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Generic relationships in the *Alooideae (Asphodelaceae)*

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Summary

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

Introduction

The subfamily *Alooideae (Asphodelaceae)* sensu Dahlgren & al. (1985) includes seven genera and approximately 450 species (Table 1). It is fundamentally an Old World group with most genera occurring in sub-Saharan Africa. The genus *Aloe* is also found on the Arabian Peninsula, Madagascar and Socotra, while *Lomatophyllum* has been reported from the Aldabra Islands, Madagascar and Mauritius. The greatest concentration of genera and of species is in southern Africa, that is, roughly, the region south of the Kunene, Okavango and Limpopo Rivers. In this region the *Liliaceae*, in which the alooid taxa have previously been included, form a major part of the petaloid monocotyledons and contribute substantially to the size of the flora (Goldblatt, 1978; Gibbs Russell, 1985, 1987).

Most research workers recognize the *Alooideae* as a taxonomically difficult subfamily. The morphology of these leaf succulents often varies considerably depending on environmental conditions (cf. Schelpe, 1958, and Bayer, 1980 on *Gasteria* Duval) and in some instances taxa seem to intergrade (cf. Bayer, 1975, and Glen & Hardy, 1987 on *Aloe* ser. *Saponariae* A. Berger; and Bayer, 1973, and Scott, 1981, on the *Haworthia reinwardtii* Haw. – *H. coarctata* Haw. complex). Recent studies, notably in the principal genera *Aloe*, *Gasteria* and *Haworthia*, have been primarily taxonomic in nature and have involved the study of variation in morphology (G. W. Reynolds, 1966, 1982; Van Jaarsveld, 1989; Bayer, 1982; Scott, 1985), leaf exudate chemistry (reviewed

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by T. Reynolds, 1985a, b; cf. T. Reynolds, 1990), leaf surface sculpturing (cf. Cutler, 1972, 1982) and cytogenetics (cf. Riley & Majumdar, 1979). Furthermore, apart from recent contributions by Smith (1988, 1990, 1991), the smaller *Alooideae* genera (Table 1) have been omitted from most previous taxonomic and biosystematic investigations of this group (see also Beaumont & al., 1985). Since the initial work in the larger genera was concerned with the basic problem of patterns of variation and how the variation could best be recognized taxonomically, little attention was given to possible phyletic relationships.

The genera of *Alooideae* have recently been analized phenetically in numerical-taxonomic studies (Rowley, 1967a, 1969). Due to the uncertain taxonomic status of some of the genera recognized, the results of these studies are inconclusive (Bayer, 1972; Rowley, 1976a; Ivimey-Cook, 1971). A few previous studies on the evolution of some genera of the *Alooideae* have been presented (Kok, 1973; Holland, 1978). However, these are often highly speculative and open to conjecture (Newton, 1973). The present cladistic analysis has been conducted to obtain a better understanding of the relationships of the members of the *Alooideae* and to present for the first time a hypothesis of phylogenetic relationships within the subfamily.

Materials and methods

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

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

Gasteria Duval (1809: 6; cf. Van Jaarsveld, 1989). Syn.: *Atevala* Rafinesque (1840: 136).

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

Table 1. Genera of the *Asphodelaceae* sensu Dahlgren & al. (1985).

Taxon	Approximate No. of species	Geographical distribution	Data source
Asphodeloideae			
Asphodeline Reichenb.	14	Mediterranean, W. Asia	Tuzlaci (1987)
Asphodelus L.	12	Mediterranean, W. Asia	Dahlgren & al. (1985)
Bulbine Wolf	60	S. Africa, Australia	Watson (1987)
Bulbinella Kunth	16	S. Africa, New Zealand	Perry (1987)
Bulbinopsis Borzì	—	Congeneric with *Bulbine*	Watson (1986a)
Eremurus M. Bieb.	35	C. Asia	Dahlgren & al. (1985)
Jodrellia Baijnath	3	Tropical Africa	Baijnath (1978)
Kniphofia Moench	70	S. & E. Africa, Madagascar, S. Arabia	Codd (1968); Marais (1973)
Simethis Kunth	1	W. Europe, W. Mediterranean	Dahlgren & al. (1985)
Trachyandra Kunth	50	S. Africa	Obermeyer (1962)
Verinea Pomel	—	Congeneric with *Asphodelus*	Jackson (1894-1895)
Alooideae			
Aloe L.	333	S. & E. Africa, Madagascar, S. Arabia	G. W. Reynolds (1966, 1982)
Astroloba Uitew.	7	S. Africa (fynbos & succulent karoo)	Roberts Reinecke (1965)
Chortolirion A. Berger	1	S. Africa (mainly grassland)	Smith (1988)
Gasteria Duval	14	S. Africa (mainly fynbos)	Van Jaarsveld (1989)
Haworthia Duval	68	S. Africa (mainly fynbos)	Bayer (1982)
Lomatophyllum Willd.	12	Madagascar, Mauritius	Jacobsen (1986)
Poellnitzia Uitew.	1	S. Africa (succulent karoo)	Smith (1985)

Lomatophyllum Willdenow (1811: 166; cf. Jacobsen, 1986). Syn.: *Phylloma* Ker (1813: t. 1585).

Chortolirion Berger (1908: 72; cf. Smith, 1985).

Poellnitzia Uitewaal (1940: 61; cf. Smith, 1985).

Astroloba Uitewaal (1947a: 53; cf. Roberts Reinecke, 1965). Syn.: *Apicra* Haworth (1819: 61) non Willdenow: 167 (1811).

The seven genera were considered as units of study (EU's, Evolutionary Units, fide Estabrook, 1977), but the assumption of the genera being monophyletic emerged as a fundamental problem of the traditional generic delimitation, particularly with regard to *Aloe* and *Haworthia.*

Data employed. – The sources of the data used in the cladistic analysis are listed in Table 1. Additional information was obtained from Coetzee & Van der Schijff (1969),

Table 2. Postulated transformation series of 16 characters used in constructing the cladogram in Fig. 2.

Number	Character	States recognised
1	Habit	acaulescent = 0; caulescent = 1
2	Leaf arrangement	congested = 0; widely spaced = 1
3	Leaf consistency	mesophytic = 0; succulent = 1
4	Leaf tuberculation	absent = 0; present = 1
5	Outline of leaf cross-section	V-shaped = 0; crescent-shape/cymbiform = 1
6	Inflorescence compaction	dense = 0; lax = 1
7	Flower shape	Not tubular = 0; tubular = 1
8	Fusion of perianth segments	free = 0; fused = 1
9	Flower colour	yellow-red = 0; green-white = 1
10	Flower disposition	not slanted upwards = 0; slanted upwards = 1
11	Perianth symmetry	not bilabiate = 0; bilabiate = 1
12	Floral fragrance	present = 0; absent = 1
13	Anther position	exserted = 0; included = 1
14	Nectar sugars	sucrose almost absent = 0; sucrose dominant = 1
15	Nectar sugars	glucose equals fructose = 0; glucose >> fructose = 1
16	Basic chromosome number *(x)*	6 = 0; 7 = 1

Baijnath (1980) and Van der Riet (1977). Nectar sugar composition was analysed by one of us (B-E. Van Wyk). The chromosomal data come principally from De Wet (1960), Sharma & Mallick (1966), Jones & Smith (1967), Brandham (1971) and Riley & Majumdar (1979). Sources of distributional information are given in the captions of Fig. 3-7.

All characters of a taxon are potentially valuable for inferring evolutionary trends. However, only some of them are strong enough indicators of evolutionary directionality to be useful for cladistic analysis. For the present study the 16 characters listed in Table 2 were used, i.e., all those for which we could confidently assign primitive and advanced states. Anatomical characters have been excluded, despite their potential value as supporting evidence for the monophyly of the *Alooideae* and the distinction between the latter and *Kniphofia*. Leaf surface sculpturing and bundle sheath types are particularly important in this regard (Dr. D. F. Cutler, personal communication), but the inclusion of these characters should be based on a more rigorous comparison of all genera. The basic data matrix is shown in Table 3.

Polarization of character states. – The selection of operational criteria by which to assign primitive (plesiomorphic) and advanced (apomorphic) conditions to character states is one of the most difficult, but critical steps in inferring a phylogeny (cf. Cronquist, 1987). Due to the absence of fossils in the *Alooideae* and the relatively uniform, bimodal karyotype of its members ($x = 7$; one long submetacentric, three long acrocentrics and three short acrocentrics; cf. Brandham & Johnson, 1977; and Brandham, 1983), the branching pattern of evolution in this group was inferred by evaluating character states in extant taxa for their evolutionary significance. Character state polarization was achieved by reference to a chosen outgroup taxon (Maddison & al., 1984) – in this case the genus *Kniphofia*. Monophyly of *Kniphofia* and the genera

Table 3. Phylogenetic character states of the genera *Kniphofia* (Knip), *Aloe* (Aloe), *Astroloba* (Astr), *Chortolirion* (Chor), *Gasteria* (Gast), *Haworthia* (Hawo), *Lomatophyllum* (Loma) and *Poellnitzia* (Poel). Characters are numbered as in Table 2. Hypo = hypothetical ancestor. Character states: 0 = plesiomorphic; 1 = apomorphic; ? = state uncertain, data not available.

	Character number															
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Hypo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Knip	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Aloe	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1
Astr	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Chor	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Gast	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1
Hawo	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Loma	1	1	1	0	1	0	1	1	0	0	0	?	0	0	0	1
Poel	1	0	1	0	1	1	1	1	0	0	0	1	1	0	0	1

of the *Alooideae* is demonstrated by two synapomorphies, namely the tubular perianth (character 7; Table 2) and the fusion of the perianth (character 8; Table 2).

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

Results and discussion

The 16 characters and their states (Table 2) used in the basic data matrix (Table 3) are listed and discussed below. In the present analysis of relationships amongst the genera of *Alooideae*, an attempt is made to combine all available information amenable to phylogenetic interpretation. These data are expressed as a cladogram (Fig. 2). Using the "ie" option of "Hennig86" the data lead to a single, robust cladogram with a consistency index value of 88 and a length of 18 character state changes.

1. Habit. – Subfamily *Alooideae* includes taxa displaying a wide range of habit, from geophytes *(Chortolirion)*, small, highly specialized, rosulate leaf succulents (for example *Aloe* [sect. *Aloe*] subsect. *Humiles* A. Berger, *Astroloba*, *Haworthia*), shrubs (for example shrubby Madagascan *Aloe* species, such as *A. acutissima* Perr.) and climbers (*Aloe* [sect. *Aloe*, subsect. *Prolongatae* A. Berger] ser. *Macrifoliae* Haw.) to small to large trees (for example *Aloe* sect. *Dracoaloe* A. Berger). On the basis of G. W. Reynolds's (1950a, 1966) keys to *Aloe*, Holland (1978) assumed that the arborescent forms of this genus (comprising ca. 13 % of the species) are more advanced than the herbaceous forms. It is noteworthy that Reynolds did not support this point of view as he interpreted *A. suzannae* Decary, the tallest of the Malagasy aloes with a stem length of 3-4 m, as the most primitive (G. W. Reynolds, 1966). Holland's (1978) assumption is also not borne out by cytogenetic data presented by Brandham (1983), who proposes that the species of *Aloe* with a scandent habit and usually relatively mesophytic leaves, such as *A. tenuior* Haw. and *A. ciliaris* Haw. (Hunt, 1978), represent the primitive state. We in large part support the point of view of Brandham (1983) and propose that in the *Alooideae* as a whole, both small, highly succulent taxa and arborescent forms were derived from a mesophytic, comparatively acaulescent taxon.

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

In *Kniphofia* one or two species, such as *K. northiae* Baker, could develop an aerial stem rarely more than 0.5 m long (Roux, 1985). However, the large majority of *Kniphofia* species are acaulescent (Codd, 1968). By reference to *Kniphofia* (the outgroup), *Chortolirion*, which has a short vertical axis bearing slightly fleshy leaf bases, is scored as primitive (a reversal). The variable *Aloe* also has a few bulbous species, for example *A. buettnerri* A. Berger (Jankowitz, 1975) and *A. kniphofioides* Baker (Dyer, 1951). However, more than 90 % of species of *Aloe* develop a stem, even if very short (for example *A. juvenna* Brandham & Carter, 1979). In all other *Alooideae* taxa, notably *Astroloba*, *Haworthia* subg. *Hexangulares* Uitew. ex M. Bayer, *Lomatophyllum* and *Poellnitzia*, caulescent species occur. *Gasteria* has few caulescent species, *G. rawlinsonii* Oberm. and *G. bicolor* Haw. being such exceptions. They form long, leafy stems instead of basal (rosulate or distichous) rosettes (Obermeyer, 1976). It is noteworthy that the tree or shrub habit has also evolved independently in other monocotyledonous taxa, such as *Yucca* L. in the *Agavaceae* (Dahlgren & Clifford, 1982).

While it might be expected that secondary thickening will be linked to plant habit, these characters are not perfectly correlated in the subfamily *Alooideae*. Thus, Coetzee & Van der Schijff (1969) have shown that geophytic asphodelaceous taxa, such as *Chortolirion stenophyllum* (Baker) A. Berger, *Bulbine coetzeei* Oberm. and *Trachyandra saltii* (Baker) Oberm., all exhibit secondary thickening which is, however, much less pronounced in these taxa than in the well-known arborescent taxa, for example in *Aloe* (G. W. Reynolds, 1950b; Cutter, 1971; Esau, 1977; Jankowitz, 1985; Rebelo & al., 1989). Secondary thickening also occurs in *Kniphofia* (Dahlgren & al., 1985). As in the case of the development of the arborescent habit, the faculty of secondary thickening probably evolved independently a number of times in several distinct monocotyledonous families, such as *Asphodelaceae* (Dahlgren & Rasmussen, 1983), *Iridaceae* (Rudall, 1984, 1989; Manning & al., 1990) and *Dracaenaceae* (Dahlgren & al., 1985.). Its distribution in the *Alooideae* is insufficiently known to allow this character to be used as a generic synapomorphy.

2. Leaf arrangement. – In general the dorsiventral leaves of most taxa of *Alooideae* are strongly tufted in terminal (arborescent species) or basal rosettes. The non-succulent leaves of *Kniphofia* are usually densely congested in basal rosettes and arranged in distinct ranks. Furthermore, with the exception of *Aloe* and *Lomatophyllum*, the leaves of most *Alooideae* taxa are closely compressed, whether arranged on a leafy stem or in a basal rosette. Both *Aloe* and *Lomatophyllum* have species in which the leaves are comparatively widely spaced. Window-leaved species (Schönland, 1910a, b; Hutchison, 1951; Rauh, 1974; Krulik, 1980; Cutler, 1985) occur in only a few species of *Haworthia* and are consequently uninformative of generic relationships. Similarly, a neotenic retention of distichous leaf arrangement has evolved in isolated species in both *Aloe* and *Gasteria* (Takhtajan, 1976; Rauh, 1977).

3. Leaf consistency. – The *Alooideae* are wholly composed of leaf succulents. The succulent leaves of *Alooideae* taxa represent a character specialization hypothesized to have evolved in response to aridity in combination with fire (Laubscher, 1973a; Thomas & Goodson, 1986; Scholes, 1988; Weisser & Deall, 1989; but see Bond, 1983 on *Aloe ferox* Miller, and Van Jaarsveld, 1987 on *A. plicatilis* (L.) Miller) and other environmental variables such as high levels of irradiance (Pearson, 1914; Lewis & Nobel, 1977; Eller & al., 1983; Larcher, 1983; Cutler, 1985; Nobel, 1989).

Some taxa of *Alooideae* which occur in (often high rainfall) grasslands, notably *Aloe* sect. *Graminialoe* G. Reyn. and *Aloe* sect. *Leptoaloe* A. Berger (Laubscher, 1973a, b), and *Chortolirion*, seem to have reverted to a less succulent leaf consistency. Most of these species have contractile roots and tend to be geophytic.

4. Leaf tuberculation. – The presence of distinctive, white or concolorous tubercles on the leaves of some species of *Astroloba*, *Gasteria* and *Haworthia* is hypothesized to be a derived condition. The rare occurrence of this character in *Aloe* (for example *A. aristata* Haw.) is here considered to be a parallel development. This character may have evolved in response to herbivore pressure. Especially *Gasteria* leaves are sought after by herbivores (Van Jaarsveld, 1989), since they lack the bitter constituent found in leaves of species of *Aloe* (Watt & Breyer-Brandwijk, 1962). The presence of conspicuous, rigid tubercles, often confluent in bands, probably makes leaves less palatable and may represent a form of mechanical defence. In species of *Gasteria* the leaf tubercles are most prominent in the juvenile condition, the leaves of mature specimens often being smooth, for example in *G. acinacifolia* (Jacq.) Haw. In such cases the leaves of mature specimens are usually copiously spotted, perhaps as a camouflage against herbivores. Secondly, similar to the reflective function of a surface layer of wax particles or hairs, which can increase reflectance from leaves of the leaf succulent *Cotyledon orbiculata* L. by 22 % (visible spectrum) and 12 % (infrared spectrum) (Sinclair & Thomas, 1970), tubercles may be an adaptation to prevent irradiation and heat damage to underlying tissues. It is noteworthy that leaf tuberculation is a dominant character, as evidenced by first filial crosses between the smooth-leaved *Haworthia cymbiformis* (Haw.) Duval and a species with prominent leaf tubercles, *H. attenuata* Haw. The absence of leaf tubercles in *Chortolirion* and some species of *Haworthia* is here considered to be a reversal.

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

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

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

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

Although the flowers of both *Gasteria* and *Poellnitzia* are also brightly coloured, the racemes of these taxa are not nearly as dense as those of most species of *Aloe* and *Kniphofia*. The flowers of species of *Astroloba, Chortolirion* and *Haworthia* are usually fairly inconspicuous and laxly dispersed in a wiry raceme. This appears to be an adaptation to a specialized pollination syndrome and is hypothesized to be the apomorphic condition.

7. *Flower shape.* – Variations in flower structure of the various *Alooideae* genera are shown in Fig. 1. Even though a few distinct trends in floral structure are evident in the *Alooideae* (for example towards zygomorphy in *Chortolirion, Gasteria* and *Haworthia*; see also Rowley, 1967b, on *Bulbine*), the flowers of all taxa of *Alooideae* and *Kniphofia* are tubular. The tubular perianth is an excellent reservoir for the copious amounts of nectar that the flowers of most species produce. Furthermore, the desiccating perianth tube serves to guide nectar from the ovary towards the apex where it accumulates in a glistening droplet. This usually coincides with the ripening of the stigma of the protandric flowers and serves as an additional attractant to potential anemophilous pollinators (Mottram, 1977; Van Jaarsveld, 1987).

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

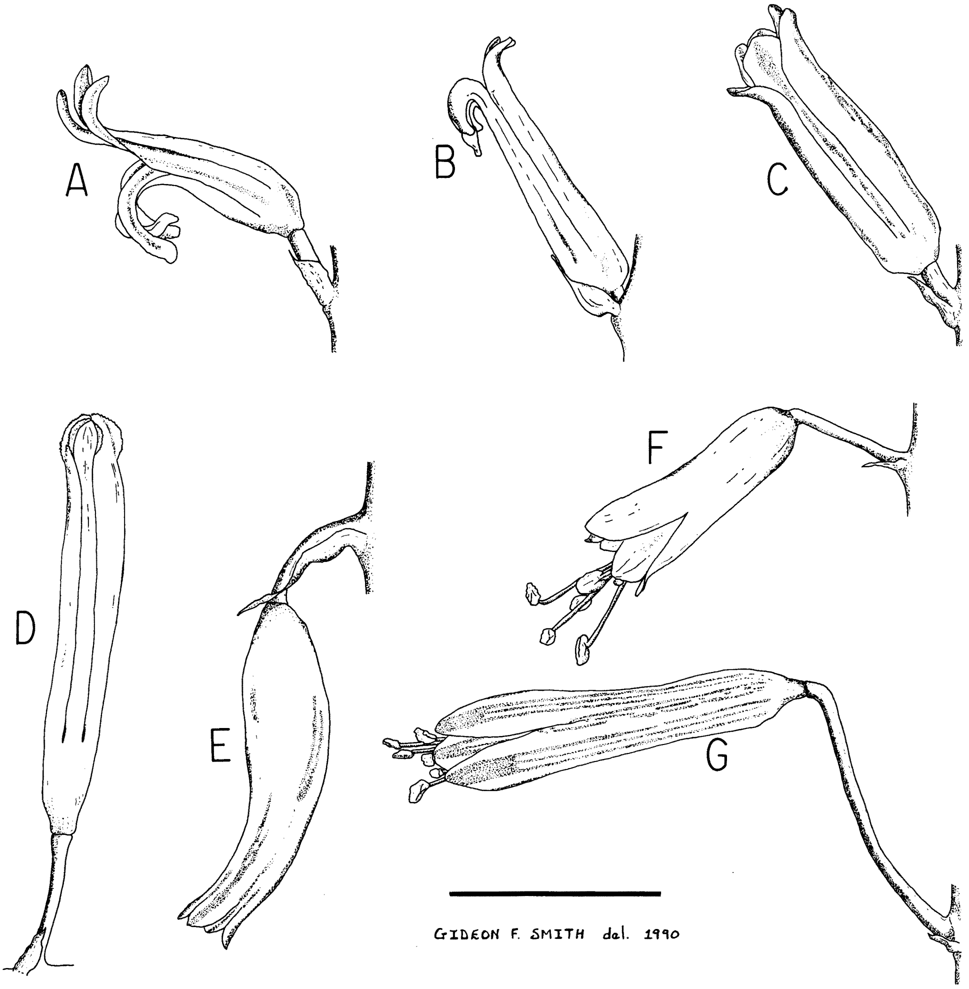

Fig. 1. Flowers from one representative of each of the genera *Aloe*, *Astroloba*, *Chortolirion*, *Gasteria*, *Haworthia*, *Lomatophyllum* and *Poellnitzia*, as seen in lateral view. With the exception of *Chortolirion* and *Poellnitzia* there is considerable intrageneric variation in the size, shape and disposition of individual flowers. Some variants have in the past been split off as monotypic genera (e.g, *Chamaealoe* and *Guillauminia* from *Aloe*). The basic perigon structure is, however, fairly constant within genera and is of taxonomic value at generic level. A, *Haworthia gracilis* Poelln.; B, *Chortolirion angolense* (Baker) A. Berger; C, *Astroloba foliolosa* (Haw.) Uitew.; D, *Poellnitzia rubriflora* (L. Bolus) Uitew.; E, *Gasteria pulchra* (Haw.) Haw.; F, *Aloe tenuior* Haw. var. *rubriflora* G. Reyn.; G, *Lomatophyllum* cf. *purpureum* (Lam.) T. Durand. All drawings were made from live material. Scale bar = 5 mm.

synapomorphy for these taxa and suggests a close phylogenetic affinity amongst them.

8. Fusion of perianth segments. – The fusion of the petaline tepals is the second character shared by *Kniphofia* and the *Alooideae* which suggests monophyly. However, this character varies considerably, even within a single genus. In some species of *Aloe*, for example *A. pictifolia* Hardy (1976), the perigon segments are free to the base whereas in other taxa fusion extends almost to the tips of the flowers (*Aloe* ser. *Macrifoliae* Haw.). Yet other species of *Aloe* (for example *A. albiflora* Guillaumin from Madagascar) are characterised by the absence of a distinct perianth-tube (Mathew, 1974). Although the basic morphology of the flowers of species of *Alooideae* is very simple and fairly constant, the occurrence of a number of aberrant floral morphologies have previously led to the splitting off of monotypic genera from especially *Aloe* (*Aloinella* Lemée non Cardot, *Guillauminia* A. Bertrand, *Chamaealoe* A. Berger). However, all these genera are currently included in *Aloe*.

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

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

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

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

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

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

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

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

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

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

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

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

14 and 15. Nectar sugars. – Individual flowers of most taxa of *Kniphofia* and *Alooideae* are nectariferous and last from one to several days. In the subfamily nectar secretion occurs by means of septal nectaries (Schnepf & Pross, 1976). Flower size is correlated with nectar volume, the large-flowered species of *Aloe* producing nectar in much larger quantities than representatives of, for example, *Chortolirion* and *Haworthia* (cf. Beyleveld, 1973, on selected species of *Aloe* ser. *Saponariae*; and Mottram, 1977, Fox & Norwood Young, 1988, and Hoffman, 1988, on *A. ferox*).

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

16. Basic chromosome number. – The majority of species of *Alooideae* has been investigated cytologically. These studies were initiated early in the 20th century (cf. Taylor, 1925) and have resulted in an extensive bibliography on the cytology of this group (for reviews see Muller, 1941; Riley, 1959a, b, c; Brandham, 1971, 1983; Riley & Majumdar, 1979). The *Alooideae* are one of the most uniform groups as regards chromosome number and the markedly bimodal karyotype. All species have the same basic chromosome number ($x = 7$), with four long and three short chromosomes. In the entire subfamily the basic diploid karyotype ($2n = 14$) is only very rarely altered (Brandham, 1969). This character represents a synapomorphy for all the taxa of *Alooideae*. A large number of intra- and intergeneric hybrids have been produced in the *Alooideae* (Rowley, 1982). This clearly testifies to the close cytogenetical relationship which exists amongst species of the subfamily (Rollins, 1953).

Based on overall genome size and increased bimodality, Brandham (1983) has shown that, at least in *Aloe*, there is a gradation from smaller chromosomes in species which have retained a number of plesiomorphic characters (*A. tenuior*: actinomorphic flowers; weak scandent stems; mesophytic) to larger ones in species with morphological apomorphies (*A. peckii* Bally & I. Verd.: stemless; extreme xerophyte).

In contrast to the *Alooideae*, *Kniphofia* has a basic set of six chromosomes ($2n = 12$). This represents a sharp discontinuity between the two taxa and suggests a distinct barrier to gene interchange (De Wet, 1960). With reference to the outgroup, *Kniphofia*, the basic chromosome set of $x = 7$ is scored as apomorphic.

Phylogenetic implications. – No attempt at cladistic analyses of the *Alooideae* has previously been made and the results of phenetic analyses are inconclusive (see our introduction for references). The subfamily *Alooideae* as a whole is proposed to be monophyletic on the basis of the distinctive karyotype and the characteristic leaf morphology. In this regard *Bulbine* (subfam. *Asphodeloideae*) appears to be problematical, since some of its species have karyotypes and morphologies similar to that of certain taxa of *Alooideae* (cf. Spies & Hardy, 1983, on *B. latifolia* (L. f.) Schultes & Schultes f.; and Rowley, 1954, on *Bulbine* in general). Our exclusion of *Bulbine* from the *Alooideae* is based on the non-tubular and usually uniformly yellow flowers

(Trager, 1984), free tepals, and lack of nectar production, suggesting that the similarities with *Alooideae* are non-homologous.

In contrast to the *Alooideae*, leaf succulence is absent in *Kniphofia*, the leaf outline in transverse section is V-shaped (not crescent-shaped or cymbiform), and the basic chromosome number is $x = 6$ (not $x = 7$). We regard the tubular flowers and fusion of the perianth segments as sufficient evidence to justify the choice of *Kniphofia* as outgroup for the *Alooideae*. *Kniphofia* has been separated from the *Alooideae* on the basis of, amongst others, differences in the anatomical construction of the leaves (Baijnath, 1980; Dahlgren & al., 1985). Typically the vascular bundles of taxa of *Alooideae* sensu Dahlgren & al. (1985) have a well-developed cap of thin-walled parenchyma cells at the phloem pole. These are often referred to as aloin cells. In contrast, *Kniphofia* has well-defined fibres present in a cap at both the xylem and phloem poles (Beaumont & al., 1985). The presence of aloin cells varies considerably within and amongst taxa (and sometimes even within a leaf of a single provenance) of the

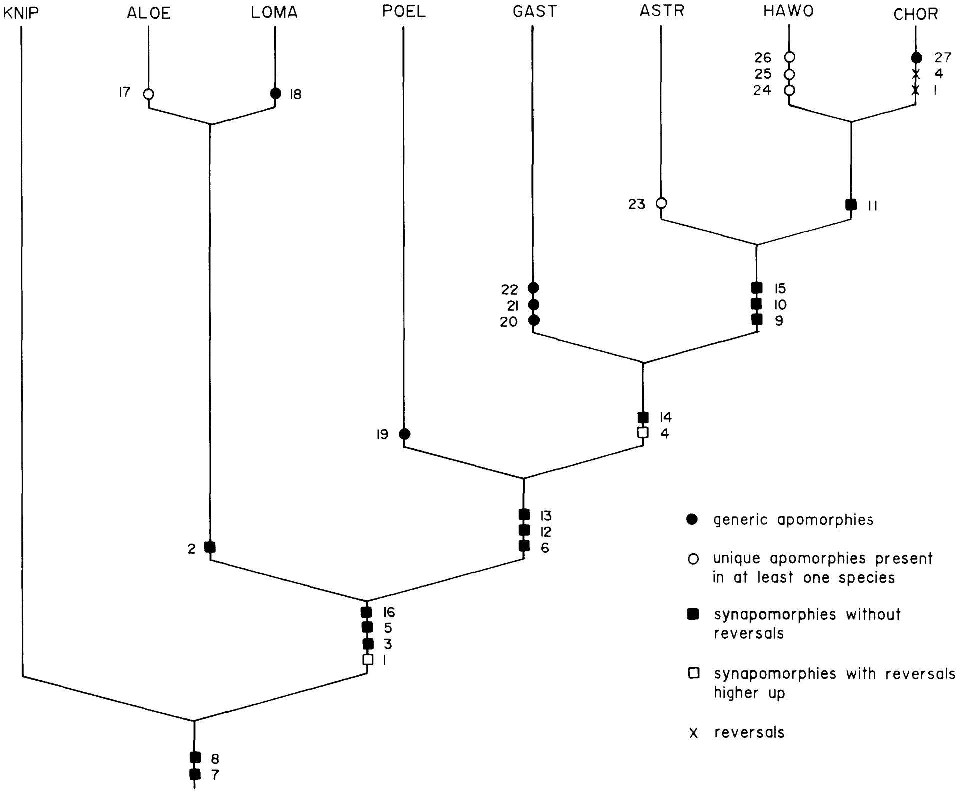

Fig. 2. Cladogram of hypothetical phylogenetic relationships among the genera *Aloe, Astroloba, Chortolirion, Gasteria, Haworthia, Kniphofia, Lomatophyllum* and *Poellnitzia*. Numbers 1-16 refer to characters given in Table 2. Character states and character polarization for the genera are listed in Table 3. Genera are labelled with the first four letters of their names (see Table 3). Generic apomorphies and unique apomorphies present in at least one species of a genus are: 17, flowers tomentose; 18, fruit baccate; 19, tips of perianth segments connivent; 20, pedicels pendulous at anthesis; 21, perianth curved upwards; 22, perianth basally gasteriform; 23, perianth with inflated tissue; 24, leaf tips retuse; 25, leaves with windows; 26, perianth curved downwards; 27, capsule acuminate.

Alooideae, and this character is not readily amenable for phylogenetic interpretation. However, the conclusion of Beaumont et al. (1985) that the parenchymatous condition (presence of thin-walled cells rather than schlerenchyma) is derived corroborates our choice of *Kniphofia* as outgroup for the *Alooideae*.

In the cladogram (Fig. 2) *Aloe* and *Lomatophyllum* are shown as basal to the rest of the subfamily. In contrast, *Astroloba*, *Chortolirio*n and *Haworthia* are the most derived genera, with *Gasteria* and *Poellnitzia* in an intermediate position. The *Alooideae* line is defined by four apomorphies, one of which (caulescent habit) has a reversal higher up *(Chortolirion)*. The controversy that has surrounded generic delimitation in the *Alooideae* is reflected by the lack of autapomorphies for some of the genera upheld in this study. Only *Gasteria* (three distinct apomorphies), *Chortolirion*, *Lomatophyllum* and *Poellnitzia* (one distinct apomorphy each) are reasonably well defined. However, it is noteworthy that three of these genera, *Chor-*

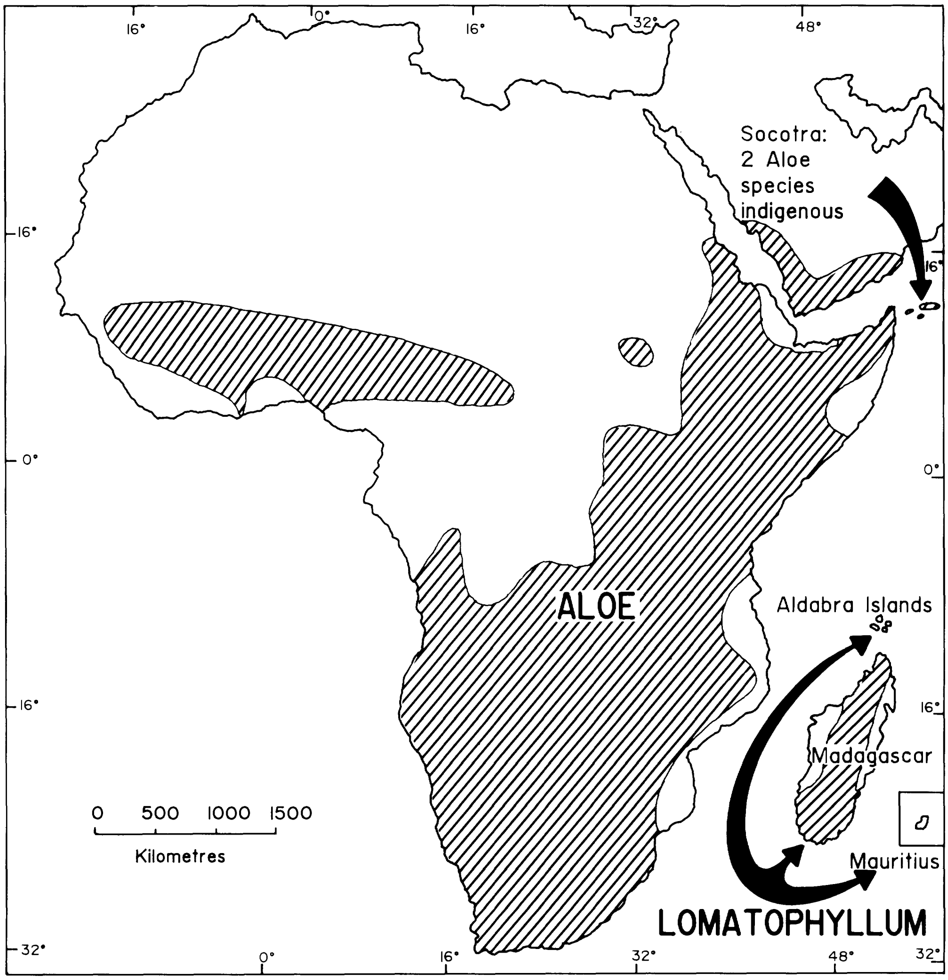

Fig. 3. Approximate geographical distribution of the genera *Aloe* and *Lomatophyllum* (information for *Aloe* from G. W. Reynolds, 1950a, 1966; Lavranos, 1969; Holland, 1978; and Wood, 1983; and for *Lomatophyllum* from Jacobsen, 1986).

tolirion, Lomatophyllum and *Poellnitzia*, are notorious for taxonomic confusion. In the past they have been variously combined with and separated from *Aloe*, *Astroloba* and *Haworthia*. Reverting to a Duvalian concept of alooid classification in which only three "supergenera", *Aloe, Gasteria* and *Haworthia*, are recognized would be inconsistent with our result. Inclusion of *Astroloba* and *Chortolirion* in *Haworthia* would, however, furnish the genus with at least two apomorphies (characters 11 and 15), and would therefore improve generic delimitations within the subfamily. There is no convincing evidence that *Haworthia* sensu stricto is monophyletic, and the eventual broadening of the generic concept seems unavoidable. Similarly, the present generic concept of *Aloe* is open to speculation. Our result highlights a major weakness in the present system – that *Aloe* and *Haworthia* may not be monophyletic. Future studies should address this basic problem.

Geographical considerations. – The approximate geographical distributions of *Aloe, Astroloba, Chortolirion, Gasteria, Haworthia, Lomatophyllum* and *Poellnitzia* are shown in Fig. 3-7. *Aloe* occurs over much of sub-Saharan Africa, ranging from the southern tip of Africa to west and northeast Africa and the Arabian Peninsula. It is also found on Madagascar and Socotra. The distribution of *Kniphofia* is also mainly palaeotropical (Sudano-Angolan and Namib-Karroo regions of the African subkingdom, Palaeotropical kingdom, sensu Takhtajan, 1969) and largely overlaps with that of *Aloe*, but the genus is absent from Socotra, Namibia and Botswana (Codd, 1968). The species of *Kniphofia* seem to favour moist habitats and are found mainly along the mountain ranges. In contrast *Aloe* is ecologically heterogeneous within its range of distribution and has diversified into almost every possible habitat, ranging from deserts, grassland and savanna to comparatively high-rainfall coastal forest types. In terms of number of species both *Aloe* and *Kniphofia* are presently concentrated in southern Africa. The fleshy-fruited *Lomatophyllum* is restricted to a few of the Mascarene Islands off the south-east coast of Africa.

The distribution patterns of *Astroloba*, *Gasteria* and *Haworthia* are fairly similar. These three genera are endemic to southern Africa and are more or less restricted to the summer-dry, semi-arid coastal regions below the inland escarpment of the subcontinent. *Gasteria* and *Haworthia* have outliers in the arid river valleys of Natal, Swaziland and the eastern Transvaal, with a single taxon of *Haworthia*, *H. venosa* subsp. *tessellata* (Haw.) M. Bayer, occurring in the climatically severe central-southern Africa. The distribution of *Astroloba* is more restricted than those of *Gasteria* and *Haworthia*, and it is usually found in slightly more arid environments of the fynbos and succulent karoo biomes of southern Africa. These three genera and *Aloe* have relatively large numbers of species indigenous and endemic to the arid subtropical transitional thickets of the eastern Cape where they show signs of active speciation (see Court, 1981; Smith & Marx, 1990; and references therein).

Of the genera of *Alooideae*, the monotypic *Poellnitzia* has the most restricted distribution. This genus is found only in the Robertson and Bonnievale districts of the south-western Cape Province. In contrast, the other monotypic genus, *Chortolirion*, is widely distributed in the summer-rainfall grasslands of southern Africa. The genus does, however, enter the winter-rainfall region in southern Namibia.

The distribution pattern of the *Alooideae* suggests three major components: Africa, Madagascar and associated islands, and southern Africa. As shown in Fig. 8, there is some evidence of vicariance in the phytogeographical history of the subfamily. Two major events are indicated, even though the effects seem to have been partly

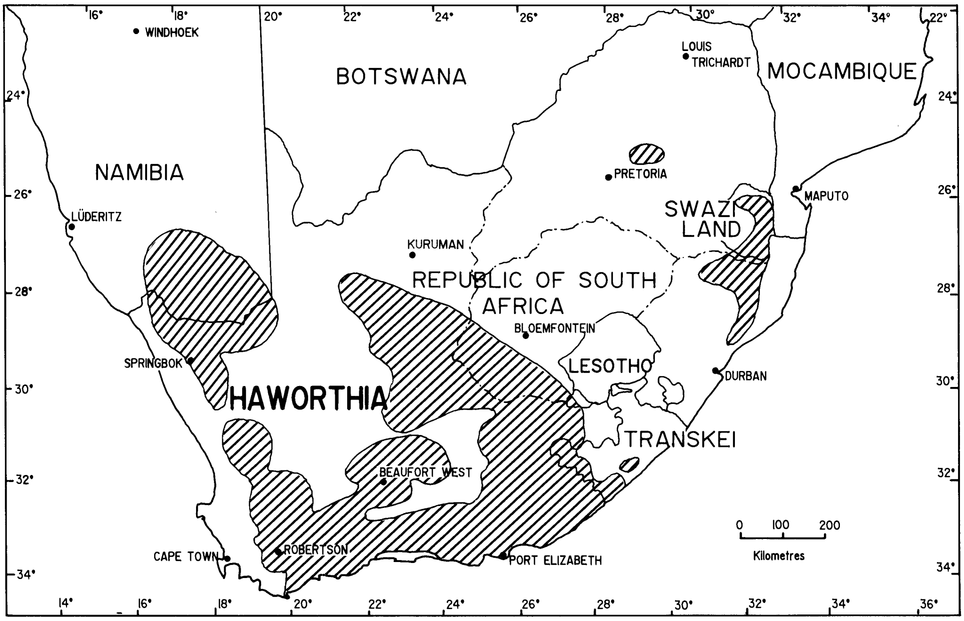

Fig. 4. Approximate geographical distribution of the genus *Haworthia* (information from Pilbeam, 1983; but see Bayer, 1986).

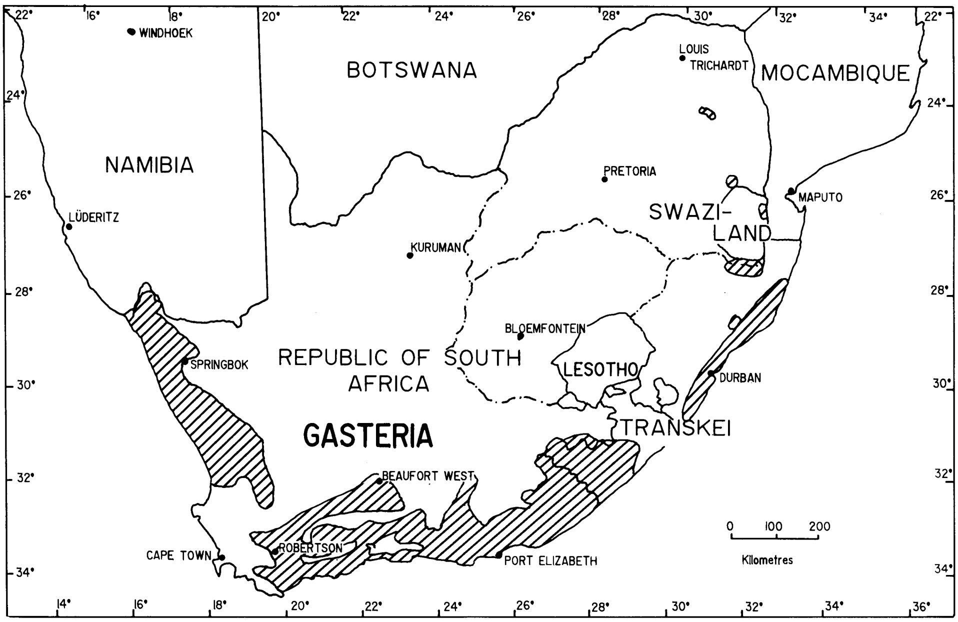

Fig. 5. Approximate geographical distribution of the genus *Gasteria* (information from Van Jaarsveld, 1989).

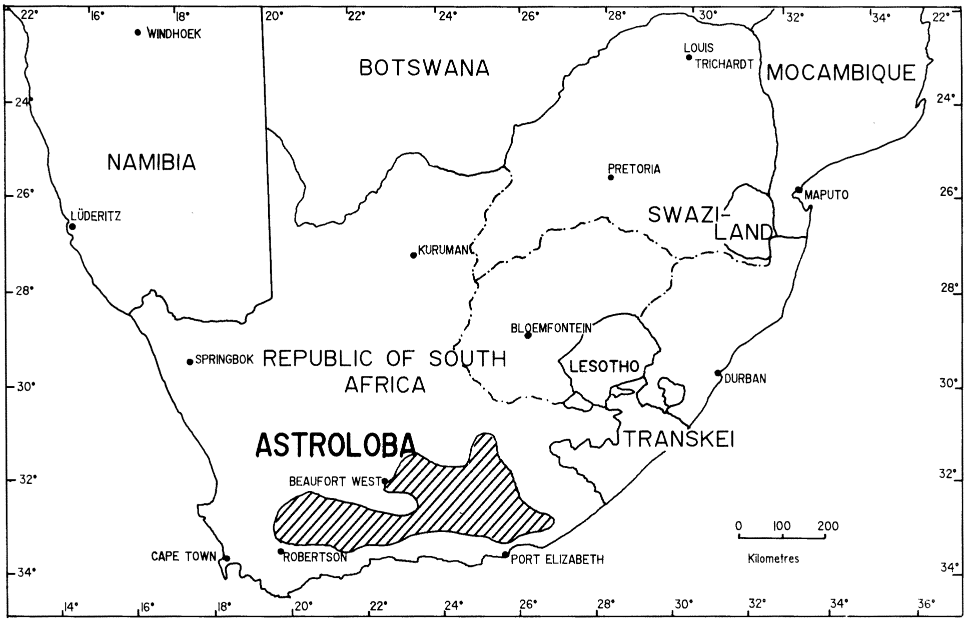

Fig. 6. Approximate geographical distribution of the genus *Astroloba* (information from Roberts Reinecke, 1965).

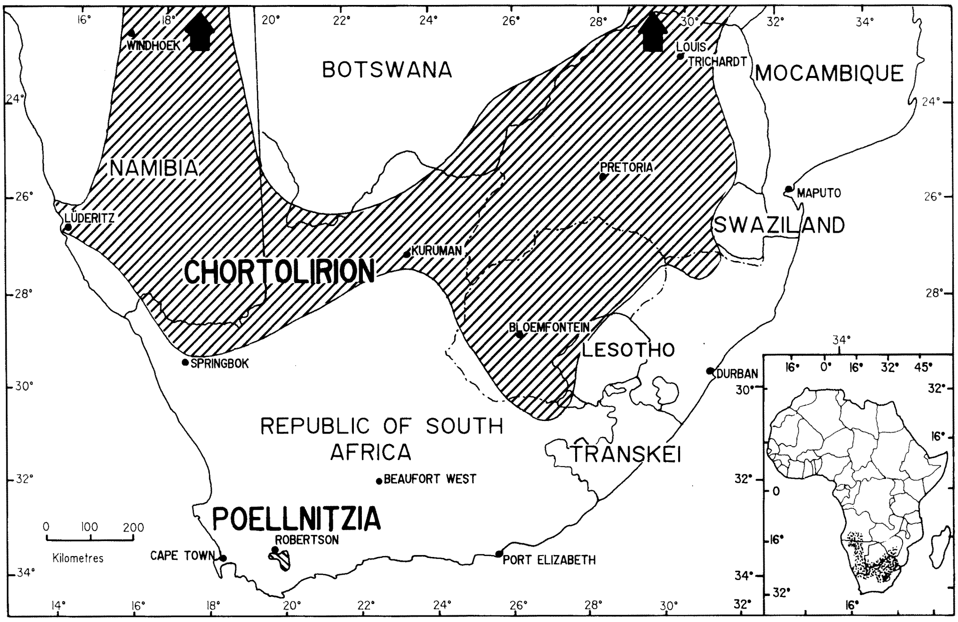

Fig. 7. Approximate geographical distribution of the genera *Chortolirion* and *Poellnitzia* (information for both genera from Smith,1985). It is not unlikely that *Chortolirion* occurs further north in Botswana and further south in Natal. When not in flower its likeness to a small tufted grass is remarkable and it could easily go undetected.

obscured by subsequent events: (1) the separation of Madagascar from the African mainland (mid-Cretaceous, c. 100 million years before present; cf. Flores, 1970, and McElhinny & al., 1976); (2) the separation of southern Africa from the rest of Africa, possibly as a result of aridification which commenced during the Oligocene (c. 38-26 million years before present) and continued through the Miocene and Pliocene (c. 26-7 and 7-2 million years before present, respectively) (Goldblatt, 1978; Deacon, 1983; Raven 1983; Van Jaarsveld, 1987). The present-day distributions of the genera are uninformative with respect to the sequence of these events, i.e., whether the separation of southern Africa occurred before or after the separation of Madagascar.

Conclusion

Available evidence suggests only one obvious generic phylogeny for the *Alooideae.* It is clear from our result that the inclusion of *Lomatophyllum* in *Aloe* and the inclusion of *Chortolirion* and *Astroloba* in *Haworthia* can be justified, but that there can be little doubt about the generic status of *Poellnitzia.* We suggest, however, that the generic concepts as used in this study be retained until detailed taxonomic revisions of, particularly, *Aloe, Haworthia* and *Lomatophyllum* becomes available.

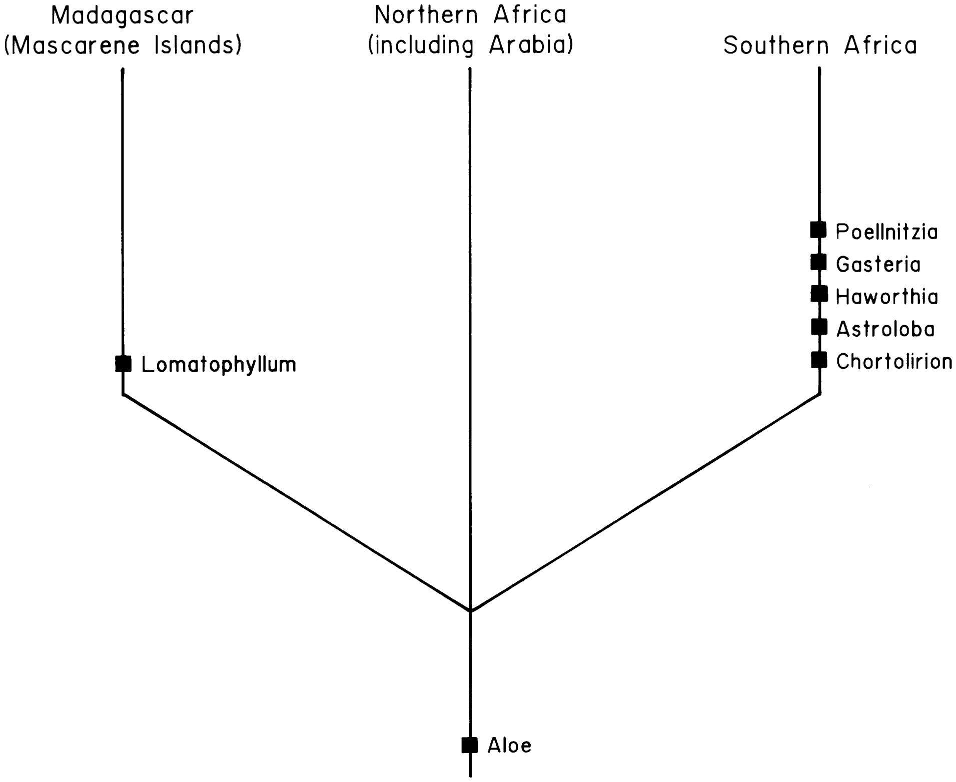

Fig. 8. Unresolved area cladogram for the subfamily *Alooideae*, showing three major components. The generic phylogeny in Fig. 2 is uninformative about the sequence of the two main events, i.e. the separation of Madagascar from Africa and the separation of southern Africa from the rest of the continent.

Similarly, the transfer of *Kniphofia* to the *Alooideae* seems premature at this stage, because only an analysis of the family as a whole could demonstrate whether such a transfer is the most parsimonious solution. The broad conceptual approach taken in this study has nevertheless provided some clarity on the infrasubfamilial phylogeny of the *Alooideae*.

The following key should serve to distinguish amongst *Kniphofia* (outgroup) and genera of the *Alooideae* recognized in this study.

1. Leaves herbaceous, soft, non-succulent, immaculate, lacking distinct spines, in basal rosettes (apical in *Kniphofia northiae* Baker) .... *Kniphofia*
1. Leaves thick, rigid, succulent, maculate, often margined with prickly teeth, in basal or apical rosettes, or cauline 2
2. Fruit a berry .... *Lomatophyllum*
2. Fruit a capsule 3
3. Capsule apically acuminate, underground parts bulbous, flowers usually < 15 mm long, zygomorphic .... *Chortolirion*
3. Capsule apically rounded or obtuse, underground parts rhizomatous (if rarely bulbous then flowers > 15 mm long, actinomorphic) 4
4. Perianth segments apically connivent .... *Poellnitzia*
4. Perianth segments apically spreading or recurved 5
5. Flowers pendulous at anthesis, perianth tube curved upwards .... *Gasteria*
5. Flowers erect, suberect or spreading at anthesis, perianth tube straight or curved downwards 6
6. Perianth bilabiate, < 15 mm long, mouth not upturned .... *Haworthia*
6. Perianth regular (if rarely weakly bilabiate then flowers > 15 mm long, mouth upturned) 7
7. Flowers usually brightly coloured, fleshy, stamens as long as or longer than the perianth .... *Aloe*
7. Flowers dull-coloured, flimsy, stamens included .... *Astroloba*

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