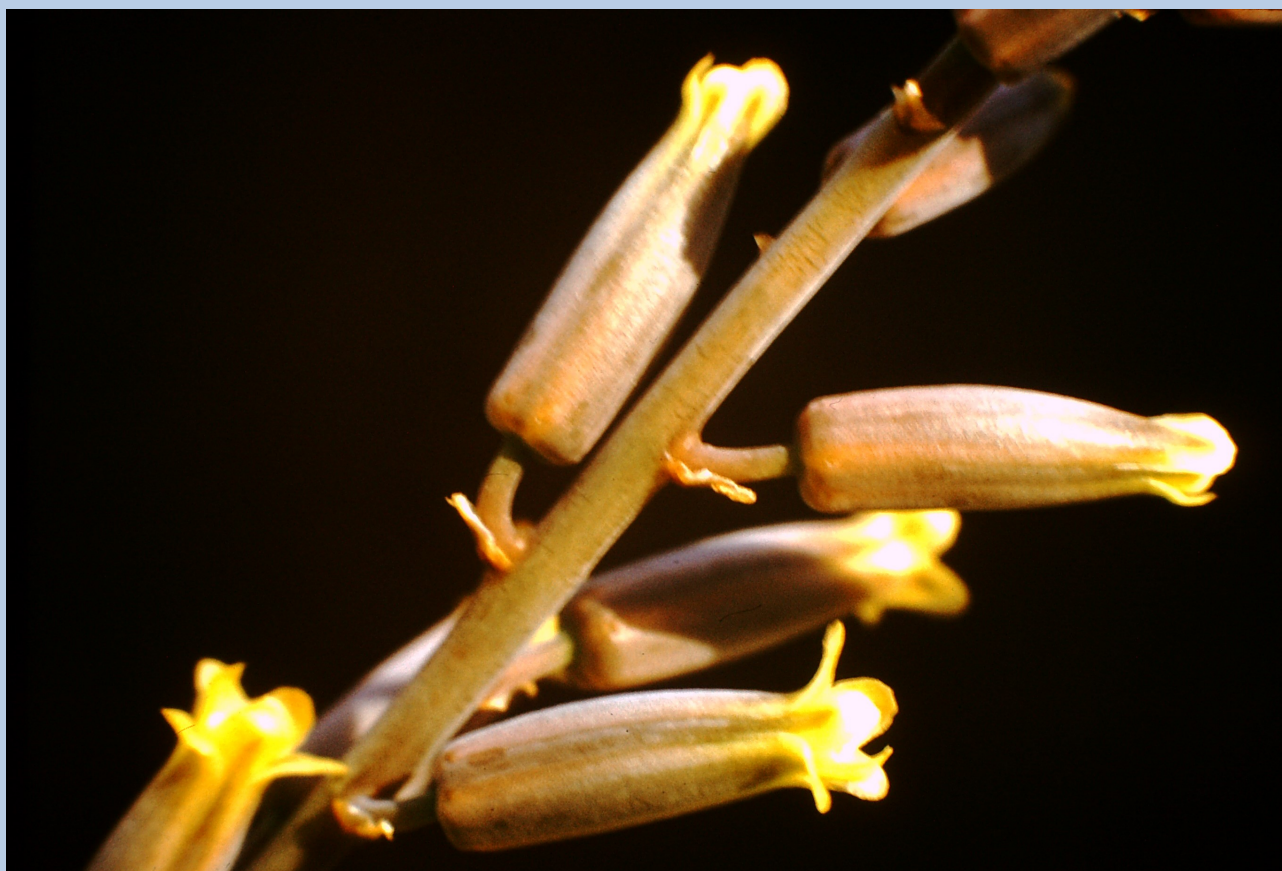


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Tulista bullulata flowers. Photo Rowley.

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ASTROLOBA Uitewaal: INFERRED RELATIONSHIPS FROM EXTENSIVE HYBRIDIZATION

David M Cumming

Keywords: Relatedness, intergeneric hybridization, *Astroloba*, *Aloe*, *Gasteria*, *Haworthia*, *Poellnitzia*.

Abstract

Intergeneric hybrids within **Aloaceae** have been achieved with most genera (Cumming 1999a, 2005, 2006), a few have been recorded with *Astroloba*. The following experiments were compiled from notes on hybridizations carried out over a period in excess of thirty years and explore relatedness between *Astroloba* and the other genera. Due to the almost unique situation found in Aloaceae concerning the ease of genesis of interspecific and intergeneric hybrids it is thought that where barriers are present, that these should be treated as of taxonomic worth in this specific case.

Introduction: *Astroloba* Uitewaal, from Greek, 'aster, astros' star and 'lobos', lobe for the stellately spreading perianth lobes. Thirteen species were listed (Jacobsen 1960), reduced later to eleven (Jacobsen 1974) this has since been reduced to six (Meyer & Smith 2001) pending a new revision being undertaken by N.L.Meyer. The genus has been revised in an unpublished thesis by Roberts Reinecke in 1965, the most recent revision being by Groen (1986, 1987). *Astroloba* has also been incorporated within *Haworthia* by various authors, (Parr 1971) (Hayashi 2004).

Astroloba is to be found in the Western Cape and Eastern Cape provinces of South Africa. Records show the following **X** *Aloloba* G.D.Rowley (1967) for *Aloe* **X** *Astroloba*, see Rowley (1982) for a list of hybrids, **X** *Astroworthia* G.D.Rowley (1967), for *Astroloba* **x** *Haworthia*, one natural occurring hybrid is listed, **X** *A. bicarinata*, *Astroloba corrugata* **x** *Haworthia maxima*. It is noted that many plants in cultivation under this name do not appear to have *A. corrugata* as one of their parents. **X** *Gastroloba* D.M. Cumming (1974), for *Astroloba* **x** *Gasteria*, **X** *Maysara* D.M. Cumming (1999) for a trigeneric cross *Astroloba* **x** (*Gasteria* **x** *Haworthia*).

Methods & Materials: these were previously discussed, (Cumming 2005). However the plants used and not previously listed (Cumming 2006), were as follows:-

Aloe rauhii Reynolds, *A millotii* Reynolds, *A. thompsonii* Groenewald, *A. sladeniana* Pole-Evans, *A. (millotii x bellatula* Reynolds) **x** *haworthioides* Baker, *A. haworthioides* **x** *descoingsii* Reynolds, *G* 'Little Warty', *G*. 'Old Man Silver', *G*. 'Big Brother', *G*. hybrid as 'sulcata' were all from horticulture. *Aloe calcairophylla* Reynolds I.S.I 789, *Gasteria carinata* v. *verrucosa* (Miller) van Jaarsveld, DMC 4234 Mudlark.

Table 1 <i>ASTROLOBA congesta</i> x <i>ALOE</i>										
Pollen	Pod Parent									
		1	2	3	4	5	6	7	8	9
<i>Astroloba congesta</i>	1		0/6	0/10	0/5	0/5	0/10	0/6	0/10	0/9
<i>Aloe rauhii</i>	2	1/5		X	X	X	X	X	X	X
<i>Aloe jucunda</i>	3	2/6	X		X	X	X	X	X	X
<i>Aloe variegata</i>	4	2/6	X	X		X	X	X	X	X
<i>Aloe calcairophylla</i>	5	5/10	X	X	X		X	X	X	X
<i>Aloe millotii</i>	6	3/9	X	X	X	X		X	X	X
<i>Aloe descoingsii</i>	7	3/8	X	X	X	X	X		X	X
<i>Aloe thompsonii</i>	8	2/5	X	X	X	X	X	X		X
<i>Aloe jacksonii</i>	9	3/8	X	X	X	X	X	X	X	

Results: 5/10 denotes five successful attempts out of 10 attempts. Wherever possible 10 attempts were made to achieve any one cross with three flowers being used on any

one day, pollinations taking place in the morning and in the late afternoon.

Table 2 <i>ASTROLOBA herrei</i> x <i>ALOE</i>										
Pollen	Pod Parent									
		1	2	3	4	5	6	7	8	9
<i>Astroloba herrei</i>	1		0/4	0/5	0/5	0/5	0/7	0/5	0/10	0/5
<i>Aloe calcaireophylla</i>	2	4/6		X	X	X	X	X	X	X
<i>Aloe jucunda</i>	3	5/10	X		X	X	X	X	X	X
<i>Aloe bellatula</i>	4	2/6	X	X		X	X	X	X	X
<i>Aloe descoingsii</i>	5	3/10	X	X	X		X	X	X	X
<i>Aloe rauhii</i>	6	2/6	X	X	X	X		X	X	X
<i>Aloe thompsonii</i>	7	4/10	X	X	X	X	X		X	X
<i>Aloe variegata</i>	8	1/3	X	X	X	X	X	X		X
<i>Aloe jacksonii</i>	9	2/10	X	X	X	X	X	X	X	

Table 3 X <i>ASTROWORTHIA</i> & various <i>ASTROLOBA</i> x <i>ALOE</i>										
Pollen	Pod Parent									
		1	2	3	4	5	6	7	8	9
<i>Astroloba spiralis</i>	1		X	X	0/5	X	0/5	0/4	0/5	X
<i>Astroloba foliosa</i>	2	X		X	0/5	0/5	0/8	X	0/5	X
X <i>Alsterworthia</i> (B)*	3	X	X		X	0/6	0/5	X	0/1	0/2
<i>Aloe descoingsii</i>	4	3/8	0/10	X		X	X	X	X	X
<i>Aloe (millotii</i> x <i>bellatula</i>) x <i>haworthioides</i>	5	X	2/6	4/10	X		X	X	X	X
<i>Aloe haworthioides</i> X <i>descoingsii</i>	6	1/5	4/10	5/9	X	X		X	X	X
<i>Aloe sladeniana</i>	7	4/8	X	X	X	X	X		X	X
<i>Aloe bellatula</i>	8	4/10	2/5	3/7	X	X	X	X		X
<i>Aloe jucunda</i>	9	X	X	1/5	X	X	X	X	X	

Table one, two & three.

These represent a selected sample that demonstrate the pattern of this cross, many others were achieved, see listing of 'named' crosses. This cross is relatively easy to achieve, under suitable conditions, seed being set on the species/genus with the shortest style, in this case the

genus *Astroloba*. Compare these to those results achieved with the sub genera of (Cumming 2006 in prep). (unfortunately this was not completed at that time, look to Cumming 2015)

Table 4. *X ALOLOBA* Cultivar names assigned to plants distributed in Australia, prior to 1994

Parentage		Cultivar name given
<i>Astroloba herrei</i>	x <i>Aloe calcairophylla</i>	'Ardillo'
<i>Astroloba herrei</i>	x <i>Aloe jucunda</i>	'Bram'
<i>Astroloba congesta</i>	x <i>Aloe variegata</i>	'Chunky'
<i>X Astroworthia</i> (B)	x <i>Aloe</i> (<i>millotii</i> x <i>bellatula</i>) <i>X haworthioides</i>	'Cledwyn'
<i>Astroloba spiralis</i>	x <i>Aloe descoingsii</i>	'Creon'
<i>Astroloba congesta</i>	x <i>Aloe descoingsii</i>	'Deen'
<i>X Astroworthia</i> (B)	x <i>Aloe</i> (<i>millotii</i> x <i>bellatula</i>) <i>X haworthioides</i>	'Dovel'
<i>Astroloba congesta</i>	x <i>Aloe jacksonii</i>	'Dyani'
<i>Astroloba congesta</i>	x <i>Aloe thompsonii</i>	'Ilde'
<i>Astroloba congesta</i>	x <i>Aloe rauhii</i>	'Jelena'
<i>Astroloba herrei</i>	x <i>Aloe bellatula</i>	'Jofrid'
<i>Astroloba spiralis</i>	x <i>Aloe sladeniana</i>	'Leo'
<i>Astroloba congesta</i>	x <i>Aloe sp.</i>	'Nicol'
<i>X Astroworthia</i>	x <i>Aloe haworthioides</i> x <i>descoingsii</i>	'Odette'
<i>Astroloba herrei</i>	x <i>Aloe descoingsii</i>	'Thorold'
<i>Astroloba herrei</i>	x <i>Aloe descoingsii</i>	'Toole'
<i>Astroloba congesta</i>	x <i>Aloe jucunda</i>	'Towering Beauty'
<i>Astroloba congesta</i>	x <i>Aloe millotii</i>	'Tyson'
<i>Astroloba herrei</i>	x <i>Aloe thompsonii</i>	'Western Justice'
<i>Astroloba congesta</i>	x <i>Aloe millotii</i>	'Xenek'

Table 5. *ASTROLOBA X GASTERIA*

Pollen parent.	Pod parent									
		1	2	3	4	5	6	7	8	9
<i>Astroloba congesta</i>	1		X	X	0/5	X	0/10	0/5	X	0/8
<i>Astroloba herrei</i>	2	X		X	0/5	0/9	0/5	0/6	X	0/5
<i>Astroloba spiralis</i>	3	X	X		0/6	X	0/5	X	0/5	0/10
<i>Gasteria bicolor v. liliputana</i>	4	4/10	4/10	4/8		X	X	X	X	X
<i>Gasteria carinata v. verrucosa</i>	5	X	3/6	X	X		X	X	X	X
<i>Gasteria</i> 'Little Warty'	6	4/10	4/5	6/8	X	X		X	X	X
<i>Gasteria</i> 'Old Man Silver'	7	3/7	3/8	X	X	X	X		X	X
<i>Gasteria</i> hybrid as "sulcata"	8	X	X	2/5	X	X	X	X		X
<i>Gasteria</i> 'Big Brother'	9	4/8	2/2	4/5	X	X	X	X	X	

These crosses are also easy to achieve under suitable conditions, again seed is only set on the *Astroloba*.

Table 6. *X Gastroloba* Cultivar names assigned to plants distributed in Australia.

Parentage		Cultivar name given
<i>Astroloba congesta</i>	x <i>Gasteria</i> 'Old man Silver'	'Aina'
<i>Astroloba congesta</i>	x <i>Gasteria</i> 'Little Warty'	'Delbat'
<i>Astroloba congesta</i>	x <i>Gasteria</i> 'Old Man Silver'	'Grugwyn'
<i>Astroloba herrei</i>	x <i>Gasteria</i> as 'humilis'	'Jaytee'
<i>Astroloba congesta</i>	x <i>Gasteria bicolor v liliputana</i>	'Leith'
<i>Astroloba herrei</i>	x <i>Gasteria</i> unnamed hybrid	'La Poquita'
<i>Astroloba spiralis</i>	x <i>Gasteria</i> as "sulcata"	'Verde Nigrita'
<i>Astroloba herrei</i>	x <i>Gasteria bicolor v liliputana</i>	'Regulus'
<i>Astroloba herrei</i>	x <i>Gasteria bicolor v liliputana</i>	'Rook'
<i>Astroloba herrei</i>	x <i>Gasteria carinata v verrucosa</i>	'Sheengh'

Table 7 <i>Astroloba</i> x <i>Haworthia</i> subgenus <i>Hexangulares</i> & <i>Robustipedunculares</i>										
Pollen Parent			Pod Parent							
		1	2	3	4	5	6	7	8	9
<i>Astroloba herrei</i>	1		X	X	0/4	0/2	X	X	4/5	X
<i>Astroloba congesta</i>	2	X		X	0/5	X	0/4	X	X	0/2
<i>Haworthia scabra</i>	3	3/4	3/5		X	X	X	X	X	X
<i>Haworthia fasciata</i>	4	2/5	1/4	X		X	X	X	X	X
<i>Haworthia attenuata</i>	5	2/5	X	X	X		X	X	X	X
<i>Haworthia viscosa</i>	6	4/5	X	X	X	X		X	X	X
<i>Haworthia sordida</i> x sp	7	1/5	2/6	X	X	X	X		X	X
<i>Haworthia maxima</i>	8	X	2/5	X	X	X	X	X		X
<i>Haworthia minima</i>	9	2/5	X	X	X	X	X	X	X	

Success was achieved in this case only with the *Haworthia* as the seed parent and the *Astroloba* as the pollen donor, this is likely as in previous cases due to the style being longer in

Astroloba and failure of the pollen tubes to grow the full length of the style.

Table 8. <i>Astroloba</i> x <i>Haworthia</i> subgenus <i>Haworthia</i>										
Pollen Parent.			Pod Parent.							
		1	2	3	4	5	6	7	8	9
<i>Astroloba herrei</i>										
<i>Astroloba congesta</i>	1		X	X	0/5	X	0/10	0/6	0/5	0/2
<i>Astroloba bullulata</i>	2	X		X	0/5	0/2	0/2	0/2	0/4	X
<i>Astroloba foliosa</i>	3	X	X		0/10	0/10	X	0/3	0/10	0/6
<i>Haworthia cymbiformis</i>	4	0/5	0/5	0/3		X	X	X	X	X
<i>Haworthia cooperi</i>	5	0/3	0/3	X	X		X	X	X	X
<i>Haworthia magnifica</i>	6	0/5	0/6	0/5	X	X		X	X	X
<i>Haworthia gracilis</i>	7	0/5	X	0/3	X	X	X		X	X
<i>Haworthia mucronata</i>	8	0/5	0/5	0/6	X	X	X	X		X
<i>Haworthia pygmaea</i>	9	0/2	0/4	0/2	X	X	X	X	X	

Many more unsuccessful attempts were made, though it may be possible that with many more attempts, such a cross could be achievable.

X <i>Astroworthia</i> Cultivar names assigned to plants distributed in Australia				
Parentage			Cultivar Name given	
<i>Astroloba herrei</i>	x	<i>Haworthia scabra</i>	'Auriga'	
" "	x	" <i>fasciata</i>	'Fasher'	
" "	x	" <i>attenuata</i>	'Herat'	
" "	x	" <i>viscosa</i>	'Hervis'	
" "	x	" <i>reinwardtii</i> v <i>brevicula</i>	'Herwart'	
" "	x	" <i>starkiana</i>	'Verdeclara'	
" "	x	" <i>sordida</i> x sp.	'Monoceros'	
" <i>congesta</i>	x	" <i>maxima</i>	'Eneas'	
" <i>bullulata</i>	x	" <i>limifolia</i>	'Limerg'	
<i>Haworthia maxima</i>	x	<i>Astroloba herrei</i>	'Papher'	

Conclusions: With the exception of *Gasteria*, *Astroloba* exhibits the greatest willingness to form intergeneric hybrids, many of these have proved to be fertile to varying degrees. Only hybrids with *Poellnitzia* have proved to be unachievable,

furthermore this does not provide any evidence for the subsumation of *Poellnitzia* into *Astroloba*. Those with *Chortilirion* have so far not been attempted, however it is expected that such a cross would prove fruitful

Leaf arrangement in *Aloe striatula*

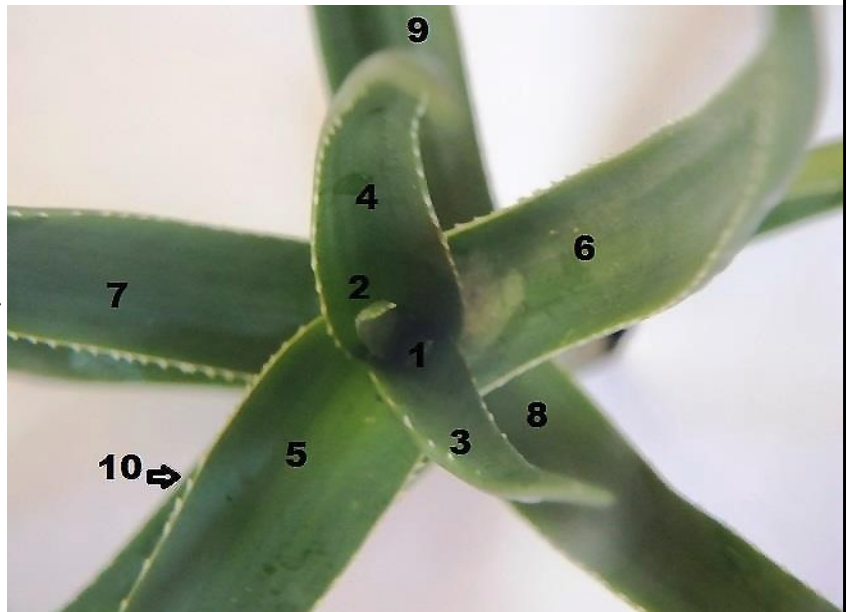
Bruce Bayer

Herewith is an image of the leaf arrangement in *Aloe striatula*.

I have numbered the leaves in inverse order to show that the leaves are as much distichous as trifarious i.e in two rows or three. The primary set is 1 through 10, the distichous set is 1, 3, 5, 7, 9 and 2, 4, 6, 8, 10. The trifarious set is 1, 4, 7, 10; 2, 5, 8 and 3, 6, 9.

I have also added a picture of the leaf insertion – here it is entire and there is a leaf sheath around the stem – the actual point of insertion is at the pointer although the “veins” continue through that point to the stem itself. In this species the next leaf is inserted just below the opening of the previous sheath. Despite the leaves being alternate, they are spirally arranged.

In *Aloe broomii* the leaf insertion is continuous and you can peel all the leaves off the stem in one piece. In most haworthias the leaves are imbricate (overlapping alternately) but always in a spiral sequence. *H. wittebergensis* has leaves that have entire insertion and by memory the same is true for *H. blackburniae* and maybe for *H. viscosa*.



Continued from page 5

There appears to be no indication that there is any more worth in incorporating the genus *Astroloba* within *Haworthia* as to doing so within *Aloe* or *Gasteria*. Again it is stated that unless all the genera within Aloaceae are subsumed under the genus *Aloe* to form one super genus then *Astroloba* should remain a recognised genus.

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ALOE AND GOODBYE: A NEW EVOLUTIONARY CLASSIFICATION OF THE ALOOIDS

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Introduction

The philosophical boundaries of the genera of the alooids (subfamily Alooideae of the family Asphodelaceae) have shifted kaleidoscopically ever since Carl Linnaeus named *Aloe* in 1753. Working from a mix of dried and cultivated specimens plus illustrations, Linnaeus aimed to catalogue the large and ever-increasing diversity of living organisms that confronted him and his colleagues in Europe in such a way that each species could be easily identified and named. Names as a shorthand for indicating evolutionary relationships was still a long time in the future.

The taxonomic pigeonhole that Linnaeus labelled '*Aloe*' contained a mixed group of lily-like plants with tubular flowers and leathery or succulent, sword-shaped leaves. Four of the 16 species that he included in it are not alooids at all (three species of *Sansevieria* and one of *Kniphofia*). The remaining dozen, which he grouped by flower size and shape, included four species of *Aloe*, one species of *Gasteria*, one species of *Astroloba* and five species of *Haworthia* (following a more recent classification of genera). His preliminary grouping of the alooid species by flower form set the stage for the later generic classification of the alooids: Salm-Dyck (1836–63) treating the groups as sections within *Aloe* but Duval (1809) electing to upgrade two of them to generic status, as *Gasteria* (those species with moderately large, curved flowers more or less swollen at the base) and *Haworthia* (those species with very much smaller, whitish flowers). *Haworthia* itself was subsequently split when the species with more or less radially symmetrical flowers were separated as the genus *Astroloba* from those with two-lipped flowers by Uitewaal (1947). Three additional small genera were also named, viz. *Chortolirion*, *Lomatophyllum* and *Poellnitzia*, but *Lomatophyllum* has now been subsumed back into *Aloe*, and *Poellnitzia* is included in *Astroloba*. Until the recent developments that we describe below, most botanists segregated the species of alooids among the five genera *Aloe*, *Astroloba*, *Chortolirion*, *Gasteria* and *Haworthia*, defined mainly by the shape, size and colouring of the flowers (Table 1).

The emergence of techniques for inferring relationships among living species through the analysis of DNA

TABLE 1 Traditionally recognised genera of alooids

Genus	No. Species	Features	Distribution
<i>Aloe</i>	±400	<p>Growth form: trees, shrubs and stemless perennials.</p> <p>Leaves: tough, mostly with spiked or toothed margins, surface smooth to warty.</p> <p>Flowers: small to large, mostly yellow to red, bell-shaped to tubular or swollen, radially symmetrical to 2-lipped with anthers exerted or included.</p>	Africa, Arabian peninsula, Madagascar, islands in western Indian Ocean

Genus	No. Species	Features	Distribution
<i>Astroloba</i>	7	Growth form: multi-stemmed. Leaves: hard, spirally arranged, untoothed. Flowers: small, dull or reddish, suberect, tubular and radially symmetrical with anthers included.	Western and Eastern Cape of South Africa.
<i>Chortolirion</i>	1–4	Growth form: stemless. Leaves: grass-like with bulb-like swelling and weakly toothed margins. Flowers: small, whitish, 2-lipped with anthers included.	Grasslands of Angola, Botswana, Namibia and the summer rainfall areas of South Africa.
<i>Gasteria</i>	23	Growth form: stemless or stemmed. Leaves: firm-textured with hard, untoothed margins, dark green with bands of whitish spots. Flowers: medium to large, tubular and curved, swollen at base, with anthers included.	Eastern Cape of South Africa, southern Namibia.
<i>Haworthia</i>	± 61	Growth habit: dwarf, mainly stemless. Leaves: rosette-forming, variable in size and shape, without hard teeth. Flowers: small, whitish, radially symmetric or 2-lipped, with anthers included.	Western and Eastern Cape, Mpumalanga and Limpopo Provinces of South Africa; Swaziland, Mozambique and Namibia.

introduced a powerful new tool for reconstructing the evolutionary history of groups of organisms. The first botanists to look at the evolutionary (or phylogenetic) relationships in the Asphodelaceae were Chase & al. (2000), who analysed DNA sequence data from the chloroplasts of a small sampling of species in the family. Their results confirmed that the alooids represented a single evolutionary lineage, with *Haworthia* evidently mostly closely related to *Gasteria*. The limited number of species included in the analysis prevented further conclusions. A second study by Treutlein & al. (2003) of a larger sample of species, using chloroplast DNA sequence data supplemented by DNA fingerprinting techniques, went further by suggesting that both *Aloe* and *Haworthia* were artificial assemblages of species associated by appearance and not heritage. Their analysis of relationships showed that the species of *Haworthia* subg. *Haworthia* were more closely related to some species of *Aloe* than to other species of *Haworthia*, whereas the members of *Haworthia* subg. *Hexangulares* were most closely related to *Gasteria*, *Astroloba* and *Aloe aristata*. The genus *Chortolirion* grouped with the grass-like species of *Aloe*, and *Lomatophyllum* was firmly placed among another group of *Aloe* species. A third study, by Ramdhani & al. (2011), focussed on evolutionary relationships in the genus *Haworthia* by analysing DNA sequences from three separate gene regions in 26 species from all three subgenera *Haworthia*, *Hexangulares* and *Robustipedunculares*. They confirmed the earlier findings that *Haworthia* was a superficial collection of species in which the three subgenera represented separate and independent evolutionary groups not directly related to one another. The *Haworthia* flower was thus a false indicator of relationships, as had already been shown with *Chortolirion*.

These intriguing hints at evolutionary relationships among the alooids pointed to the urgent need to re-examine the boundaries of the genera if there was any hope of defining them as real evolutionary lineages.

Natural vs unnatural classifications.

At this stage we need to pause to consider the framework for defining genera and other ranks of organisms. In

other words, what is the role of a classification? At one extreme, it can be treated as a filing system serving to retrieve the names of organisms with maximum reliability. At the other extreme, it reflects the evolutionary relationships of each organism at every level. Charles Darwin addressed this dichotomy with his characteristic clarity of expression in *The Origin of Species* as follows:

'Naturalists ... try to arrange the species, genera and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike ... as an artificial method of enunciating ... general propositions... The ingenuity and utility of this system are undisputable. But many naturalists think that something more is meant by the Natural System... Expressions such as that famous one by Linnaeus ... that the characters do not make the genus, but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance. I believe that this is the case, and that community of descent — the one known cause of close similarity in organic beings — is the bond, which through various degrees of modifications, is partially revealed to us by our classifications.'

For Darwin, therefore, classifications mirror the evolutionary history of organisms as closely as possible. In this view, systems of classification should be derived from the unique evolutionary past of each group rather than reflect the superficial patterns developed among the survivors. A natural (or phylogenetic) classification, based on shared genealogy, will be maximally useful in understanding and predicting other characteristics of the organisms, from their chemical composition to their geographic origins. Accepting this philosophy, we can now turn to the vexed issue of the classification of the alooids, in which it was becoming ever clearer that some of the genera were artificial groupings of species in a scheme that relied on selected aspects of their appearance rather than on community of descent.

A New Order Emerges.

With this aim, Daru et al. (2013) examined the evolutionary relationships among the largest sampling of alooids to date, including 20 species of *Gasteria*, 69 species of *Haworthia* from all three subgenera, 60 species *Aloe* selected from 20 sections (including *Lomatophyllum*), four species of *Astroloba* (including *Poellnitzia*) and one species of *Chortolirion*, using four different gene regions (ITS1 from the nucleus, and *matK*, *rbcLa*, and *trnH-psbA* from plastids). Their findings were clear: *Aloe* was a grab-bag of species from which all other genera of alooids had evolved; and *Haworthia* was an artificial assemblage of three separate lineages corresponding to the subgenera that were currently recognized. They identified eight primary evolutionary lineages among the alooids, corresponding largely to the following currently recognised groups: (1) *Aloe* sect. *Dracoaloe* + sect. *Aloidendron*; (2) *A.* sect. *Kumara*; (3) *A.* sect. *Macrifoliae*; (4) *Haworthia* subg. *Haworthia*; (5) *A.* sect. *Aristatae* + *H.* subg. *Robustipedunculares* + *Astroloba*; (6) *H.* subg. *Hexangulares*; (7) *Gasteria*; (8) the remaining species of *Aloe* (including *Chortolirion*).

Seven of these eight primary lineages are endemic to southern Africa, with only *Aloe* in the strict sense extending beyond the region, suggesting that the early diversification of the subfamily took place in the subcontinent, which remains the main centre of distribution for the subfamily.

The picture was now clear but what was to be made of it? Two options presented themselves for redefining the genera to reflect their evolutionary history: revert to Linnaeus and Salm-Dyck and sweep everything into the genus *Aloe*, or look at other ways of dismembering the subfamily. Both had their advantages. The single-genus option would not significantly increase the variation already accepted within *Aloe* and would permit infinite shuffling of species within it without the risk of incurring any further name-changes. The multi-genus option would preserve at least some of the generic names popular among growers, and would highlight the fundamental diversity of the group in southern Africa. The work by Daru & et. (2013) stimulated an immediate reaction among students of the alooids. Grace & al. (2013) proceeded promptly to dismember *Aloe*, raising sects. *Dracoaloe* (= *Aloidendron*), *Macrifoliae*, and *Kumara* to generic level as *Aloidendron* (six species), *Aloiampelos* (seven species), and *Kumara* (one species), respectively. Hard on their heels, and basing his opinions directly on the phylogenetic tree published by Daru & al. (2013), Rowley (2013) restricted the genus *Haworthia* to members of *H.* subg. *Haworthia*, transferred most members of subg. *Hexangulares* to his new genus *Haworthiopsis*, and amalgamated the remaining species of *Haworthia* with *Astroloba* and *Aloe aristata* in the genus *Tulista*. This rush to carve up *Aloe* and *Haworthia* revealed a clear preference for a multi-genus solution but raised a cloud of nomenclatural dust that is only now beginning to settle.

We proceeded by adding two additional unusual species of *Aloe* to our analysis and to sequence a further gene region

in an attempt to clarify the evolutionary picture to a point where no further changes in the pattern could reasonably be expected to emerge by adding more species to the mix. This analysis has now just been published (Manning et al. 2014) (Figure 1). The basic picture remains unchanged but our inclusion of the two odd aloes added two important details. *Aloe haemanthifolia*, a narrow endemic of the southwestern Cape, is immediately related to *A. plicatilis*; and the relationships of *A. variegata* lie with *A. aristata* and *Astroloba*. Both of these associations are supported by general vegetative resemblances, and it appears that flowers are rather less than ideal reflectors of relationships among groups of alooids!

Our expanded evolutionary analysis forms the basis for the first complete phylogenetic classification of the alooids. Accepting the precedents initiated by Grace et al. (2013) and Rowley (2013) in the interests of developing a single, maximally acceptable classification for the subfamily, we recognise eleven major lineages within the alooids as genera (Figure 1).

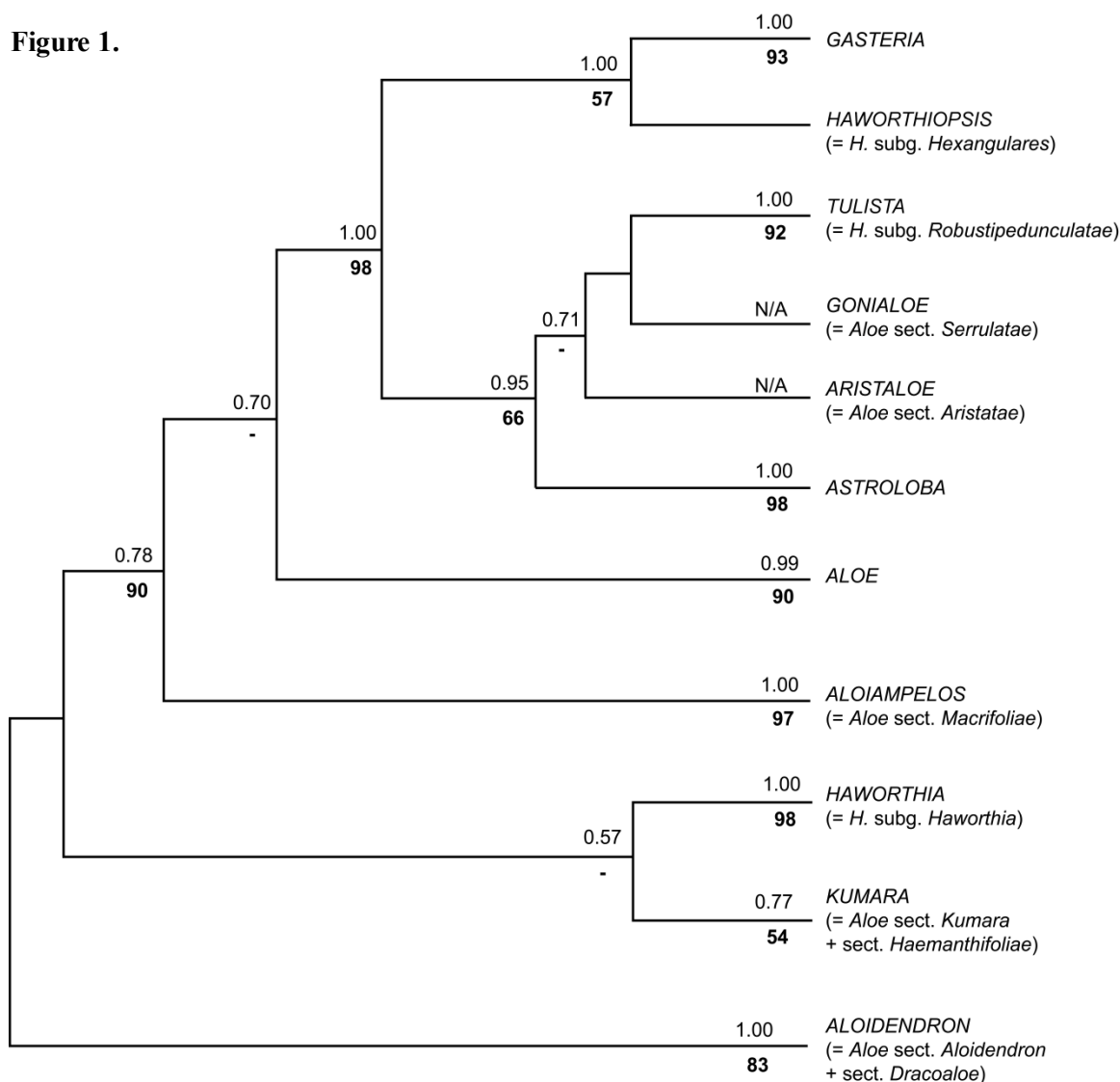


Figure1.

Summary tree of major lineages within Alooideae and the genera proposed by Manning & al. (2014) (uppercase). Bayesian posterior probabilities are indicated above branches and maximum parsimony bootstrap support below.

We accept the recognition of *Aloiampelos*, *Aloidendron*, and *Kumara*, but expand the circumscription of *Kumara* to include *A. haemanthifolia*. Although this species differs dramatically from the tree-like *Kumara plicatilis* in its stemless habit, *Aloe haemanthifolia* is otherwise vegetatively very similar to that species in its 2-ranked, tongue-shaped leaves without marginal teeth.

Astroloba and *Gasteria* remain unchanged, but *Haworthia* is restricted to the typical subgenus, with the subgenera *Hexangulares* and *Robustipedunculatae* treated as the genera *Haworthiopsis* and *Tulista*, respectively. We place both *H. koelmaniorum* and *H. pungens* in *Haworthiopsis*, in contrast with Rowley (2013), who associated both species without comment with *H. subg. Robustipedunculatae* in the genus *Tulista*.

We recognise the new genera *Aristaloe* for *Aloe aristata* and *Gonialoe* for *A. variegata* and its allies, based on their isolated evolutionary position between *Astroloba* and *Haworthia* subg. *Robustipedunculatae*. They share a dwarf habit and similar flowers with the outer tepals joined more than halfway but differ substantially in their foliage and fruit, with *A. aristata* characterised by softly prickly leaves with dry, awn-tipped apices, and *A. variegata* and allies in sect. *Serrulatae* by leaves with cartilaginous margins, and relatively large capsules and seeds. In this treatment we again diverge from Rowley (2013), who adopted a broad circumscription of *Tulista* to include not only *Haworthia* subg. *Robustipedunculatae* plus two species of subg. *Hexangulares*, but also *Astroloba* and *Aloe aristata*. No explanation was offered for this decision, which was made without any knowledge of the close relationship between *A. variegata* and these taxa. Including these morphologically and historically distinct lineages in a single genus is contrary to all arguments for the adoption of the multi-genus classification.

We provide a summary of our new classification below, including lists of species in some of the new genera. We follow the taxonomic concepts used by Glen and Hardy (2000) and Reynolds (1966, 1969) for species previously treated in *Aloe*, and those of Bayer (1999) and Bayer and Manning (2012) for species previously treated in *Haworthia*.

The New Taxonomy.

Key to the genera of Aloioideae.

1. Anthers and styles deeply included, often more than halfway; leaves never prickly on margins; herbs, often dwarf.....2
 2. Perianth ± radially symmetric3
 3. Plants with stems and stiff, pointed leaves, usually eccentrically keeled beneath; flowers usually < 15 mm long and whitish, rarely larger and orange but then not swollen at the base6. *Astroloba*
 3. Plants with or without stems, with smooth, rough, or velvety leaves; flowers > 20 mm long, pink to orange with greenish tips, swollen at the base with the tepals ± completely joined 11. *Gasteria*
 2. Perianth 2-lipped4
 4. Flowers curved; inner and outer tepal whorls not adhering; style curved; leaves smooth, velvety, or rough3. *Haworthia*
 4. Flowers straight; inner and outer tepal whorls adhering; style straight; leaves smooth or with white, subtuberculate to subspinescent spots on lower or both surfaces5
 5. Flowers abruptly contracted below and abruptly joined to the pedicel 9. *Tulista*
 5. Flowers narrowing more gradually below and tapering to the pedicel10. *Haworthiopsis*
1. Anthers and styles usually exserted or just included (flowers small and strongly bilabiate with included anthers and styles in *Aloe* sect. *Chortolinion* but then almost stalkless); leaves often prickly on margins; herbs, shrubs, or trees6
 6. Leaves 2-ranked, tongue-shaped with rounded tips, without spots; outer tepals joined more than halfway2. *Kumara*
 6. Leaves spirally inserted or 3-ranked, sharp, unspotted or variously marked; outer tepals variously free or joined7
 7. Trees or large shrubs with equally forked branches and leafless stems; leaves unspotted ..1. *Aloidendron*
 7. Herbs or shrubs, sometimes tree-like but not equally forked; leaves spotted or not8
 8. Several-stemmed shrubs or climbers; leaves scattered along the stems, distinctly sheathing at the base, unspotted, with soft marginal teeth; flowers with outer tepals almost completely joined 4. *Aloiampelos*
 8. Mostly single-stemmed herbs or shrubs; leaves not scattered along the stems; flowers with outer tepals free or variously joined9

9. Dwarf, stemless herbs; leaves white-spotted or with hairlike prickles from white tubercles; outer tepals joined more than halfway; anthers not or hardly protruding10
 10. Leaves 3-ranked, without prickles, margins cartilaginous; peduncles with numerous sterile bracts8. Gonialoe
 10. Leaves spirally arranged, lower surface and margins with soft prickles; peduncles without sterile bracts7. Aristaloe
 9. Plants without the above combination of characters 5. Aloe

1. Aloidendron (A.Berger) Klopper & Gideon F.Sm.—Type species: *Aloidendron barberae* (Dyer) Klopper & Gideon F.Sm.

Aloe section *Aloidendron* A.Berger. *Aloe* section *Dracoaloe* A.Berger. *Aloe* section *Sabaealoe* A.Berger

Dichotomously much-branched shrubs or trees with leafless stems, not suckering. *Leaves* in rosettes, unspotted, margins finely toothed. Inflorescence a panicle, usually few-branched, peduncles without sterile bracts, racemes cylindric. *Flowers* cylindric-ventricose, 25–40 mm long, yellow or pink, outer tepals joined in lower half, inner tepals ± free. *Anthers* long-exserted. *Style* long-exserted.

(6 or 7 spp.; southern and east tropical Africa)

Species: *Aloidendron barberae* (Dyer) Klopper & Gideon F. Sm., *A. dichotomum* (Masson) Klopper & Gideon F. Sm. (incl. *A. ramosissimum* (Pillans) Klopper & Gideon F. Sm.), *A. eminens* (Reynolds & P.R.O.Bally) Klopper & Gideon F.Sm., *A. pillansii* (L. Guthrie) Klopper & Gideon F. Sm., *A. sabaea* (Schweinf.) Boatwr. & J.C. Manning, *A. tongaensis* (Van Jaarsv.) Klopper & Gideon F.Sm.

2. Kumara Medik.—Type species: *Kumara plicatilis* (L.) G.D.Rowley

Aloe subgenus *Kumara* (Medik.) Baker. *Aloe* section *Haemanthifolia* (A.Berger) Glen & D.S.Hardy

Dichotomously much-branched shrub or tree with leafless stems, or stemless. *Leaves* 2-ranked, tongue-shaped, blunt, unspotted, margins entire or brown-denticulate. Inflorescence a lax or head-like raceme, peduncles with or without sterile bracts. *Flowers* cylindric, 23–45 mm long, reddish pink, tepals ± free or outer joined in lower half. *Anthers* included or scarcely exserted. *Style* included or shortly exserted.

(2 spp.; moist sandstone slopes in winter rainfall, southwestern South Africa)

Species: *Kumara haemanthifolia* (A.Berger & Marloth) Boatwr. & J.C.Manning, *K. plicatilis* (L.) G.D.Rowley

3. Haworthia Duval—Type species: *Haworthia arachnoidea* (L.) Duval.

Dwarf, stemless herbs. *Leaves* rosette-forming, more or less soft and juicy, smooth, hairy, or rough. *Inflorescence* a raceme, peduncles slender and flexible, with few sterile bracts. *Flowers* < 15 mm long, 2-lipped, curved, ascending, triangular-tapering to the pedicel, brownish or whitish, outer and inner tepals joined at base, the two whorls not adhering. *Anthers* included. *Style* curved, included.

(42 spp.; winter rainfall, southwestern South Africa)

4. Aloiampelos Klopper & Gideon F.Sm.—Type species: *Aloiampelos ciliaris* (Haw.) Klopper & Gideon F.Sm.

Aloe series *Macrifoliae* Haw.

Shrubs or climbers with distantly leafy, cane-like stems. *Leaves* laxly spirally arranged, thin-textured, sheathing, unspotted, margins toothed or fringed in one species. *Inflorescence* lateral, racemose, cylindrical, peduncles ± without sterile bracts. *Flowers* cylindric, 10–40 mm long, yellow to red, outer tepals ± completely joined, inner tepals ± free. *Anthers* included or shortly exserted. *Style* included or shortly exserted.

(7 spp.; southern and eastern South Africa)

Species: *Aloiampelos ciliaris* (Haw.) Klopper & Gideon F.Sm., *A. commixta* (A.Berger) Klopper & Gideon F.Sm., *A. decumbens* (Reynolds) Klopper & Gideon F.Sm., *A. gracilis* (Haw.) Klopper & Gideon F.Sm., *A. juddii* (Van Jaarsv.) Klopper & Gideon F.Sm., *A. striatula* (Haw.) Klopper & Gideon F.Sm., *A. tenuior* (Haw.) Klopper & Gideon F.Sm.

5. Aloe L.—Type species: *A. perfoliata* L.

Perennial herbs or shrubs, branched or unbranched. *Leaves* in a rosette, unmarked or variously spotted or streaked, margins smooth or prickly. *Inflorescence* spicate or racemose, simple or branched, peduncles with or without sterile bracts. *Flowers* regular or 2-lipped, bell-shaped, cylindric or with a basal swelling, mostly > 15 mm long, often brightly coloured, outer tepals mostly joined in lower half, inner tepals \pm free. *Anthers* mostly exserted. *Style* mostly exserted.

(\pm 400 spp.; widely distributed through Africa, Arabia, Madagascar, and Socotra)

6. *Astroloba* Uitewaal—Type species: *Astroloba pentagona* (Ait.) Uitewaal (= *Astroloba spiralis* (L.) Uitewaal)

Poellnitzia Uitewaal

Dwarf, stemmed herbs, clump-forming. *Leaves* spirally inserted, overlapping, leathery or hard, deltoid and sharply pointed, smooth or tuberculate, usually eccentrically keeled beneath, margins smooth or toothed. *Inflorescence* a raceme or panicle, *peduncles* with sterile bracts. *Flowers* tubular, straight, ascending, usually < 15 mm long and brownish or whitish, rarely longer and reddish, outer and inner tepals joined in lower half. *Anthers* included. *Style* straight, included.

(6 spp.; mainly winter rainfall, southern and southwestern South Africa)

Species: *Astroloba bullulata* (Jacq.) Uitewaal, *A. congesta* (Salm-Dyck) Uitewaal, *Astroloba corrugata* N. L. Mey. & Gideon F. Sm., *Astroloba foliolosa* (Haw.) Uitewaal, *Astroloba herrei* Uitewaal, *A. rubriflora* (L. Bolus) Gideon F. Sm. & J. C. Manning, *Astroloba spiralis* (L.) Uitewaal.

7. *Aristaloe* Boatwr. & J.C.Manning—Type species: *Aristaloe aristata* (Haw.) Boatwr. & J.C. Manning. *Aloe* section *Aristatae* (A.Berger) Glen & D.S.Hardy

Dwarf, stemless, clump-forming herb. *Leaves* rosette-forming, with white subtuberculate to subspinescent spots on both surfaces, margins with soft white prickles. *Inflorescence* a panicle, peduncles without sterile bracts. *Flowers* arcuate-nodding, constricted above ovary, 30–40 mm long, dull orange but paler beneath, outer tepals joined for most of length, inner tepals \pm free. *Anthers* not or scarcely exserted. *Style* shortly exserted.

(1 sp.; montane, southeastern South Africa)

Species: *Aristaloe aristata* (Haw.) Boatwr. & J. C. Manning

8. *Gonialoe* (Baker) Boatwr. & J.C.Manning. *Aloe* subgenus *Gonialoe* Baker. *Aloe* section *Serrulatae* Salm-Dyck

Dwarf, stemless, mostly clump-forming herbs. *Leaves* 3-ranked, deltoid to V-shaped in section, with white subtuberculate spots on both surfaces, margins thickened and minutely toothed. *Inflorescence* a simple or branched raceme, peduncles with sterile bracts. *Flowers* nutant, slightly swollen or constricted above ovary, 20–45 mm long, pink, orange, or scarlet, outer tepals joined for most of length, inner tepals joined to outer. *Anthers* not or scarcely exserted. *Style* shortly exserted.

(3 spp.; arid South Africa and Namibia)

Species: *Gonialoe dinteri* (A. Berger) Boatwr. & J.C.Manning, *G. sladeniana* (Pole-Evans) Boatwr. & J.C.Manning, *G. variegata* (L.) Boatwr. & J.C.Manning

9. *Tulista* Raf.—Type species: *Tulista pumila* (L.) G. D. Rowley. *Haworthia* subgenus *Robustipedunculatae* (Uitewaal) M.B. Bayer [as *Robustipedunculares* Uitewaal ex M. B. Bayer]

Dwarf, stemless herbs. *Leaves* in a dense rosette, smooth or with white subtuberculate to subspinescent spots on lower or both surfaces, margins similarly ornamented. *Inflorescence* a raceme, peduncle stiff, with few sterile bracts. *Flowers* < 15 mm long, weakly 2-lipped, straight, ascending, abruptly joined to pedicel, brownish or whitish, outer and inner tepals joined at base, both whorls adhering. *Anthers* included. *Style* straight, included.

(4 spp.; winter rainfall, southwestern South Africa)

Species: *Tulista kingiana* (Poelln.) G.D.Rowley, *T. marginata* (Lam.) G.D.Rowley, *T. minima* (Ait.) Boatwr. & J.C.Manning, *T. pumila* (L.) G.D.Rowley

10. *Haworthiopsis* G.D.Rowley—Type species: *Haworthiopsis coarctata* (Haw.) G. D. Rowley. *Haworthia* subgenus *Hexangulares* (Uitewaal) M.B.Bayer [as Uitewaal ex M. B. Bayer]

Dwarf, stemless or stemmed herbs. *Leaves* rosette-forming or spirally inserted, smooth or with white subtuberculate to subspinescent spots on lower or both surfaces, margins similarly ornamented. *Inflorescence* a raceme, peduncle stiff, with few sterile bracts. *Flowers* < 15 mm long, bilabiate, straight, ascending, tapering to the pedicel, brownish or whitish, outer and inner tepals joined at base, both whorls adhering. *Anthers* included. *Style* straight, included.

(18 spp.; winter rainfall, southwestern South Africa)

Species: *Haworthiopsis attenuata* (Haw.) G.D.Rowley, *H. bruynsii* (M.B.Bayer) G.D.Rowley, *H. coarctata* (Haw.) G.D.Rowley, *H. fasciata* (Willd.) G.D.Rowley, *H. glauca* (Baker) G.D.Rowley, *H. granulata* (Marloth) G.D.Rowley, *H. koelmaniorum* (Oberm. & Hardy) Boatwr. & J.C.Manning, *H. limifolia* (Marloth) G.D.Rowley, *H. longiana* (Poelln.) G.D.Rowley, *H. nigra* (Haw.) G.D.Rowley, *H. pungens* (M.B.Bayer) Boatwr. & J.C.Manning, *H. reinwardtii* (Salm-Dyck) G.D.Rowley, *H. scabra* (Haw.) G.D.Rowley, *H. sordida* (Haw.) G.D.Rowley, *H. tessellata* (Haw.) Boatwr. & J.C.Manning, *H. venosa* (Lam.) G.D.Rowley, *H. viscosa* (L.) G.D.Rowley, *H. woolleyi* (Poelln.) G.D.Rowley

11. *Gasteria* Duval—Type species: *Gasteria disticha* (L.) Haw.

Stemless or stemmed caulescent herbs. Leaves rosette-forming rosulate or 2-ranked, smooth, rough, velvety, or with white subtuberculate spots on both surfaces, margins similarly ornamented. Inflorescence a raceme or panicle, often slanting, peduncles with few sterile bracts. *Flowers* tubular, pendulous, arcuate with a basal swelling, ± pink or reddish with green tips, outer and inner tepals ± completely joined. *Anthers* included. *Style* curved, included.

(23 spp.; South Africa)

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Living with Changes.

No!! This is not about plant classification, but about the representation of *Alsterworthia* International (A.I.).

When A.I. was inaugurated at the beginning of 2001 we were heavily reliant on Honorary Representatives for recruitment and the collection of subscriptions and other payments. They were the basis of our success and we are extremely grateful to them. To assist them, the original annual membership fees were fixed for one year or more in both Sterling and the currencies of countries which had representatives. This worked fine for some time, but gradually events outside our control began to have an effect.

The electronic world continued to expand rapidly and became much more widely accepted, particularly as the influence of younger generations expanded and businesses seized opportunities. Web sites, Facebook, e-mail etc. made communication much easier, quicker and cheaper. PayPal introduced new methods of international payments, much less costly than bank transfers and quicker.

This resulted in some members sending money direct to the UK and new members joining directly.

The recent economic and financial crises, which are still with us, have had more profound effects than might have been expected. More frequent and significant fluctuations in exchange rates have presented problems, resulting in the fixed exchange rates we use becoming out-of-date. In their efforts to ensure that A.I. received the correct Sterling amounts some representatives found they were losing money and some members changed to sending money in Sterling direct by PayPal.

How this has worked out in different parts of the world has varied, but the overall effect is that more payments are being made direct to *Alsterworthia* International and more members are joining directly.

Honorary Representatives are important ambassadors for A.I. but, in the light of uncertainty and changing conditions, we are in the process of consulting them about the future.

We should also like to have member's views, particularly on methods of publicising A.I., making payments and keeping down costs. Would on-line publication of the journal in addition to the printed versions be desirable?

Do please let the editor have your comments and suggestions: hmays@freenetname.co.uk

Intergeneric Hybrids in the Asphodelaceae

Subfamily Alooideae - 2014 Update.

Gordon Rowley

Much has changed in the aloe world since this review was first compiled, eight years ago (Rowley 2006). DNA sequencing and phylogenetic classification have come into their own and provide a basis on which to build new systems based upon common ancestry.

How far one accepts the findings, which often play havoc with traditional concepts, depends upon where in a cladogram one sets the level at which hierarchical branches (clades) diverge.

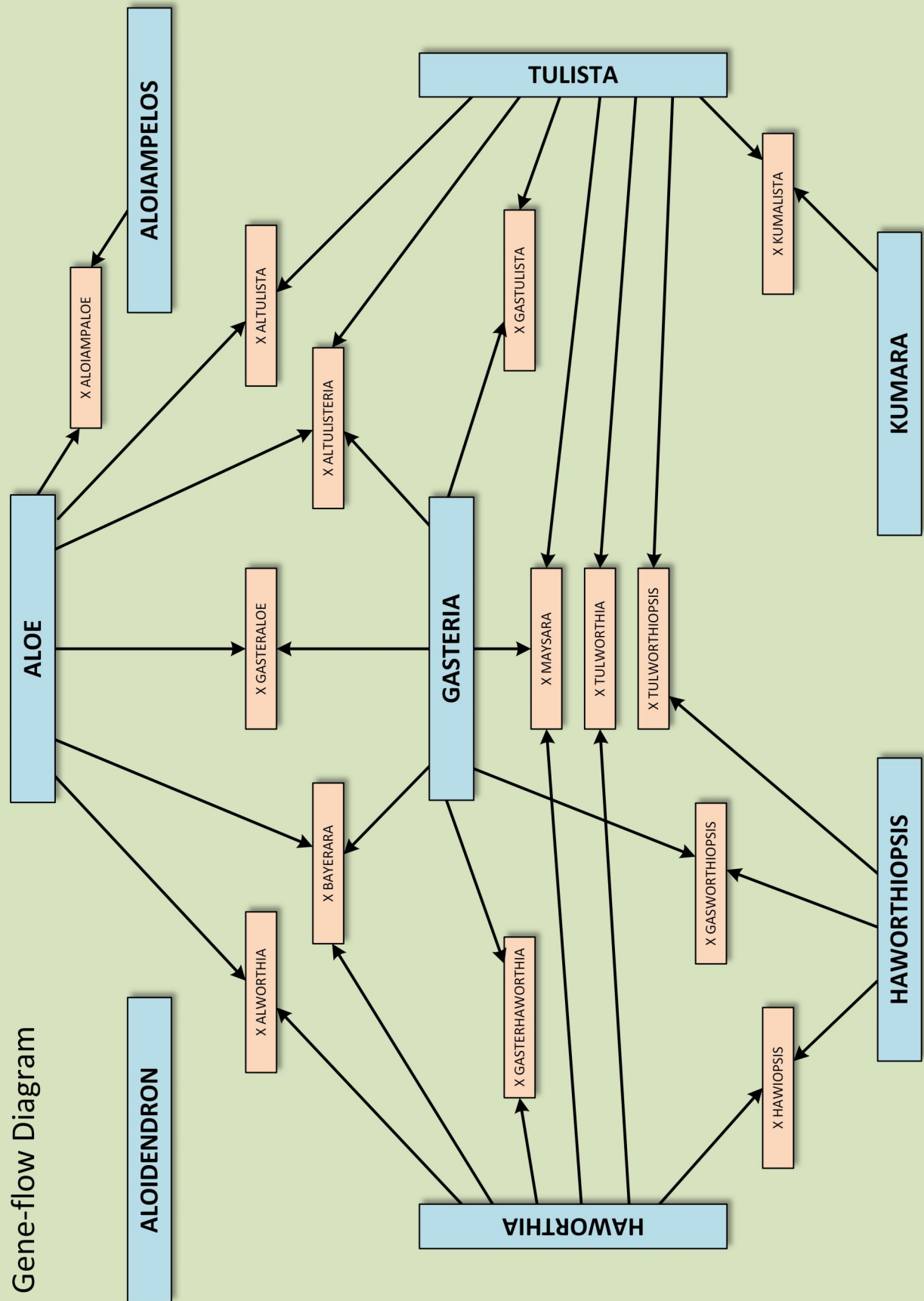
The team headed by Manning, Boatwright and Daru explored the best of two worlds. In 2012 they proposed extreme lumping of the whole subfamily into a single genus *Aloe*, with some 55 new combinations (Daru 2012), but two years later opted for splitting into 11 genera (Manning et al. 2014A & B). I favour a less radical split, resulting in 8 genera, and retaining *Tulista* in the broader sense. This seems a happy compromise, with the opportunity for retrieving *Astroloba* and other splits as Subgenera or Sections later.



Figs.2-3. *Tulista (Aloe) aristata* - “Odd man out” in the *Aloe* complex but parent of many hybrids. Photos Peter Arthurs.

These provide the foundations for the classification of hybrids that follows. Every change in genera may bring with it changes in the names of hybrid genera (nothogenera). Although these names are governed by the nomenclature codes, they should not be confused with botanical genera. They are formula names, compiled from all or parts of the names of the parent genera. As such they are self-explanatory and serve ideally as labels for boxes into which to file cultivars of known origin, Fig. 1, opposite page, shows the 14 best documented nothogenera linking the 8 genera. Note that 3 of these are trigeneric, combining species belonging to three separate genera, for which commemorative names ending in -ara are permissible. As yet I have found no credible record of hybrids among the tree aloes of *Aloidendron*, although shrubby *Kumara* has obliged with a single impressive cross.

Figure 1
Gene-flow Diagram



Historical flashback.

By the end of the nineteenth century many hybrids within the Aloooideae, both infra- and inter-generic, were in cultivation in Europe. Thomas Hanbury's famous garden in La Mortola enabled some of the larger-growing plants to flourish and flower. A few came from habitat; others arose from seed, by hand-pollination or by chance, in which case the parentage can only be surmised. The species are nearly all diploid and amenable to crossing. Salm Dyck provided illustrations for some of the earliest, such as *X Gasterhaworthia bayfieldii*; J.G. Baker documented others growing at Kew Gardens. Abbé Béguin of Brignoles in France supplied nurserymen Haage & Schmidt in Germany with *X Gasteraloes*, and a classic paper by Radl (1896) documents more intergeneric crosses. Alwin Berger's classic monograph of the Aloooideae in 1908 gives rare attention to cultigens as well as indigens. He recalls (p. 316) how he went in June 1903 to visit the nonagenarian hybridist J.B.A. Deleuil, raiser of the largest of all aloe cultigens, with leaves 1.0-1.25 m long. *A. X deleuilii* was named in his honour. He also describes five other aloe hybrids from Deleuil's catalogues of 1898-1902. They flourished at La Mortola and one wonders if they survive there today. Some propagations were offered for sale at high prices.

New Nothogenera.

X *Aloiampaloe* nothogen. nov. *Aloe* L. X *Aloiampelos* Klopp. & Smith.

Poindexter reports *Aloiampelos* (*Aloe*) *striatula* x *Aloe* (*Leptaloe*) sp.. in Cact.Succ.J. (U.S.) 6(6): 92-93, 1934. Resende in Mem.Soc.Brot. 2: 5-117, 1943 mentions several intergeneric crosses in passing, including *Aloiampelos* (*Aloe*) *striatula* x *Aloe* (*Chortolirion*) *subspicata*. His innovations include cultivars *Aloiampaloe* 'Gigas', a giant pentaploid hybrid of *Aloiampelos ciliaris*, and *Aloiampelos* 'Conimbricensis' an almost toothless variant of *A. striatula*.

Syn. X *Alolirion* Rowl. 1973.

X *Altulista* nothogen. nov. *Aloe* L. x *Tulista* Raf.

X *A. 'Desmetiana'* is based upon *Aloe X desmetiana* Baker in Fl.Cap.6: 329, 1896; Berger 1908: 191, as *Tulista* (*Aloe*) *variegata* x *Aloe humilis* and x *A. 'Weingartii'* (Berger l.c.) is credited with similar parentage.

Reynolds (1970) records and illustrates (Fig. 352) a natural hybrid of *Tulista* (*Aloe*) *variegata* x *Aloe hereroensis*, and notes another X *Altulista* involving *T. variegata* and *A. microstigma* (p. 210). A triple hybrid involving *T. variegata* and two aloes is recorded by E. Henze in Monatss.f.Kakteenk.11: 55-56,1901 (See Fig. 7) At least 4 cultivars belong here, too, as transfers from X *Aloloba*: see Rowley 1982; 46. Russell Scott (2000) states that *T. (Aloe) aristata* "seems to hybridise easily with other aloe species", but regrettably gives no details.

Syn. X *Aloloba* Rowl. 1982.

X *Altulisteria* nothogen. nov. *Aloe* L. x *Gasteria* Duv. x *Tulista* Raf. At least 2 cultigens exist: see Eggli 2001: 103 under X *Algastoloba* Cumming.

X *Gastulista* Rowl. 2013C: 111. *Gasteria* Duv. x *Tulista* Raf.

To the 19 cultigens listed from the early days of hybridisation by Radl 1896 we can now add:-

X *G. 'Apicroides'* based upon *Gasteria X apicroides* Baker in J. Linn.Soc.l8: 197, 1880 and Fl.Cap.6; 302, 1896 *Gasteria* sp. x *Tulista* sp. (Fig 8),

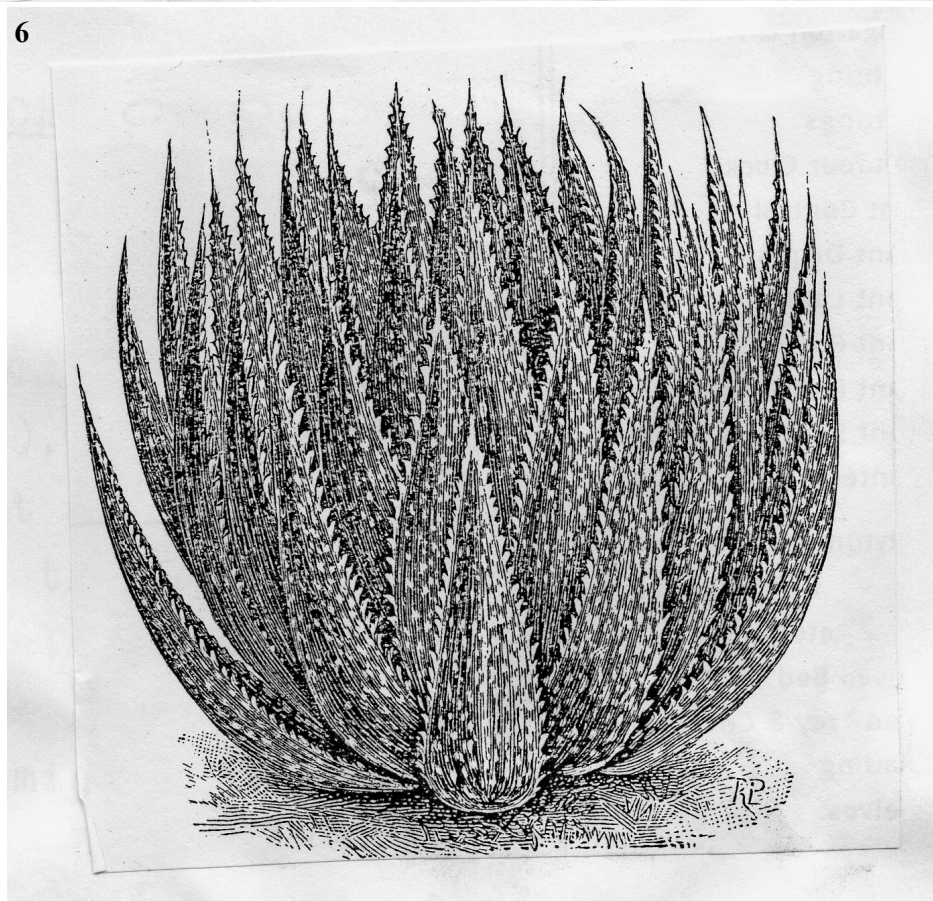
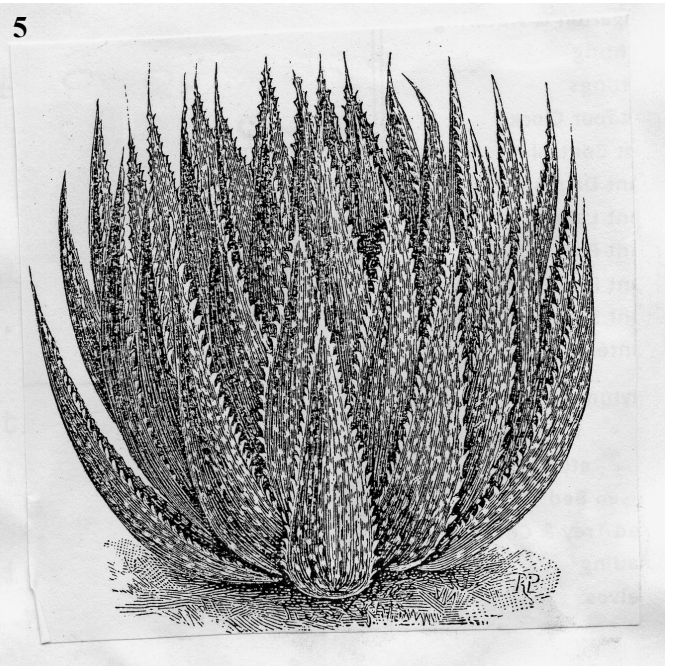
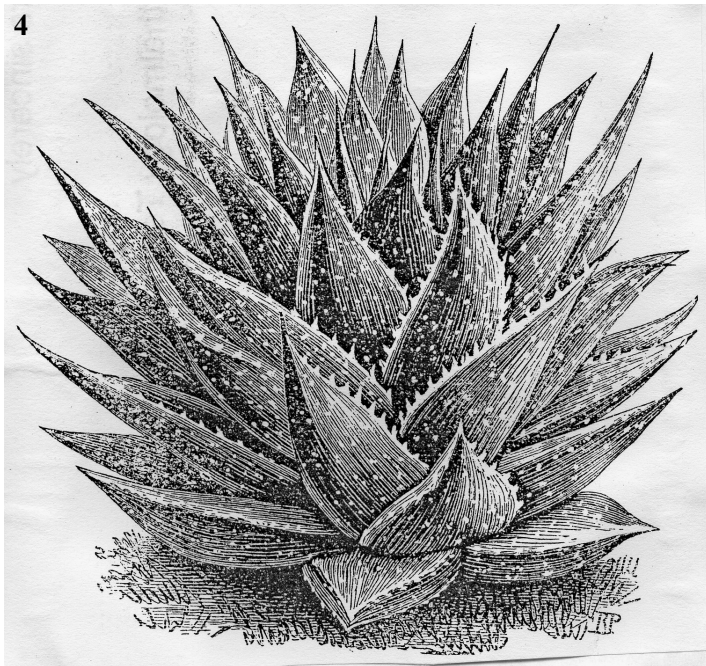
X '*Mortolensis*' Berger l.c. (*Tulista variegata* x *Gasteria acinacifolia*).

X *G. 'Rebutii'* based upon *Aloe X rebutii* Berger l.c. (*Tulista variegata* x *Gasteria* sp.).

X *G. 'Sculptilis'* (*Tulista variegata* x *Gasteria cheilophylla*), see Haseltonia 5: 94, 1997.

X *G. 'Simoniana'* based upon *Aloe X simoniana* Deleuil in Wiener Ill.Gartztg. 1893: 194 (*Tulista aristata* X *Gasteria disticha*).

X *G. 'Smaragdina'* based upon *Aloe X smaragdina* Berger in l.c. (*Tulista variegata* X *Gasteria* ? *acinacifolia*).



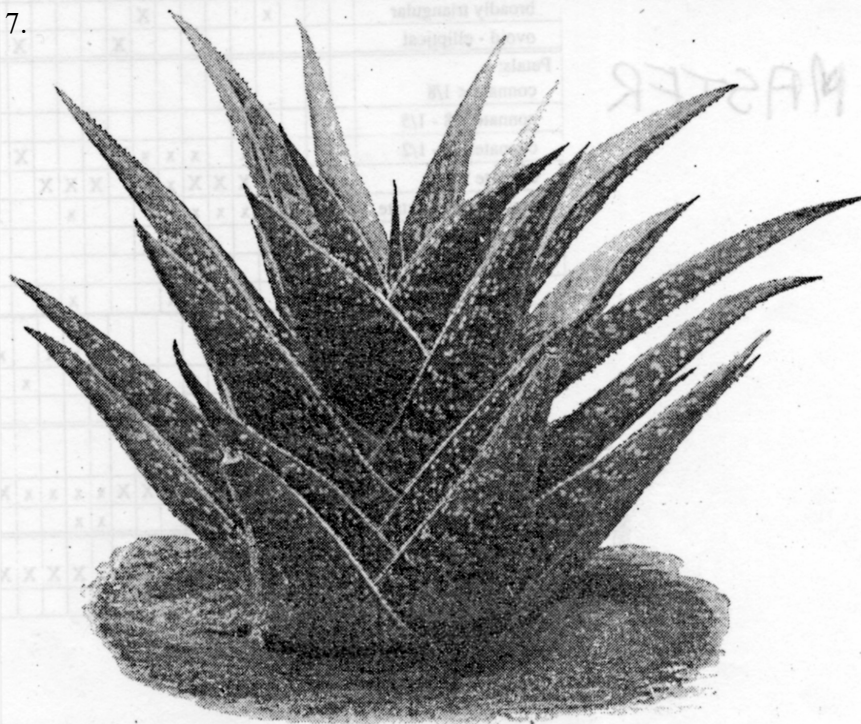
Some archetypal X *Gastulista* hybrids from Haage & Schmidt's 1896 Catalogue in Ehrfurt.

4. X *Gastulista* 'Bedinghausii'; *Gasteria disticha* (*nigricans*) x *Tulista aristata*.

5. X *Gastulista* 'Perfection'; *Gasteria disticha* (*nigricans*) x *Tulista aristata*.

6. X *Gastulista* 'Stella'; *Gasteria* sp. X *Tulista aristata*.

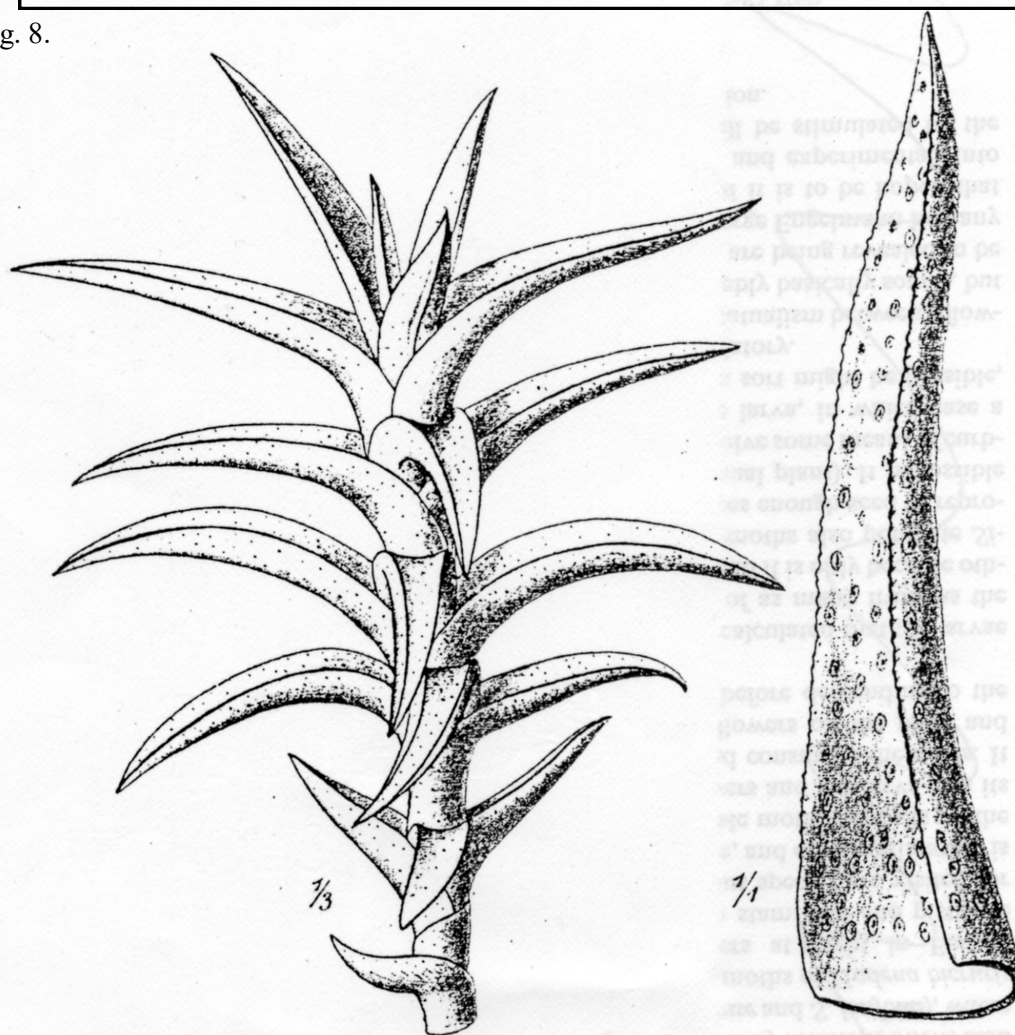
Fig. 7.



Ein Tripelbastard.
Aloe Schimperi × *humilis* × *variegata* Henze.
 Nach einer für die „Monatsschrift für Kakteenkunde“
 hergestellten Photographie.

A triple hybrid X *Altulista* involving *Tulista variegata* and two aloes, from Henze in 1901.

Fig. 8.



X *Gastulista* 'Apicroides', a nineteenth century cultigen grown at Kew, and in the private collection of J.T. Peacock.

Unnamed X *Gastulista* cultigens are also reported by Takahashi et al. in *Chromosoma* 105: 342-348, 1997, (*Tulista aristata* x *Gasteria excelsa*) along with karyotype details, and by Sato (1936) (*Tulista variegata* X *Gasteria carinata*). Modern additions to the list include X G. 'Ruby' (*Tulista rubriflora* x *Gasteria* sp.) from Bill Baker in California, and X G. 'Silky Oaks' from Burk's Nursery in the U.S.A. At Kew Cutler reports *T. (Aloe) aristata* X *Gasteria excelsa* in 1972, and Berger's "*Aloe* X *imbricata*" may belong here as a hybrid of *Tulista variegata* (Berger in Wiener 111.Gartztg,1893: 194).

Syn. X *Gastroloba* Cumming; X *Poellneria* Rowl.

X *Gasworthiopsis* nothogen. nov. *Gasteria* Duv. x *Haworthiopsis* Rowl.

At least 1 cultigen: X G. 'Figaro' Audissou in *Alsterworthia International* 12(2): 9, 2012: *Gasteria batesiana* X *Haworthiopsis scabra*.

X *Kumalista* nothogen nov. *Kumara* Med. x *Tulista* Raf. X *Kumalista corderoyi* (Berg.) n. comb.

Aloe X *corderoyi* Berger Monatss. f. Kakteenk. 14: 61, 1904 & Aloineae (Das Pflanzenreich 33): 324. 1908.

An attractive hybrid of *Kumara plicatilis* x *Tulista variegata* by Justus Corderoy that Berger records seeing in flower at La Mortola in May 1907. It has the shrubby habit of X *K. plicatilis*, but with leaves in spiral rosettes.

X *Hawiopsis* nothogen nov. *Haworthia* Duv. x *Haworthiopsis* Rowl.

Haworthia truncata Schönl. x *Haworthiopsis limifolia* (Marl.) Rowl. Pilbeam 1983: 132; 111.

X *Tulworthia* nothogen. nov. *Haworthia* Duv. x *Tulista* Raf.

At least 1 cultigen, including transfers from X *Astroworthia*.

X *T.* 'Alligator Pair' ISI 93-37, and *T.* 'Crocodile Rock' ISI 97-74 (*Haworthia pygmaea* x *Tulista koelmaniorum*).

X *Tulworthiopsis* nothogen. nov. *Haworthiopsis* Rowl. x *Tulista* Raf.

X *T.* 'Subattenuata', *Tulista pumila* (L.) Rowl. x *Haworthiopsis attenuata* (Haw.) Rowl. Pilbeam 1983: 125-127; 111.

Further research is needed to locate and document hybrids involving species of the three Sections of *Haworthia* now elevated to generic rank. Documentation is poor and scattered throughout the copious literature published by nurserymen and amateur breeders. Hybridisers from Uitewaal onwards have agreed that it is easier to cross species within each of the three Sections *Haworthia*, *Hexangularis* and *Robustipedunculares* than it is to intercross between them. As yet I have traced no credible record of *Aloe* x *Haworthiopsis*: do any candidates exist?

Nothogeneric names now referred to synonymy.

X *Algastoloba* Cumming is referred to *Altulisteria* Rowl.

X *Alolirion* Rowl. is referred to X *Aloiampaloe* Rowl.

X *Aloloba* Rowl. in referred to X *Altulista* Rowl.

X *Astroworthia* Rowl. is referred X *Tulworthia* Rowl.

X *Cummingara* Rowl. is referred to X *Maysara* Cumming.

X *Gasterlirion* Mays & Rowl. is referred to X *Gasteraloe* Rowl.

X *Gastroloba* Cumming is referred to X *Gastulista* Rowl.

X *Poellneria* Rowl. is referred to X *Gastulista* Rowl.

Additions to *Tulista*.

Tulista dinteri (Berg.) Rowl n. comb.

Syn. *Aloe dinteri* Berger in Dinter Neue Pfl. Deutsch-Südwest-Afr. 14, 1914.

Tulista sladeniana (Pole-Evans) Rowl. n. comb.

Syn. *Aloe sladeniana* Pole Evans in Ann. Bol. Herb. 3:13, 1920.

Tulista variegata (L.) Rowl. n. comb.

Syn. *Aloe variegata* L. in Sp. Pl. 321, 1753.

Tulista minima (Ait.) Boatwr. & Mann.

Syn. *Aloe margaritifera* v. *minima* Ait., *Haworthia minima* (Ait.) Haw.

Additional cultivars include:

Haworthiopsis 'Tauteae', *H. scabra* x *viscosa*. See Pilbeam p. 128; *Haworthia* x *tauteae* Arch. in Fl.Plants.Afr. 25 t.992, 1946.

Tulista 'Nain Jaune' by Audissou in *Alsterworthia International* 12(2): 8, 2012, under *Astroworthia*.

X *Gasterhaworthia* 'Towering Inferno', a recent distribution from the I.S.I., also under *Astroworthia*.

We end up with 14 nothogenera linking 8 recognised genera, as compared with 6 genera and 13 nothogenera in 2006. Here all ancient cultigens previously given Latinised binomials are rechristened as cultivars, with two exceptions. X *Kumalista corderoyi* seems outstanding enough to merit nothospecies status, and *Tulista bicarinata* is an isolated example of a much-studied indigen.

Hybrids Intergeneric and Intercladal.

DNA sequencing has given us a new insight into the significance of wide crosses, which offer more interest than a mere exercise in naming and tabulating. Attention focuses on crosses bridging the gulf between major branches of the family tree (see Daru et al. 2013 and Rowley 2013B). Many hybrids previously considered as intergeneric are now seen to cluster within the same clade. It turns out to be quite rare for plants from different major clades to be capable still of exchanging genes. We call such hybrids **intercladal** (Rowley 2014). Among succulents, *Gasteria* proves to be exceptional. A monophyletic major clade, it can still intercross with species of at least 7 other genera, the F₁ progeny in some cases still fertile enough to enable breeders to raise further generations.

Of course, everything depends on the level at which you discriminate major and minor clades and here taxonomists take different views. Manning and co-workers have offered the extremes of lumping and splitting; I prefer a middle course and less extreme carve-up. Time will tell which approach finds favour in the long run.

As Chris Thomas writes (in New Scientist Jan. 11; 28, 2014) "Genes are jumping around. Molecular genetics is finding that hybridisation between species is more common than previously suspected. Darwin talked about a tree of life, with species branching out and separating. But we are discovering it is more of a network, with genes moving between close branches as related species interbreed. This hybridisation quickly opening up evolutionary opportunities."

Acknowledgements

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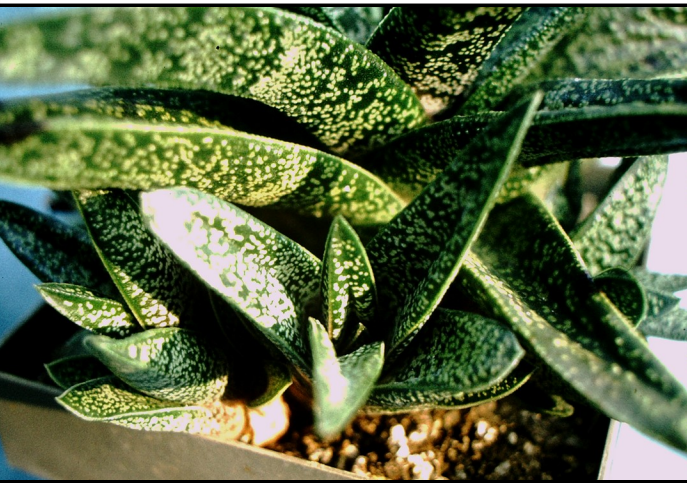
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Photographic presentation of some species of the revised genera.



X *Gastulista*

(*Gasteria batesiana* x *Tulista variegata*)



X *Gasteraloe*

(*Aloe jucunda* x *Gasteria batesiana*)



Aloidendron ramosissimum, *Aloe pearsonii* at Hellskloof. Photo Len Newton.



Aloidendron dichotomum Photo Hall 235.



Aloidendron eminens (+ *Dracaena schizantha*) Photo F. Howard.



Aloiampelos gracilis Photo Hall 448.



Tulista rubryflora Hall 849.



Tulista aristata. Photo Rowley.



Tulista variegata Photo Hall 890.



Aloe mitriformis Berkeley U.B.G.



Aloidendron pillansii