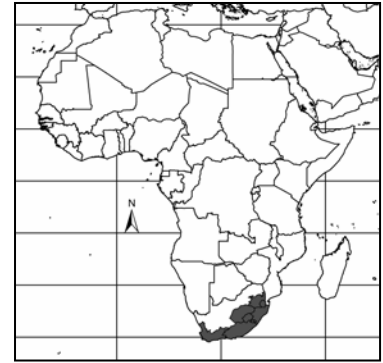
The species was resolved on a long terminal branch in the maculate group and is related to the East African species *A. ellenbeckii* and *A. lateritia* (Chapter 4) Wabuye (2006) proposed the latter should be included in this species. It is one of few maculate species in which two flavonoids have been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



***A. maculata* All.**

1773, Auct. Syn. 13.

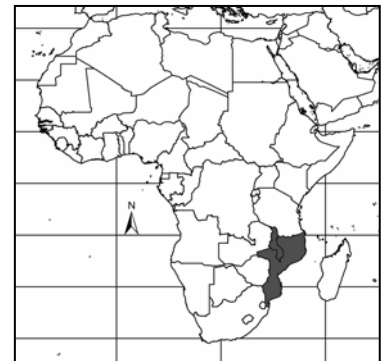
The type species for section *Pictae*. A common flavonoid is the major UV-absorbing constituent of the leaves (Chapter 5), which possess distinctive micromorphological surface features (Grace et al. 2009b).



***A. menyharthii* Baker**

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

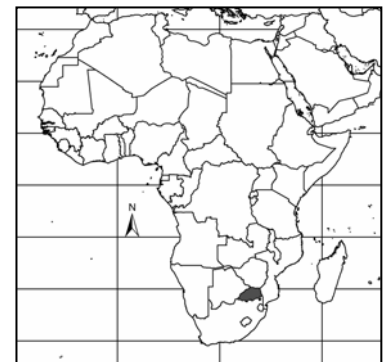
A maculate species occurring in south Tropical Africa. Data were not acquired during the present study due to a lack of material.



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

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

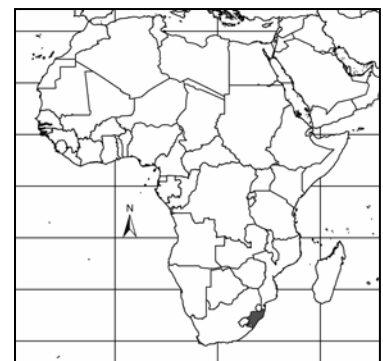
A distinctive maculate species endemic to the Northern Province (Limpopo; South Africa). It occurs in deep shade and is the only maculate species with secund racemes. However, the flowers are typical of section *Pictae* and it was recovered in the maculate group in a phylogenetic study (Chapter 4). The 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).



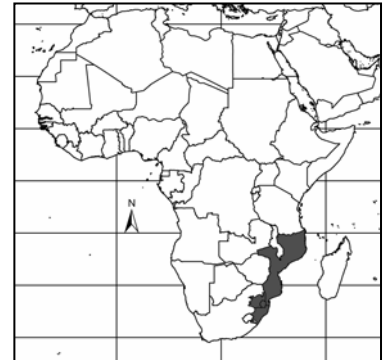


***A. parvibracteata* Schönland**

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 \equiv *Aloe parvibracteata* var. *zuluensis* (Reynolds) Reynolds.

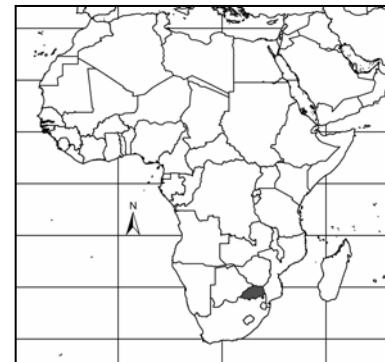
A south-east African maculate species associated with other species in the region. The major UV-absorbing constituent of the leaves is a flavonoid typical of maculate species in southern Africa (Chapter 5).



***A. petrophila* Pillans**

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

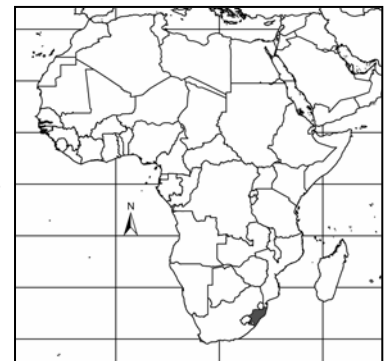
A diminutive maculate species endemic to the Northern Province (Limpopo, South Africa). Glen and Hardy (2000) included it in *A. swynnertonii*, but it has been upheld by Van Wyk and Smith (2005) and Newton (2001). Data were not acquired during the present study due to a lack of material.



***A. pruinosa* Reynolds**

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

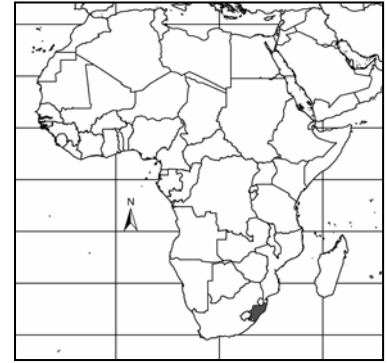
A maculate species endemic to KwaZulu-Natal (South Africa). It is closely related to other KwaZulu-Natal endemics *A. mudenensis* and particularly to *A. greenii*. This species is upheld largely on the basis of its restricted distribution and pruinosity. The flavonoid typical of southern African maculate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



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

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

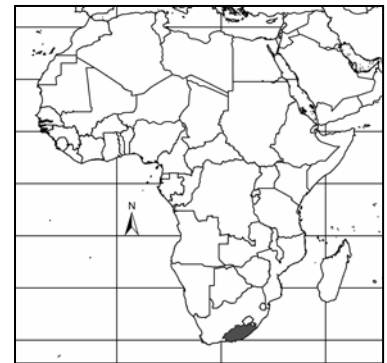
A diminutive maculate species readily distinguished by its stature, dense racemes of pale flowers, and leaf surface morphology (Grace et al. 2009b). Phylogenetic evidence and similarities in leaf chemistry suggest it is closely related to another KwaZulu-Natal endemic, *A. vanrooyenii* (Chapter 5, Grace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



***A. reynoldsii* Letty**

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

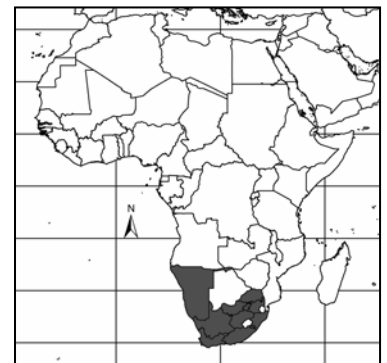
A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). See *A. striata*.



***A. striata* Haw.**

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

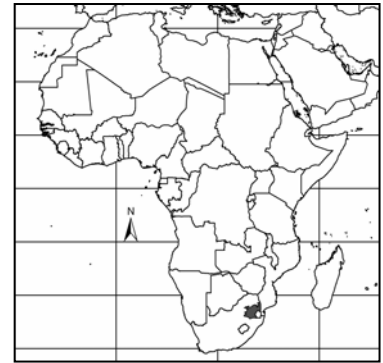
A species recognised in the segregate section *Paniculatae* which seemingly shares a recent ancestor with section *Pictae* (Chapter 4). Representatives of section *Paniculatae* possess floral characters typical of maculate species and, often, patterned leaf surfaces. However, they differ in the somewhat 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).



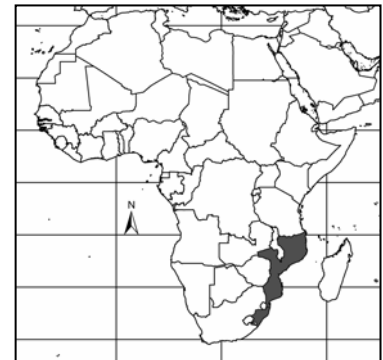
A. *suffulta* Reynolds ?

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.

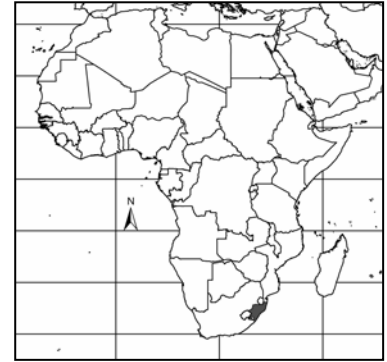
A maculate species in which flavonoids were not detected, but the leaf surfaces are similar to other maculate species (Chapter 5, Grace et al. 2009b).



***A. umfoloziensis* Reynolds**

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

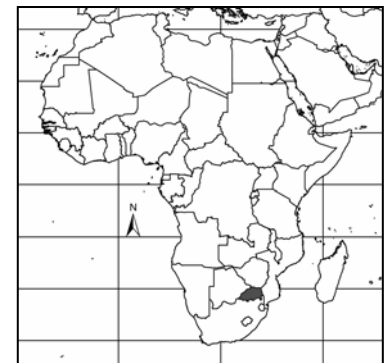
A maculate species endemic to KwaZulu-Natal and related to geographically overlapping species such as *A. dewetii*. Glen and Hardy (2000) included it in their hypothesis of *A. maculata* but differences in leaf micromorphology contest this (Grace et al. 2009b).



***A. vandermerwei* Reynolds ■**

1950, Aloes South Afr.: 267–270.

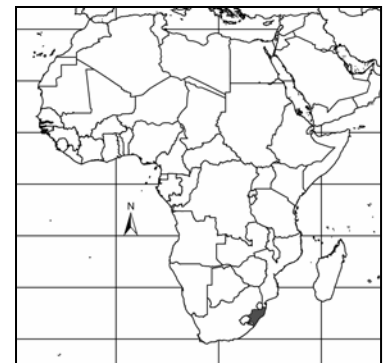
A maculate species considered an Mpumalanga variant of *A. zebrina* (Glen & Hardy 2000; Van Wyk & Smith 2005). Data were not acquired during the present study due to a lack of material.



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

2006, Bothalia 36: 73–80.

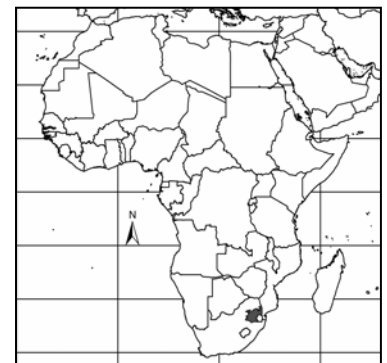
The most recently named maculate species, endemic to KwaZulu-Natal. Phylogenetic evidence and similarities in leaf chemistry suggest it is related to another KwaZulu-Natal endemic, *A. prinslooii* (Chapter 5, Grace et al. 2009b).



***A. verdoorniae* Reynolds**

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

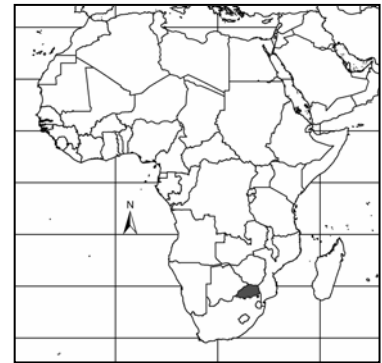
A maculate species included in *A. greatheadii* var. *davyana* by Glen and Hardy (2000) but also affiliated with *A. zebrina* (Van Wyk & Smith 2005). Constituents typical of maculate species were not found in the leaves (Chapter 5). The status of this species remains unclear.



***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).

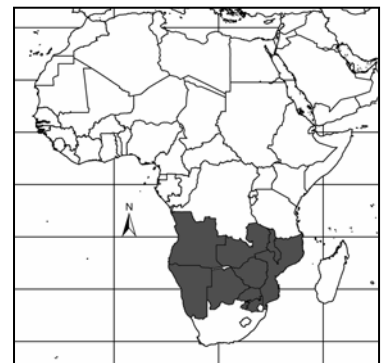


***A. zebrina* Baker**

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 (*matK*, *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*.
- Intraspecific 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 intraspecific 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. prinslooii* 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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