

## A Molecular Phylogeny and Generic Classification of Asphodelaceae subfamily Aloioideae: A Final Resolution of the Prickly Issue of Polyphyly in the Alooids?

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**Abstract**—Phylogenetic analysis of plastid (*rbclA*, *matK*, *trnH-psbA* and the *trnL* intron) and nuclear (ITS1) sequence datasets in a wide sampling of species of Asphodelaceae: Aloioideae provides a generally well-resolved phylogeny. Among traditionally accepted genera only *Astroloba* and *Gasteria* are supported as monophyletic. Species of *Haworthia* are distributed among three clades corresponding to the current subgenera. *Aloe* s. l. (including *Chortolirion*) segregates into six, well-supported clades corresponding respectively to sections *Dracoaloe* (= *Aloidendron*), *Kumara* + *Haemanthifoliae*, *Macrifoliae*, *Aristatae*, *Serrulatae*, and the remainder of the genus. The first three clades are retrieved as early branching lineages, whereas *A.* sects. *Aristatae* and *Serrulatae* are strongly supported as members of a clade including *Astroloba* + *Haworthia* subg. *Robustipedunculatae*. We examine possible options for recircumscribing the genera of Aloioideae as reciprocally monophyletic entities. Although morphological and molecular data are consistent with expansion of *Aloe* to include all members of Aloioideae, we accept and implement an alternative option maintaining historical usage in the group as far as possible. *Astroloba* and *Gasteria* are retained as currently circumscribed; *Haworthia* is restricted to *H.* subg. *Haworthia*; the genus *Tulista* is accepted for members of *H.* subg. *Robustipedunculatae*, with the new combination *T. minima*; and *H.* subg. *Hexangulares* is treated as the genus *Haworthiopsis* with the new combinations *H. koelmaniorum*, *H. pungens*, and *H. tessellata*. The genus *Aloe* is restricted to the clade comprising the ‘true aloes’, with *Aloidendron*, *Aloiampelos*, and *Kumara* accepted as segregates, the latter broadened to include *A. haemanthifolia* as *K. haemanthifolia*. *Aloe aristata* is segregated in the monotypic genus *Aristaloe* as *A. aristata* and *Aloe* sect. *Serrulatae* is treated as the new genus *Gonialoe* with the species *G. dinteri*, *G. sladeniana*, and *G. variegata*.

**Keywords**—*Aloe*, *Aristaloe*, classification, *Gonialoe*, *Haworthia*, nomenclature.

Subfamily Aloioideae (Aloaceae sensu Smith and Steyn 2004), with ca. 500 species restricted to the Old World, is the larger of two subfamilies of Asphodelaceae (sensu APGII 2003) currently recognised. Aloioideae are strongly supported as monophyletic, diagnosed by their more or less succulent foliage and a basic chromosome number of  $x = 7$  (Taylor 1925; Smith and Van Wyk 1998). They are characterised chemically by the presence of anthrone-C-glycosides in the leaves and 1-methyl-8-hydroxyanthraquinones in the roots (Smith and Van Wyk 1998).

Four core genera were recognized in the subfamily until recently (Klopper et al. 2010), with *Aloe* L. (ca. 400 species) traditionally by far the largest genus, followed by *Haworthia* Duval (ca. 70 species), *Gasteria* Duval (23 species), and *Astroloba* Uitewaal (seven species). Three additional genera, namely *Lomatophyllum* Willd. (ca. 14 species), *Chortolirion* A. Berger (three species), and *Poellnitzia* Uitewaal (one species) have also been recognised by some authorities (Smith and Van Wyk 1998). *Chortolirion*, a small genus of acaulescent species from summer-rainfall grasslands, has weakly armed, grass-like leaves with swollen, bulb-like base and *Haworthia*-like flowers (Smith and Van Wyk 1993; Smith 1995a). Although included in *Haworthia* in the past (see Obermeyer 1973), it resembles the grass-like species of *Aloe* sect. *Leptoaloe* A. Berger in vegetative morphology and leaf anatomy (Smith and Van Wyk 1993). Molecular study has shown it to be deeply nested within *Aloe* and it is now included in that genus (Daru et al. 2013; Grace et al. 2013). *Lomatophyllum*, endemic to Madagascar and the Mascarenes, was separated from *Aloe* by its fleshy fruits, but is also deeply nested in the genus (Treutlein et al. 2003a,

2003b) and is appropriately treated as a section in *Aloe* (Glen and Hardy 2000). *Poellnitzia* is vegetatively and chemically similar to *Astroloba* and was distinguished by its inclined racemes of secund, orange-red flowers with connivent tepals. It is now usually treated as a specialised, ornithophilous species of *Astroloba* (Manning and Smith 2000).

*Aloe* has recently been partially dismembered by Grace et al. (2013), with sections *Dracoaloe* (= *Aloidendron*), *Macrifoliae*, and *Kumara* raised to generic level as *Aloidendron* (A. Berger) Klopper & Gideon F. Sm. (six species), *Aloiampelos* Klopper & Gideon F. Sm. (seven species), and *Kumara* Medik. (one species), respectively. This step, taken on the basis of unpublished molecular data, receives support from the molecular phylogeny of Daru et al. (2013). Following this precedent and based on the same phylogeny, Rowley (2013) has since restricted the genus *Haworthia* to members of *H.* subg. *Haworthia*. Most members of subg. *Hexangulares* were transferred to the new genus *Haworthiopsis* G. D. Rowley, and the remaining species of *Haworthia*, comprising primarily members of subg. *Robustipedunculatae*, were amalgamated with *Astroloba* and *Aloe aristata* in the genus *Tulista* Raf.

The morphology and taxonomic history of the subfamily are well summarised by Smith and Van Wyk (1998) and Klopper et al. (2010). Genera of Aloioideae were traditionally diagnosed primarily on floral characters, namely the size, symmetry, shape, and colour of the perianth, supplemented in some instances by vegetative characters, phytochemistry, cytology, and nectar sugar composition (Smith and Steyn 2004; Klopper et al. 2010). *Aloe* in its traditional circumscription is poorly defined and lacking in evident synapomorphies. Most species in the genus have spiked or toothed

leaves with acrid/unpalatable sap, sunken stomata, bright yellow to red or sometimes bicoloured flowers usually with exerted anthers, and flattened, wind-dispersed seeds. There are, however, numerous exceptions, including taxa with almost entire leaf margins, and species with campanulate to tubular or gasteriform flowers with actinomorphic or bilabiate symmetry, and a dull to brightly coloured perianth. The recent segregation of *Aloiampelos*, *Aloidendron*, and *Kumara* from *Aloe* by Grace et al. (2013) has not substantially altered the morphological diagnosis of the genus, apart from excluding the truly arborescent forms. *Gasteria* is clearly distinguished by its inclined racemes of secund, curved flowers with well-developed perianth tube, usually swollen at the base and with included anthers, and mostly dark green leaves marked with bands of whitish maculations and with horny, untoothed margins (Van Jaarsveld 2007). Species of *Astroloba* are typically caulescent and multi-stemmed with spirally inserted, hard, smooth, pungent leaves and racemes of small, tubular flowers with included anthers (Smith 1995b; Manning and Smith 2000). There is a close vegetative similarity between *Astroloba* and some species of *Haworthia* s. l., which was distinguished by more or less strongly bilabiate flowers. Species of *Haworthia* were segregated among three subgenera on the basis of subtle differences in floral morphology, which correlate with broad patterns in vegetative morphology (Bayer 1982, 1999). *Astroloba*, *Gasteria*, and *Haworthia* s. l. are mostly endemic to the southern African, winter-rainfall region.

Phylogenetic relationships among the genera of Aloioideae have been greatly clarified by analysis of plastid and nuclear sequences, plus some genomic fingerprinting (Adams et al. 2000; Chase et al. 2000; Treutlein et al. 2003a, b; Zonneveld and Van Jaarsveld 2005; Ramdhani et al. 2011; Daru et al. 2013). We now have an adequate and well-supported understanding of the relationships of the smaller genera, but some species relationships within the larger genera *Aloe* s. l. and *Haworthia* s. l. are still incompletely resolved.

The first phylogenetic study to include more than a handful of species (Treutlein et al. 2003b) relied on chloroplast nucleotide sequence data plus genomic DNA fingerprinting. Sampling, although limited, was sufficient to conclude that *Haworthia* and *Aloe* were not monophyletic as circumscribed, with *H.* subg. *Haworthia* forming a well-supported clade nested within *Aloe*, while *H.* subg. *Hexangulares* was located in a separate clade that included *Gasteria*, *Astroloba*, and *Aloe aristata* (Treutlein et al. 2003b). *Chortolirion* was shown to cluster with the grass-like species of *Aloe* sect. *Leptoaloe*, and *Lomatophyllum* was firmly nested within an unresolved clade of *Aloe*. A later study by Ramdhani et al. (2011), focusing on phylogenetic relationships in *Haworthia* using DNA sequences from three gene regions, confirmed the paraphyly of that genus. The recent phylogenetic analysis of Aloioideae by Daru et al. (2013) used both plastid (*rbcl*, *matK*, and *trnH-psbA*) plus nuclear (ITS1) sequence datasets from a much increased sampling of taxa from all genera, covering a wide range of vegetative and floral diversity in the subfamily. Their investigation substantiated previous studies in identifying paraphyly in both *Aloe* and *Haworthia*. Preliminary steps at reducing paraphyly in these two genera have now been taken, with the segregation of *Aloiampelos*, *Aloidendron*, and *Kumara* from *Aloe* proposed by Grace et al. (2013), and the analogous treatment of *Haworthia* by Rowley (2013) in which the genera *Haworthiopsis* and

*Tulista* have been recognised. Neither of these treatments, however, provides a complete phylogenetic classification for the subfamily.

Systematic surveys of potentially useful taxonomic characters, including chemistry and fruit and seed characters, have been hampered until now by the lack of a clear understanding of relationships within Aloioideae. Here we add sequence data from the *trnL* intron to the existing datasets of Daru et al. (2013) in an attempt to improve resolution of the phylogeny. We also include three additional, morphologically distinctive species of *Aloe* (*A. haemanthifolia*, *A. kniphofioides*, and *A. variegata*). Our analysis provides a well-sampled basis from which to derive a phylogenetic classification for subfamily Aloioideae. We assess available options, based on the recognition of reciprocally monophyletic lineages, for likely popular support and elect to follow recent precedent in adopting a multi-genus classification, recognising the eleven genera *Aloe*, *Aloiampelos*, *Aloidendron*, *Aristaloe*, *Astroloba*, *Gasteria*, *Gonialoe*, *Haworthia*, *Haworthiopsis*, *Kumara*, and *Tulista*. We provide descriptions and keys to all genera, and make necessary nomenclatural adjustments and corrections.

#### MATERIALS AND METHODS

The molecular sequence data set of Daru et al. (2013) was supplemented by the inclusion of three morphologically distinctive species of *Aloe* (*A. haemanthifolia*, *A. kniphofioides*, and *A. variegata*) and by the addition of *trnL* intron sequence data in an attempt to improve resolution of the phylogenetic backbone. A total of 157 species and subspecies, representing all genera traditionally accepted in subfamily Aloioideae, were analysed for five gene regions, including nuclear ITS1 and plastid *matK*, *rbcl*, *trnH-psbA*, and the *trnL* intron. Taxon sampling included 18/23 species (78%) of *Gasteria*, 48/70 species (69%) of *Haworthia*, 66/400 species (16.5%) of *Aloe* from 20 sections (including *Lomatophyllum*), 4/7 species (57%) of *Astroloba* (including *Poellnitzia*) and 1/3 species (33%) of *Chortolirion*. The traditional taxonomic circumscriptions of *Aloe* and *Haworthia* were adopted for the analyses. The PCR amplification and sequencing protocols for the *trnL* intron followed the same methodology as that of *rbcl* and *trnH-psbA* in Daru et al. (2013). Newly generated *trnL* intron sequences are deposited in GenBank under the accession JX630178–JX630330. See Appendix 1 for all other relevant GenBank accession numbers for this study.

Phylogenetic analyses were performed for plastid, nuclear, combined datasets (plastid + nuclear), and for a reduced dataset based on all five genes. The combined data analysis was justified based on a congruence test of the separate plastid and nuclear datasets using partitioned Bremer support (DeSalle and Brower 1997) implemented in TreeRot v.3 (Sorenson and Franzosa 2007) as described in Daru et al. (2013). No significant differences were found between the Bremer support (BS) indices of major nodes of the plastid and nuclear trees. Hence the analysis was conducted on the combined dataset (*rbcl* + *matK* + *trnH-psbA* + *trnL* + ITS1). To obtain a more robust and resolved relationship in the *Astroloba*-*Gasteria* clade we carried out an additional analysis on a reduced dataset that included only members from the the *Gasteria* + *Hexangulares* + *Robustipedunculatae* + *Astroloba* clade.

All analyses (plastid, nuclear, combined, and reduced datasets) employed parsimony and Bayesian (BI) phylogenetic methods, as outlined in Daru et al. (2013), with Bremer support and Posterior probability (PP) values indicated on the resulting phylogenetic trees.

#### RESULTS

**Phylogenetic Analyses**—Analysis of the five gene regions combined for Aloioideae is topologically comparable with that retrieved by Daru et al. (2013), but with significantly improved resolution of the phylogenetic backbone. A summary of statistics for the phylogenetic framework is presented

TABLE 1. Summary of phylogenetic analysis of Alooideae obtained from Modeltest and MP analyses of separate and combined datasets (modified from Daru et al. 2013). AIC = Akaike information criterion; CI = consistency index; RI = retention index

	<i>rbcLa</i>	<i>matK</i>	<i>trnH-psbA</i>	<i>trnL</i>	Combined plastid ( <i>rbcLa</i> + <i>matK</i> + <i>trnH-psbA</i> + <i>trnL</i> )	ITS1	Combined plastid + ITS1
No. of taxa included	171	173	160	162	175	159	175
No. of included characters	552	789	768	563	2,672	409	3,081
No. of constant characters	471	529	644	314	1,958	232	2,218
No. of variable sites	81 (15%)	260 (33%)	124 (16%)	249 (44%)	714 (27%)	177 (43%)	863 (28%)
No. of parsimony informative sites	55 (10%)	165 (21%)	71 (9%)	135 (24%)	426 (16%)	98 (24%)	516 (17%)
No. of trees (Fitch)	149	1062	106	86	35	344	376
No. of steps (Tree length)	120	408	194	465	1275	346	1910
CI	0.74	0.75	0.74	0.68	0.67	0.64	0.55
RI	0.91	0.92	0.92	0.83	0.87	0.92	0.82
Average number of changes per variable site (number of steps/ number of variable sites)	1.5	1.6	1.6	1.9	1.8	2.0	2.2
Model selected by AIC	HKY + G	TVM + G	TVM + I + G	TVM + I + G	TIM + I + G	TRN + G	GTR + I + G

in Table 1 and the majority-rule consensus tree for the combined dataset is shown in Fig. 1.

The combined molecular analysis retrieves three primary clades as a basal trichotomy. *Aloe* sects. *Aloidendron* + *Dracoaloe*, the ‘tree aloes’ (clade A), are well-supported (1.00 PP, 83 BS) as one clade in this trichotomy. The second comprises *Haworthia* subg. *Haworthia* (clade C), which is well supported (1.00 PP, 98 BS) as monophyletic, plus *Aloe plicatilis* (*A. sect. Kumara*) as sister to *A. haemanthifolia* (*A. sect. Haemanthifoliae*) with moderate support (0.77 PP, 54 BS; clade B). The sister relationship between *H. subg. Haworthia* and *A. plicatilis* + *A. haemanthifolia* receives weak support only in the BI analysis (0.57 PP) and was not retrieved by Daru et al. (2013). The third clade in the basal trichotomy comprises the remaining members of the subfamily and is moderately to well supported (0.78 PP, 90 BS). It resolves the ‘rambling aloes’, *A. sect. Macrifoliae* (clade D), as strongly monophyletic (1.00 PP, 97 BS) and sister to the rest of the clade. The latter are resolved, in turn, as a well-supported clade (0.99 PP, 90 BS; clade E) comprising the bulk of the genus *Aloe*, the so-called ‘true aloes’, as sister to a well-supported clade (1.00 PP, 98 BS) comprising all remaining species in the analysis, namely *Astroloba*, *Gasteria*, *Haworthia* subg. *Hexangulares* and *Robustipedunculatae*, plus *Aloe aristata* and *A. variegata*. Among the ‘true aloes,’ *Chortolirion* is placed as sister to a group of grass aloes (*A. sect. Leptoaloe*) that includes *A. kniphofioides*.

Relationships within the *Astroloba*–*Gasteria* clade (clades F–H) are less satisfactorily resolved, notably the relationships among the species of *H. subg. Hexangulares*. In the combined analysis, both *Gasteria* (1.00 PP, 93 BS; clade H) and *Astroloba* (1.00 PP, 86 BS) are well-supported as monophyletic, as is *H. subg. Robustipedunculatae* (1.00 PP, 92 BS). *Astroloba* is moderately well-supported (0.95 PP, 66 BS) as sister to a weakly supported trichotomy (0.71 PP) comprising *Aloe aristata*, *A. variegata*, and *H. subg. Robustipedunculatae*. *Gasteria* is associated with the bulk of the species of *Haworthia* subg. *Hexangulares* with mixed support (1.00 PP, 57 BS), and subg. *Hexangulares* is, in turn, weakly supported (0.70 PP) as monophyletic only in the BI analysis.

Relationships among the remaining members of *Haworthia* subg. *Hexangulares* received no significant support: *H. venosa* and *H. attenuata* are placed with only weak BI support (51 PP) as sister to *Gasteria* plus the bulk of *H. subg.*

*Hexangulares*, and *H. koelmaniorum* is unplaced in the clade. The position of *Haworthia koelmaniorum* is inconsistent in the plastid and nuclear analyses, with the species retrieved as sister to *Astroloba* in the plastid topology (Fig. 2) but placed within *H. subg. Hexangulares* in the nuclear topology (Fig. 3).

Re-analysis of the reduced dataset increases resolution and support values in part of the *Astroloba*–*Gasteria* clade, most notably in placing *Aloe aristata* as sister to *A. variegata* + *H. subg. Robustipedunculatae*, with weak support (0.76 PP) only in the BI analysis (Fig. 4). Placement of the various elements of *Haworthia* subg. *Hexangulares* remains weakly supported: *H. koelmaniorum* is associated with the *Astroloba*–*H. subg. Robustipedunculatae* clade only in the reduced BI analysis (0.63 PP), but is unplaced within the group in the complete analysis; and *H. venosa* is weakly supported as sister to *H. attenuata* in both the complete (0.74 PP, 51 BS; Fig. 1A) and the reduced (0.75 PP, 57 BS; Fig. 4) analyses in an unsupported relationship with the remaining members of the subgenus plus *Gasteria*.

## DISCUSSION

Inclusion of the three additional taxa and the plastid sequence data from the *trnL* intron improved resolution of phylogenetic relationships within Alooideae compared to Daru et al. (2013), but support for some of the basal nodes remains poor. We conclude that the group has undergone recent and rapid diversification, as corroborated by an inadequate correlation between morphology and molecular relationships and the resultant difficulty in unequivocal generic delimitation in the group.

The evolution of taxonomically useful morphological character states in Alooideae was examined by Daru et al. (2013) and most were demonstrated to be homoplasious. More critically, *Aloe* was only negatively diagnosable, lacking any synapomorphies by which it could be recognised. Floral morphology in the subfamily is much more labile than previously thought (Daru et al. 2013), with the presumptively unique *Haworthia*-type flower having evolved independently at least three times in the subfamily (*Aloe sect. Chortolirion*, *Haworthia* subg. *Haworthia*, and again in *H. subg. Hexangulares* and *Robustipedunculatae*). Independent support for this finding comes from an analysis

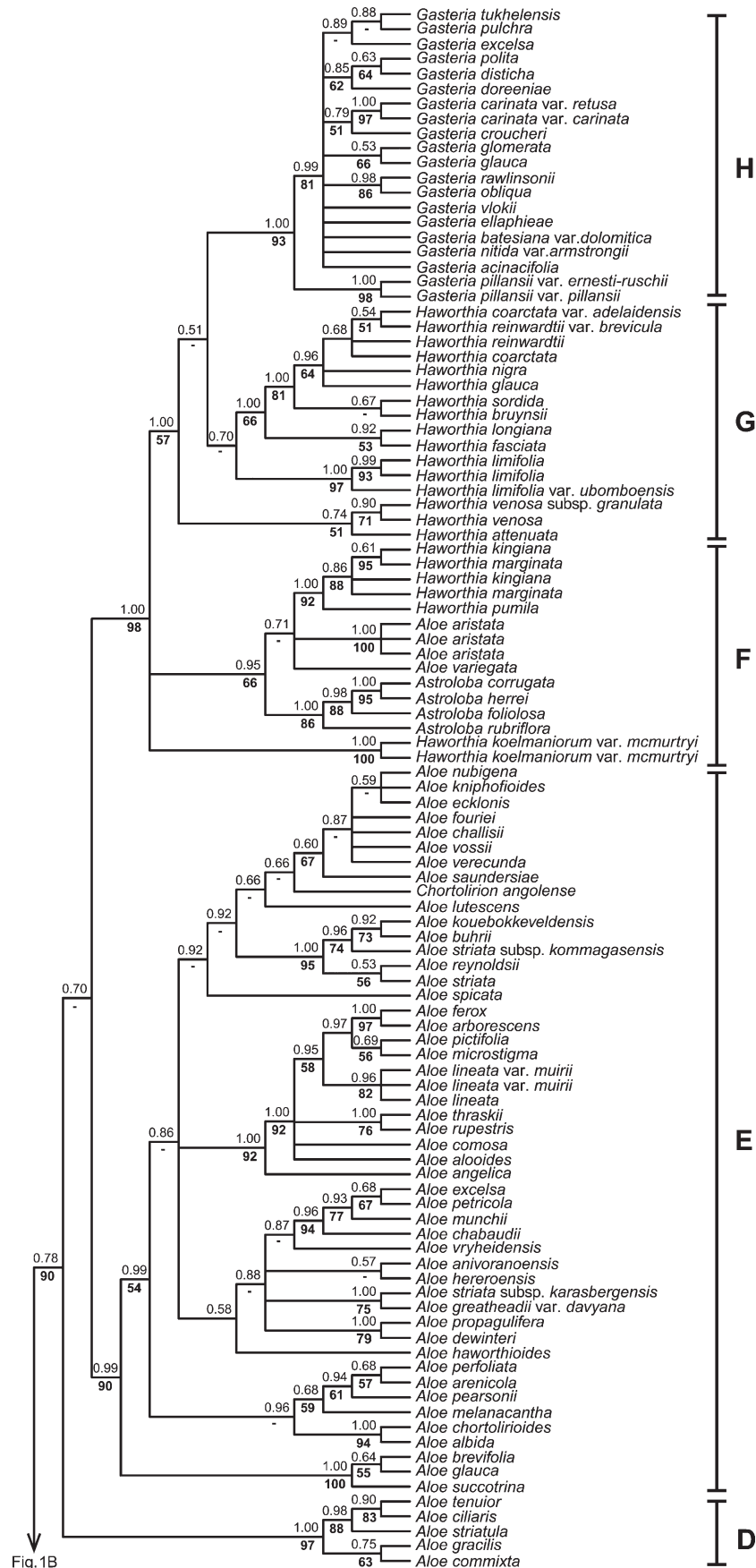


FIG. 1. Bayesian phylogram of Aloioideae estimated with concatenated matrix of ITS1, *rbcl*a, *matK*, *trnH-psbA*, and *trnL* intron. Bayesian posterior probabilities are indicated above branches and maximum parsimony bootstrap support below branches. Major clades recovered in the phylogeny are annotated with letters A–H.

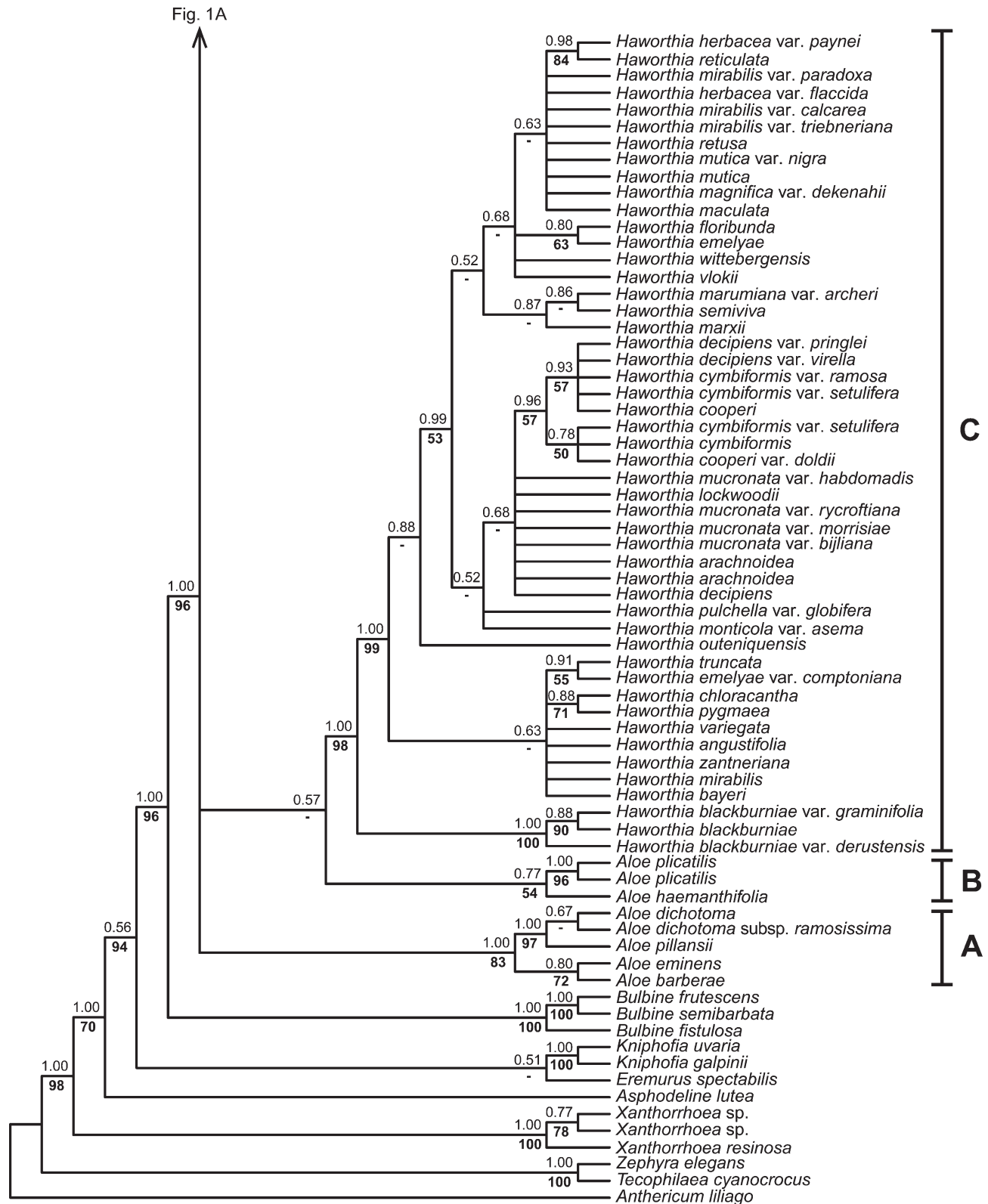


FIG. 1. Continued.

of nectar sugar content in the genus (Smith et al. 2001), which identifies two groups, the *Haworthia* type (usually < 50% sucrose) restricted to *H.* subg. *Haworthia* and the *Hexangulares* type (usually > 60% sucrose) in *H.* subg. *Hexangulares* and *Robustipedunculatae*, *Astroloba*, and *Chortolirion*.

The *Gasteria*-type flower, which is most parsimoniously interpreted as a reversion to bird-pollination from an entomophilous ancestor with *Haworthia*-type flowers, appears to have evolved just once. Similarly, the *Astroloba*-type flower appears to be unique.

It is increasingly evident that floral morphology alone is an inadequate predictor of relationships in the subfamily. The differences in floral morphology used as the primary characteristic justifying identification of various lineages in Alooideae as segregate genera almost certainly represent syndromes associated with shifts in pollination systems from bird to insect and back. Thus, *Gasteria* is defined primarily by bird-pollinated flowers with included anthers; *Astroloba* and *Haworthia* by insect-pollinated flowers with included anthers and respectively radial and bilateral perianth symmetry; and *Aloe* is distinguished by bird- or insect-pollinated flowers, mostly with exerted anthers. It is significant that *Gasteria* is one of few bird-pollinated, Old World taxa with sucrose-rich nectar (Van Wyk et al. 1993), supporting the proposition of a shift from insect to bird pollination in the genus.

Although there is general similarity in vegetative morphology among species within the smaller genera, the large genus *Aloe* displays great diversity in this regard. In the absence of clear morphological signals, molecular data have been critical in assessing phylogenetic relationships in the family. This is especially evident in the long-standing association of three separate lineages of species with *Haworthia*-type flowers as the genus *Haworthia*, and in the unpredictable relationships of the various lineages of *Aloe*.

The value of flavonoids as phylogenetic signals in *Aloe* needs to be considered with care. The flavone *isovexin* was identified as a taxonomic marker of *Aloiampelos* and *Aloe* sects. *Leptoaloe* (= *A. sect. Graminialoe*) and *Lomatophyllum* by Viljoen et al. (1998), prompting the consideration that these three groups were related. Our molecular analyses, however, suggest that the occurrence of *isovexin* in these taxa is more likely to be convergent. Although the absence of *isovexin* from the leaf exudates of *A. kniphofioides* (*A. sect. Leptoaloe*) led Viljoen et al. (1998) to raise the possibility that this species was of hybrid origin, this is not supported by our molecular analysis, which places *A. kniphofioides* unequivocally among other members of *A. sect. Leptoaloe* in both the nuclear and plastid analyses. Similarly, the presence of the unusual naphthalene derivative *plicatiliside* in various species of *Aloe* (including *A. plicatilis*) (Viljoen et al. 1999) is most parsimoniously interpreted as chemical convergence.

Treutlein et al. (2003b) described four possible options or 'scenarios' to account for the results of their preliminary phylogenetic analysis of the Alooideae, in which the possible paraphyly of *Aloe* and *Haworthia* was first demonstrated. The first scenario proposed methodological constraints, namely an inadequate diversity of gene regions included in the analysis. This is not applicable to the multi-gene analysis by Daru et al. (2013) and even less so to this analysis, which includes additional morphologically divergent species of *Aloe*. The second scenario postulated retaining the taxonomic status quo, thereby maintaining *Aloe* and *Haworthia* as demonstrably paraphyletic genera. However, as Treutlein et al. (2003b) indicate, the current subfamilial classification does not reflect available evidence from phylogenetic analyses, and the further it departs from phylogenetic evidence the more difficult it will be to integrate practice and theory. There is an increasing trend to align classifications with phylogenies at all taxonomic levels, and for taxa to be circumscribed as monophyletic lineages (Backlund and Bremer 1998), and we advocate a

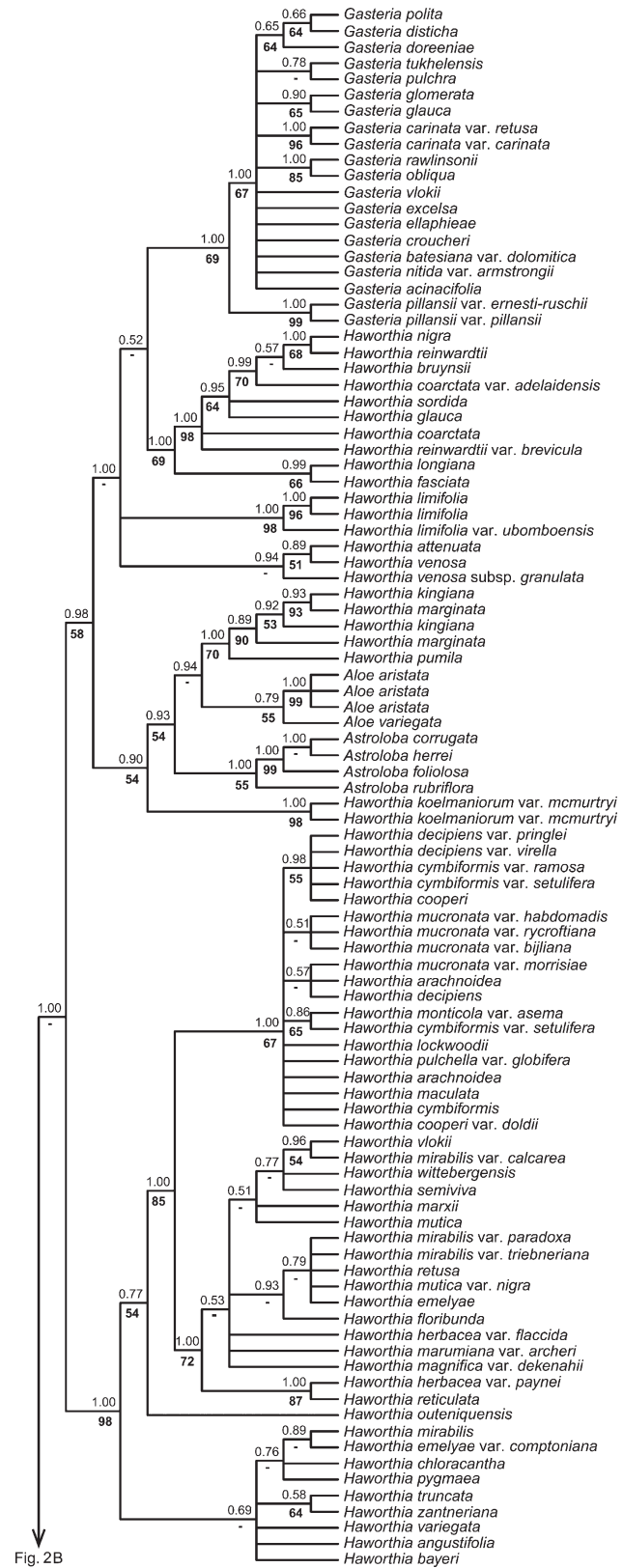


Fig. 2B

FIG. 2. Bayesian phylogram of Alooideae estimated with combined plastid matrix from *rbclLa*, *matK*, *trnH-psbA*, and *trnL* intron. Bayesian posterior probabilities are indicated above branches and maximum parsimony bootstrap support below branches.

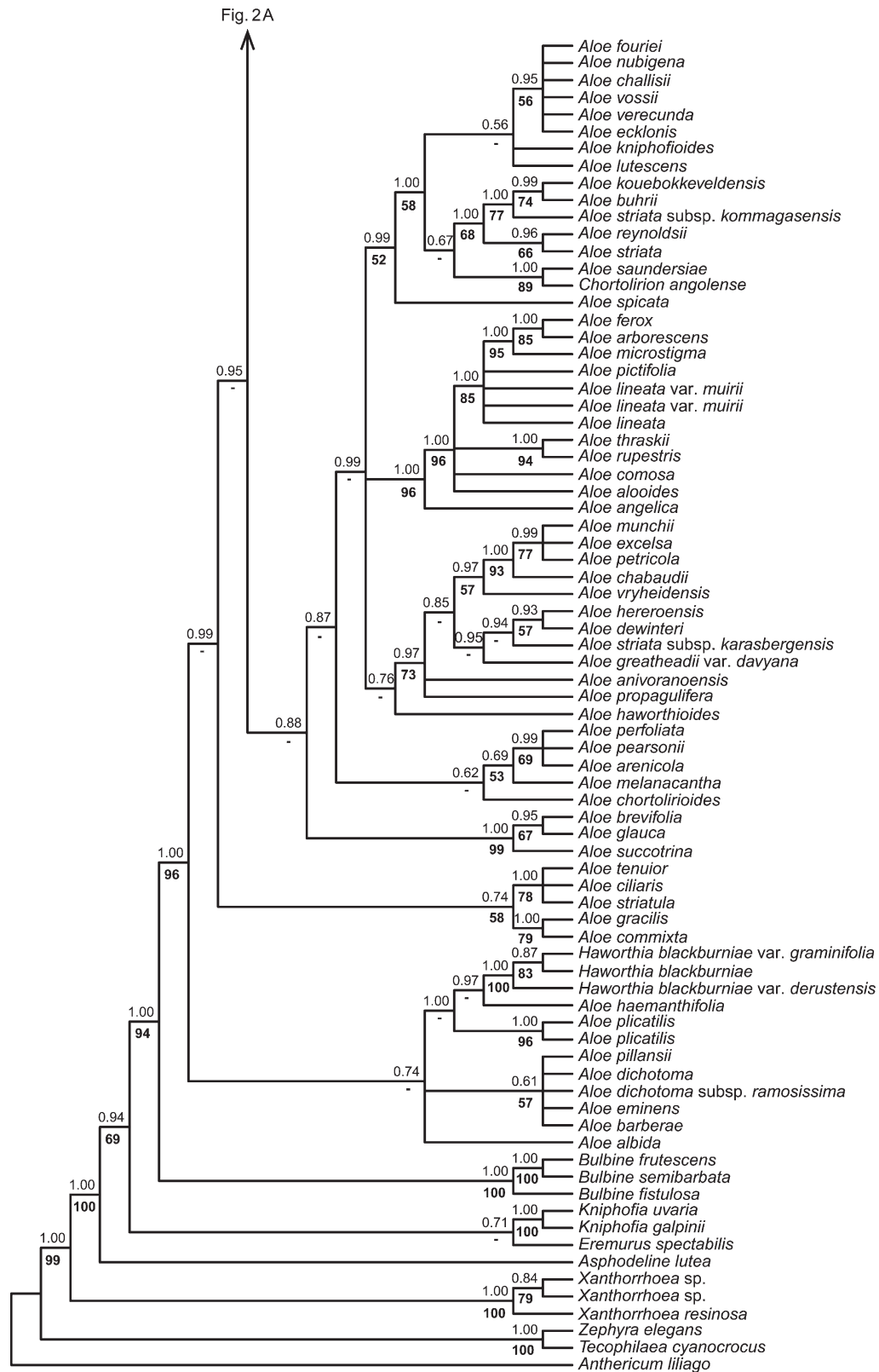


FIG. 2. Continued.

monophyletic classification of Alooiidae incorporating available phylogenetic evidence.

The remaining two options accept the principle of monophyly in deriving a generic classification and we consider them further. The five-gene analysis presented here includes

good representation of *Astroloba* (57% of species), *Gasteria* (78% of species), and *Haworthia* (69% of species), but only ca. 17% of the 400 or so *Aloe* species. These are, however, drawn from 20 of the 25 sections recognised by Glen and Hardy (2000) for southern Africa, the centre of diversity for

the genus, and thus represent the majority of the morphological, and presumably phylogenetic, diversity in the genus. We feel justified in anticipating that the addition of further species is unlikely to alter the phylogenetic framework in any meaningful way. Thus, molecular data confirm the relationship of *A. kniphofioides* to the clade that includes the vegetatively similar *A. subspicata* (= *Chortolirion*) and other grass aloes despite seemingly contrary evidence from flavonoid chemistry (Viljoen et al. 1998). Similarly, *A. haemanthifolia* is retrieved as sister to *A. plicatilis*, which it resembles in leaf morphology. At the very least, we know of no unsampled *Aloe* species that display the morphological attributes that have emerged as diagnostic for the segregate genera *Aloidendron*, *Aloiampelos*, and *Kumara*, or for the *A. aristata* and *A. variegata* clades.

Option three, the 'splitter's option', proposes the recognition of additional smaller genera within Alooideae as necessary to retain all or most of the currently accepted genera as monophyletic. Among the traditionally recognised genera, only *Astroloba* and *Gasteria* can be retained unchanged. *Haworthia* is evidently polyphyletic, despite its apparently derived flowers, and must be split into at least three smaller genera corresponding to the current subgenera (clades C, G, and part of F). There are definite, although minor, floral differences that support this treatment (see Bayer 1999 for illustrations), as well as some associated trends in vegetative morphology, notably extreme succulence and the lack of white tuberculation in *H.* subg. *Haworthia* (Rowley 2013).

The most drastic changes are required in *Aloe*, species of which are distributed among five well-supported lineages (clades A, B, D, E, and F), making a broadly circumscribed *Aloe* polyphyletic. To render *Aloe* monophyletic it is necessary to restrict the genus to the 'true Aloes' of clade E and to exclude the remaining four lineages, either as separate genera or as part of existing genera. Four of these lineages have been recognised taxonomically as *Aloe* sects. *Dracoaloe* (clade A), *Macrifoliae* (clade D), *Serrulatae*, and *Aristatae* (Glen and Hardy 2000; Van Jaarsveld 2010), with associated morphological characters, but only the first two have been recognised recently at generic level (Grace et al. 2013). The fifth lineage (clade B) includes the arborescent species *A. plicatilis* (*A.* sect. *Kumara*) plus the acaulescent *A. haemanthifolia* (*A.* sect. *Haemanthifoliae*). The association of these two monotypic sections receives support from their unusual distichous, lorate leaves with obtuse apices and smooth margins, and from their restricted distribution to moist sandstone cliffs in the Cape Fold Mountains. Although differing in inflorescence shape, both species also share included or only shortly exerted anthers. *Aloe* sect. *Kumara* has also been treated as a distinct genus, most recently by Grace et al. (2013). Two remaining lineages must be removed from *Aloe*: *A. aristata* (*A.* sect. *Aristatae*) and *A. variegata* (*A.* sect. *Serrulatae*), both of which are allied to *Astroloba* and *Haworthia* subg. *Robustipedunculatae*. These two sections are distinctive in *Aloe* in their small stature, untoothed leaf margins, and substantial fusion of the outer perianth whorl, and their placement in *Aloe* is based on superficial resemblance in perianth size and colour. The possibility that they represent ancient hybrids between *Aloe* and *Gasteria* is not supported by their consistent position in this clade in both plastid and nuclear phylogenies. Their relationship to *Haworthia* subg. *Robustipedunculatae* is

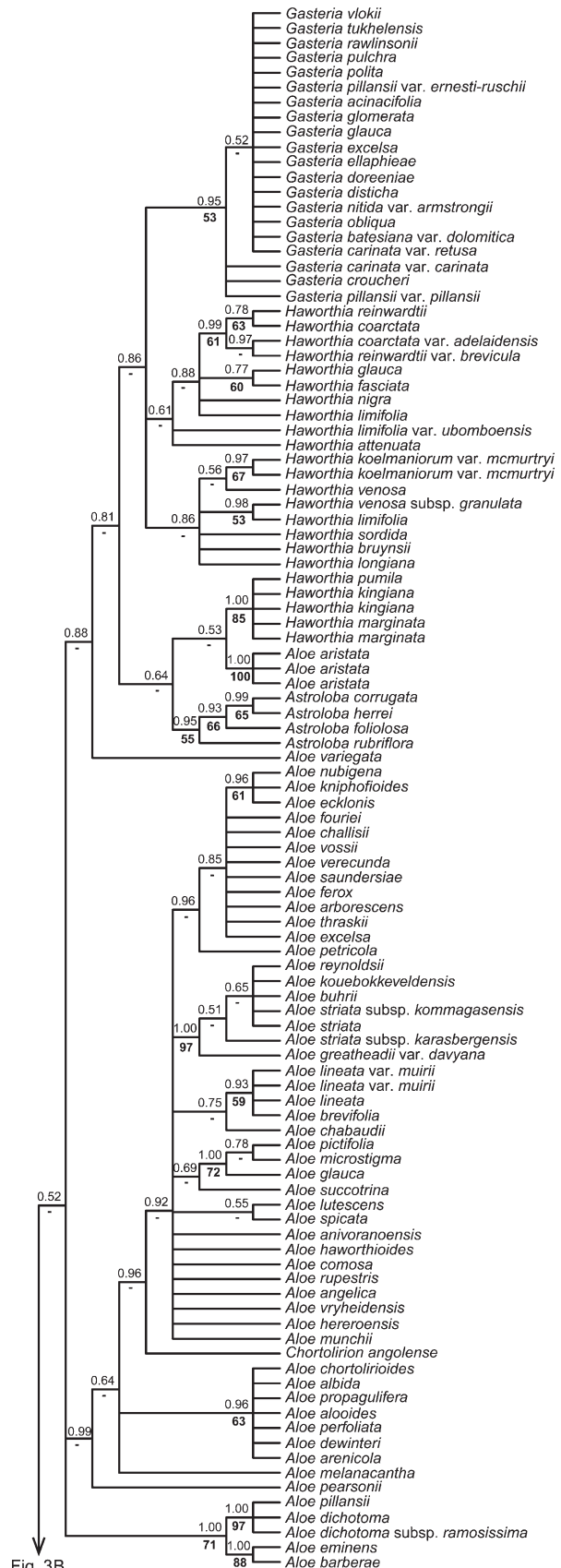


Fig. 3B

Fig. 3. Bayesian phylogram of Alooideae estimated based on nuclear dataset (ITS1). Bayesian posterior probabilities are indicated above branches and maximum parsimony bootstrap support below branches.



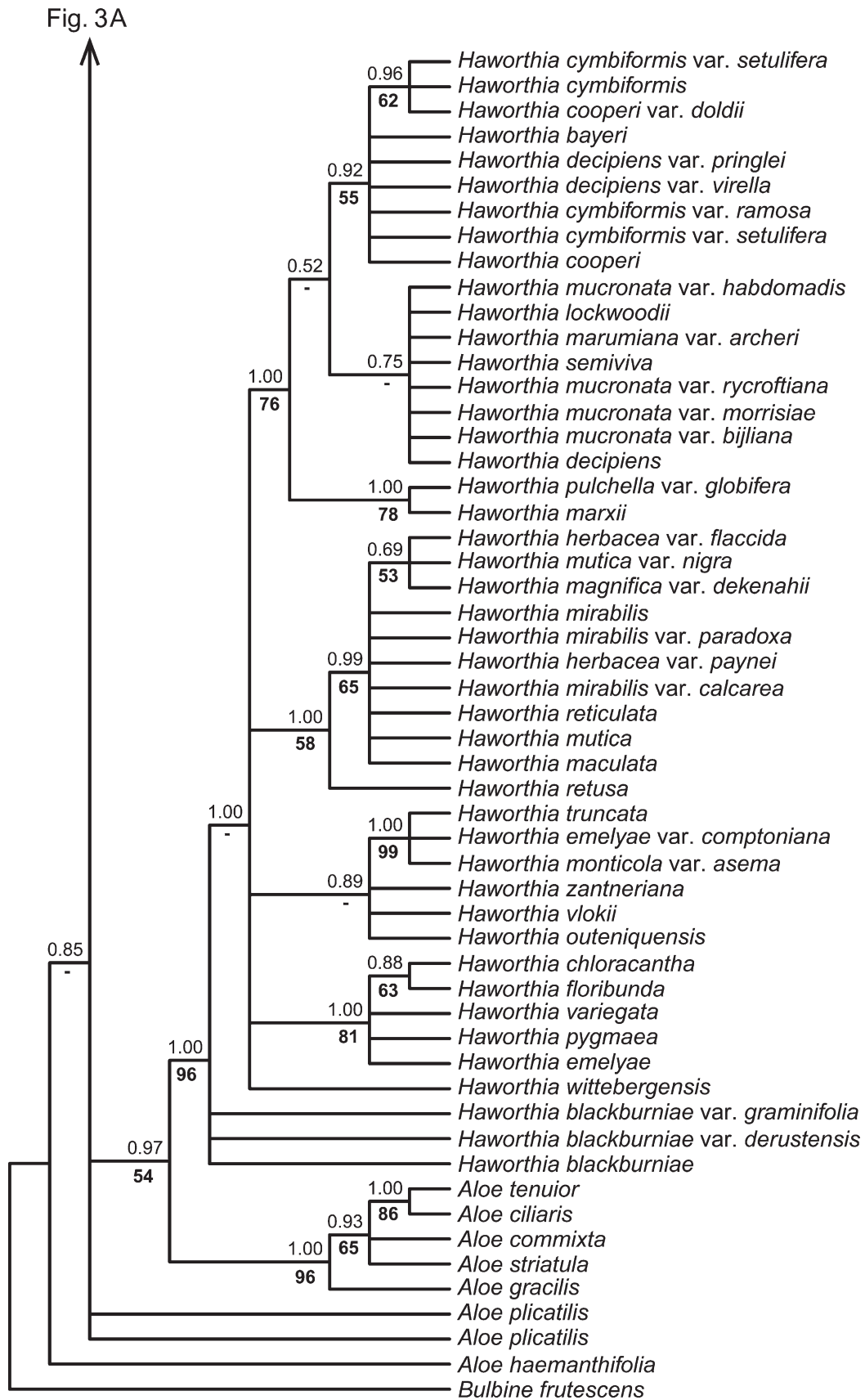


FIG. 3. Continued.

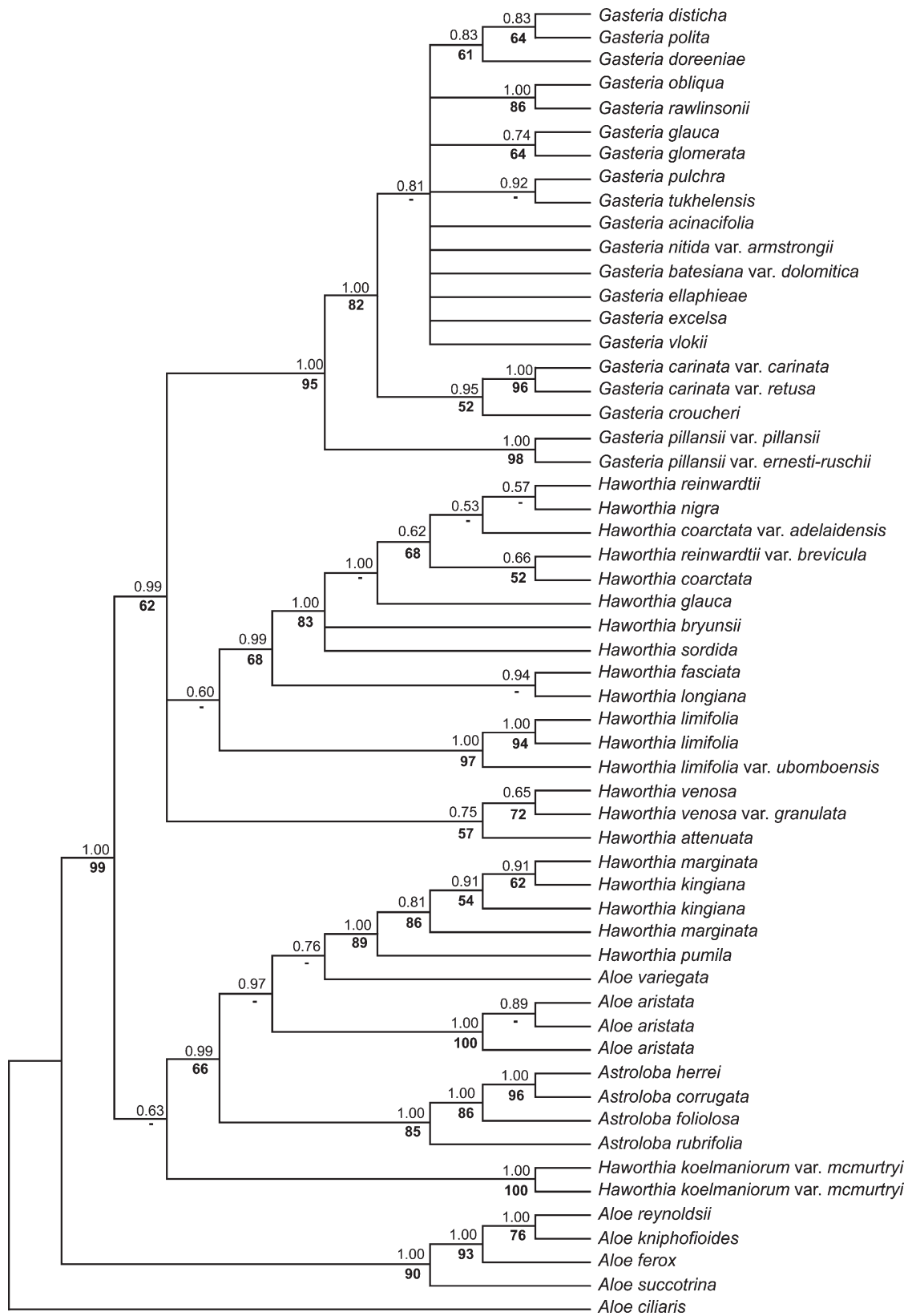


FIG. 4. Bayesian tree, based on the combined dataset, of a sub-sample of Aloioideae (Clades F, G, and H as indicated on Fig. 1). Bayesian posterior probabilities are indicated above branches and maximum parsimony bootstrap support below branches.

supported morphologically by their diminutive size and their maculate or verrucose and essentially unarmed leaves. It appears that vegetative morphology is often more relevant than floral morphology in assessing true relationships among the aloids, and that a combination of vegetative and floral characters is required to diagnose lineages and genera.

Option four, the 'lumper's option,' predicates the inclusion of all members of Alooideae in a single large genus *Aloe*. Although unwilling to adopt this solution formally, the informal taxonomic groupings proposed by Treutlein et al. (2003b) suggest such an inclination. Their articulated objection to this option turns on the practical difficulties of implementing a hierarchical classification should the evolution of the subfamily be reticulate. The congruence between the plastid and nuclear trees at higher taxonomic levels in our analysis is clear indication that reticulate evolution is not a significant issue.

Until now, neither taxon sampling nor branch support has been adequate to justify making formal changes to the taxonomy of the group, but there is no longer any reasonable expectation that the inferred relationships among the taxa will change in any meaningful way with further sampling or analysis. Given the extreme vegetative and floral variation that is present even within a narrowly circumscribed *Aloe*, and the widespread homoplasy among even the more distinctive vegetative and floral types, we favour such a wide circumscription of the genus, with the recognition of several subgenera as initiated by Baker (1878).

Generic classifications in particular need, however, to meet several, sometimes mutually incompatible, requirements (Backlund and Bremer 1998). Among groups with a significant horticultural and cultural importance such as Alooideae, it is arguable that nomenclatural continuity and historical sensitivity are disproportionately important. Although maximally stable, option four or the transfer of all species into the single genus *Aloe*, even with appropriate infrageneric groupings, is certain to cause consternation among horticulturists. An enlarged *Aloe*, termed a 'super-genus' by Treutlein et al. (2003b), would increase the size of the genus from ca. 400 to ca. 490 species, representing an inflation of just over 20%, with some 84 nomenclatural changes required. In practical terms, incorporating these genera into *Aloe* would only slightly increase the morphological diversity already accepted in the genus. Although not excessive in either number or degree, this treatment would obscure the high levels of diversity evident among the southern African representatives of the subfamily by subsuming these segregates within a single genus. It would also radically alter the popular conception of the genus. These drawbacks are avoided in option three, which continues to recognise all traditionally accepted genera, supplemented by additional genera to meet the principle of monophyly. These supplementary genera are mostly relatively minor and thus likely generally acceptable. Less than 50 nomenclatural changes are necessary in this option. The main objection here is the difficulty of diagnosing the requisite segregate genera of *Aloe*. Critically, however, this process has already been partially implemented by Grace et al. (2013), who selected this option in reorganising generic boundaries in the subfamily by recognising *Aloiampelos* (= *A.* sect. *Macrifoliae*), *Aloidendron* (= *A.* sect. *Dracoalae*), and *Kumara* (= *A.* sect. *Kumara*). Similarly, Rowley (2013) has followed suit in *Haworthia* by recognising

the segregate genera *Haworthiopsis* and *Tulista*. The precedent for dismantling both *Aloe* and *Haworthia* has therefore been set, and we accordingly complete the implementation of option three here in order to foster the development of a single, maximally acceptable generic classification for the subfamily. We recognise eleven major clades within Alooideae at generic rank (Fig. 5).

We accept the recognition of *Aloiampelos*, *Aloidendron*, and *Kumara*, but expand the circumscription of the latter to include *A. haemanthifolia* (= *A.* sect. *Haemanthifoliae*). Although differing from the arborescent *K. plicatilis* in its acaulescent habit, *A. haemanthifolia* is otherwise vegetatively very similar to that species in its distichous, lorate leaves lacking marginal teeth and is readily accommodated in an expanded circumscription of *Kumara*.

*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. Although *Haworthia attenuata* and *H. venosa* are placed as sister to the bulk of subg. *Hexangulares* plus *Gasteria*, this association received weak support only in the BI analysis and we include them in *Haworthiopsis* based on their *Haworthia*-like foliage and flowers. This treatment was also followed by Rowley (2013). Similarly, *H. koelmaniorum* is unplaced in the molecular analysis but we include it in *Haworthiopsis* on the basis of its position in the nuclear analysis, and on its floral morphology, which prompted Bayer (1999) to place it in *H.* subg. *Hexangulares*. The species shows none of the morphological characteristics of *Astroloba* that might suggest a hybrid origin and we suggest non-homologous base substitutions as an explanation for its equivocal placement in the nuclear and plastid topologies. Our treatment of *H. koelmaniorum* (and also *H. pungens*) in *Haworthiopsis* contrasts with that of Rowley (2013), who associated both species without comment with *H.* subg. *Robustipedunculatae* in the genus *Tulista*.

We describe the new genera *Aristaloe* and *Gonialoe* for *Aloe aristata* (= *A.* sect. *Aristatae*) and *A. variegata* and its allies in *A.* sect. *Serrulatae*, respectively, based on their isolated placement in a grade between *Astroloba* and *Haworthia* subg. *Robustipedunculatae*. Morphologically, they share a dwarf habit and similar flowers with the outer tepals fused more than halfway. Although not unique in *Aloe*, this condition is relatively rare in the genus. They differ substantially in their foliage and fruit, with *A.* sect. *Aristaloe* characterised by softly prickly leaves with dry, awn-tipped apices, and *A.* sect. *Serrulatae* by leaves with cartilaginous margins, and relatively large capsules and seeds. In our taxonomic treatment we differ 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 provided for this decision, which was made without any knowledge of the close relationship of *A. variegata* with these taxa. Although an argument might be made for the inclusion of *Aloe aristata* and *A. variegata* in *Tulista*, following the same logic applied to the inclusion of *Poellnitzia* in *Astroloba* (Manning and Smith 2000), their distinctive and strongly divergent vegetative and floral morphology are adequate grounds for their continued segregation, especially without historical precedence for their association with either *Astroloba* or *Haworthia*. Similarly, we



4. Flowers arcuate; inner and outer tepal whorls not adherent; style arcuate; leaves smooth, pubescent, or rugulose ..... 3. *Haworthia*
4. Flowers straight; inner and outer tepal whorls adherent; style straight; leaves smooth or with white, subtuberculate to subsperescent spots on lower or both surfaces ..... 5
5. Flowers obcapitate and abruptly joined to pedicel ..... 9. *Tulista*
5. Flowers obclavate and tapering (substipitate) to pedicel ..... 10. *Haworthiopsis*
1. Anthers and styles usually exerted or just included (flowers small and strongly bilabiate with included anthers and styles in *Aloe* sect. *Chortolirion* but then sessile); leaves often prickly on margins; herbs, shrubs, or trees ..... 6
6. Leaves distichous, lorate with rounded apex, immaculate; outer tepals fused more than halfway ..... 2. *Kumara*
6. Leaves rosulate or trifarious, acute or acuminate, immaculate or variously marked; outer tepals variously free or fused ..... 7
7. Plants dichotomously branched trees or large shrubs with stems leafless below; leaves immaculate ..... 1. *Aloidendron*
7. Plants herbs or shrubs, sometimes tree-like but not dichotomously branched; leaves maculate or not ..... 8
8. Plants several-stemmed shrubs or climbers; leaves cauline, dispersed, distinctly sheathing, immaculate, with soft marginal teeth; flowers with outer tepals almost completely connate ..... 4. *Aloiampelos*
8. Plants mostly single-stemmed herbs or shrubs; leaves not dispersed along stems; flowers with outer tepals free or variously connate ..... 9
9. Plants dwarf, acaulescent herbs; leaves white-spotted or with hairlike prickles from white tubercles; outer tepals connate more than halfway; anthers not or hardly exerted ..... 10
10. Leaves trifarious, without prickles, margins cartilaginous; peduncles with numerous sterile bracts ..... 8. *Gonialoe*
10. Leaves spirally arranged, lower surface and margins with soft prickles; peduncles without sterile bracts ..... 7. *Aristaloe*
9. Plants acaulescent or caulescent herbs or shrubs but without above combination of characters ..... 5. *Aloe*

#### TAXONOMIC TREATMENT

1. ALOIDENDRON (A. Berger) Klopper & Gideon F. Sm., *Phytotaxa* 76: 9. 2013. *Aloe* section *Aloidendron* A. Berger, *Bot. Jahrb. Syst.* 36: 56. 1905.—TYPE: *Aloidendron barberae* (Dyer) Klopper & Gideon F. Sm.

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

A genus of six or seven species from southern and east tropical Africa.

##### 1.1. Section ALOIDENDRON

*Aloe* section *Sabaealoe* A. Berger, *Bot. Jahrb. Syst.* 36: 56. 1905, syn. nov.—TYPE: *Aloe sabaea* Schweinf. (= *Aloidendron sabaea* (Schweinf.) Boatwr. & J. C. Manning).

Leaves deeply canaliculate, more than 7 times as long as wide, distantly denticulate. Flowers pink.

A section of four species from eastern and tropical Africa. [*Aloidendron barberae* (Dyer) Klopper & Gideon F. Sm., *A. eminens* (Reynolds & P. R. O. Bally) Klopper & Gideon F. Sm., *A. sabaea* (Schweinf.) Boatwr. & J. C. Manning, *A. tongaensis* (Van Jaarsv.) Klopper & Gideon F. Sm.].

***Aloidendron sabaea*** (Schweinf.) Boatwr. & J. C. Manning, comb. nov. *Aloe sabaea* Schweinf., *Bull. Herb. Boissier* 2, App. ii: 74. 1894.—TYPE: Yemen: Agara near Hodjela, 1 Feb 1889, *Schweinfurth 1010* (lectotype: G, digital image!, designated here).

- 1.2. Section ***Dracoaloe*** (A. Berger) Boatwr. & J. C. Manning, comb. nov. *Aloe* section *Dracoaloe* A. Berger, *Bot. Jahrb. Syst.* 36: 56. 1905.—TYPE: *Aloe dichotoma* Masson (= *Aloidendron dichotomum* (Masson) Klopper & Gideon F. Sm.).

Leaves biconvex to shallowly canaliculate, less than 7 times as long as wide, closely denticulate. Flowers yellow.

A section of two or three species endemic to South Africa. [*Aloidendron dichotomum* (Masson) Klopper & Gideon F. Sm. (incl. *A. ramosissimum* (Pillans) Klopper & Gideon F. Sm.), *A. pillansii* (L. Guthrie) Klopper & Gideon F. Sm.].

2. KUMARA Medik., *Theodora*: 74. 1786. *Aloe* subgenus *Kumara* (Medik.) Baker, *J. Linn. Soc., Bot.* 18: 155. 1880; Glen & D. S. Hardy, *Fl. Southern Africa* 5(1, 1): 145. 2000 [as '*A. series Kumara* (Medik.) Baker'].—TYPE: *Kumara disticha* Medik., nom. illegit. (= *Kumara plicatilis* (L.) G. D. Rowley).

*Rhipidodendron* Willd., *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk.* 15: 164. 1811, syn. nov.—TYPE: Lectotype, designated here: *R. distichum* (Medik.) Willd. (= *Kumara plicatilis* (L.) G. D. Rowley).

*Aloe* series *Haemanthifoliae* A. Berger in Engler, *Pflanzenr.* IV.38 (Heft 33): 173. 1908, syn. nov. *Aloe* section *Haemanthifolia* (A. Berger) Glen & D. S. Hardy, *Fl. Southern Africa* 5(1, 1): 23. 2000.—TYPE: *Aloe haemanthifolia* A. Berger & Marloth (= *Kumara haemanthifolia* (A. Berger & Marloth) Boatwr. & J. C. Manning).

Dichotomously much-branched shrub or tree with leafless stems, or acaulescent. Leaves distichous, lorate, obtuse, unspotted, margins entire or brown-denticulate. Inflorescence a lax or capitate raceme, peduncles with or without sterile bracts. Flowers cylindric, 23–45 mm long, reddish pink, tepals ± free or outer connate in lower half. Anthers included or scarcely exerted. Style included or shortly exerted.

A genus of two species restricted to moist sandstone slopes in winter rainfall, southwestern South Africa. [*Kumara haemanthifolia* (A. Berger & Marloth) Boatwr. & J. C. Manning, *K. plicatilis* (L.) G. D. Rowley].

- Kumara haemanthifolia*** (A. Berger & Marloth) Boatwr. & J. C. Manning, comb. nov. *Aloe haemanthifolia* A. Berger & Marloth, *Bot. Jahrb. Syst.* 38: 85. 1905.—TYPE: South Africa: Franschoek Mountains, *Marloth 3786* (holotype: BOLI; isotypes: GRA, PRE!).

3. HAWORTHIA Duval, *Pl. succ. horto Alencon.*: 7. 1809., nom. cons.—TYPE: *Haworthia arachnoidea* (L.) Duval.

*Apicra* Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 167. 1811, nom. illegit. pro *Haworthia* Duval.—TYPE: not designated.

*Haworthia* section *Retusae* Haw., Saxifrag. enum. 2: 55. 1821, syn. nov. *Aloe* section *Retusae* (Haw.) Salm-Dyck, Aloes Mesembr. 1: sect. 9. 1836.—TYPE: Lectotype, designated here: *Aloe retusa* L. (= *Haworthia retusa* (L.) Duval).

*Haworthia* section *Reticulatae* Haw., Saxifrag. enum. 2: 57. 1821, syn. nov. *Aloe* section *Reticulatae* (Haw.) Salm-Dyck, Aloes Mesembr. 1: sect. 10. 1836.—TYPE: Lectotype, designated here: *Aloe reticulata* Haw. (= *Haworthia reticulata* (Haw.) Haw.).

*Aloe* section *Limpidae* Salm-Dyck, Aloes Mesembr. 1: sect. 11. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe cymbifolia* Schrad. (= *Haworthia cymbiformis* (Haw.) Duval) [The species listed first by Duval is selected as lectotype].

*Aloe* section *Setatae* Salm-Dyck, Aloes Mesembr. 1: sect. 12. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe setosa* Schult. f. (= *Haworthia arachnoidea* (L.) Duval).

*Aloe* section *Loratae* Salm-Dyck, Aloes Mesembr. 1: sect. 13. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe chloracantha* (Haw.) Schult. f. (= *Haworthia chloracantha* Haw.).

Dwarf, acaulescent herbs. Leaves rosulate, more or less soft and juicy, smooth, pubescent, or rugulose. Inflorescence a raceme, peduncles slender and flexible, with few sterile bracts. Flowers < 15 mm long, bilabiate, arcuate, ascending, obclavate and triangular-tapering (substipitate) to the pedicel, brownish or whitish, outer and inner tepals connate at base, whorls not adherent. Anthers included. Style arcuate, included.

A genus of 42 species restricted to winter rainfall, southwestern South Africa.

4. *ALOIAMPELOS* Klopper & Gideon F. Sm., Phytotaxa 76: 10. 2013.—TYPE: *Aloiampelos ciliaris* (Haw.) Klopper & Gideon F. Sm.

*Aloe* series *Macrifoliae* Haw., Philos. Mag. J. 66: 280. 1825. *Aloe* section *Macrifoliae* (Haw.) Glen & D. S. Hardy, Fl. Southern Africa 5(1, 1): 92. 2000.—TYPE: *Aloe ciliaris* Haw. (= *Aloiampelos ciliaris* (Haw.) Klopper & Gideon F. Sm.).

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

A genus of seven species from southern and eastern South Africa. [*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., Sp. Pl.: 319. 1753.—TYPE: *A. perfoliata* L.

Perennial herbs or shrubs, branched or unbranched. Leaves rosulate, unmarked or variously spotted or streaked, margins entire or prickly. Inflorescence spicate or racemose, simple or branched, peduncles with or without sterile bracts. Flowers regular or bilabiate, campanulate, cylindrical or with a basal swelling, mostly > 15 mm long, often brightly coloured, outer tepals mostly connate in lower half, inner tepals ± free. Anthers mostly exerted. Style mostly exerted.

A large genus of ca. 400 species widely distributed through Africa, Arabia, Madagascar, and Socotra.

**Note**—The genus *Chortolirion* was formally included in *Aloe* as sect. *Chortolirion* by Daru et al. (2013). Combinations for the three species were published independently and almost simultaneously by Grace et al. (2013) and Daru et al. (2013), the former appearing while the latter was in press. This resulted in the publication of one unnecessary new name (noted by Rowley 2013) and an additional nomenclatural error that we correct here.

*ALOE* sect. *CHORTOLIRION* (A. Berger) Boatwr. & J. C. Manning, Taxon 62: 74. 2013. *Chortolirion* A. Berger in Engler, Pflanzenr. IV.38 (Heft 33): 73. 1908.—TYPE: *Chortolirion angolense* (Baker) A. Berger (= *Aloe welwitschii* Klopper & Gideon F. Sm.).

**Aloe bergeriana** (Dinter) Boatwr. & J. C. Manning, comb. nov. *Chortolirion bergerianum* Dinter, Neue Pfl. Deutsch-Südwest-Afr.: 24. 1914.—TYPE: Namibia: Voigtland, Dinter 4295 (holotype: B).

*Haworthia tenuifolia* Engl., Bot. Jahrb. Syst. 10: 2, t. 1. 1889. [non *Aloe tenuifolia* Lam., Encycl. 1: 87. 1783]. *Chortolirion tenuifolium* (Engl.) A. Berger in Engler, Pflanzenr. IV.38 (Heft 33): 73. 1908. *Aloe barendii* Klopper & Gideon F. Sm., Phytotaxa 76: 12. 2013, nom. superfl. *Aloe tenuifolia* (Engl.) Boatwr. & J. C. Manning, Taxon 62: 75. 2013, nom. illegit., non *A. tenuifolia* Lam., Encycl. 1: 87. 1783.—TYPE: South Africa: near Kuruman, Marloth 1049 (holotype: B; isotype: PRE).

*Haworthia stenophylla* Baker, Hook. Icon. Pl., ser. 3, 20: t. 1974. 1891. [non *Aloe stenophylla* Schult. f., Syst. Veg. ed. 15, 7(1): 641. 1829]. *Chortolirion stenophyllum* (Baker) A. Berger in Engler, Pflanzenr. IV.38 (Heft 33): 72. 1908.—TYPE: South Africa: Barberton, 17 Mar 1890, Galpin 858 (holotype: K; isotype: PRE).

**Note**—The existence of both *Aloe tenuifolia* Lam. (1783) and *A. stenophylla* Schult. f. (1829) precludes the transfer of these epithets to *Aloe*, but the replacement name *A. barendii* Klopper & Gideon F. Sm. (2013) is superfluous since *Chortolirion bergerianum* Dinter (1904), as a synonym, is an earlier available epithet and should have been used [Art. 11.4: McNeill et al. (2006)].

*ALOE* *JEPPEAE* Klopper & Gideon F. Sm., Phytotaxa 76: 12. 2013, as a new name for *Chortolirion latifolium* Zonn. & G. P. J. Fritz, Bradleya 28/2010: 32. 2010 [non *Aloe latifolia* (Haw.) Haw., Syn. pl. succ.: 82. 1812]. *Aloe aestivalis* Boatwr. & J. C. Manning, Taxon 62: 75. 2013, nom. superfl. [as a new name for *C. latifolium*].—TYPE:

South Africa: Bloemfontein near airport, 24 Apr 2009, Fritz 1025 (holotype: PRE).

**Note**—The replacement name *A. jeppeae* Klopper & Gideon F. Sm. (2013) antedates the proposed replacement name *A. aestivalis* Boatwr. & J. C. Manning (2013) and is therefore the correct name for the species in *Aloe*.

*ALOE SUBSPICATA* (Baker) Boatwr. & J. C. Manning, *Taxon* 62: 75. 2013. *Haworthia subspicata* Baker, *Bull. Herb. Boiss.*, sér. 2, 4: 998. 1904.—TYPE: South Africa: Modderfontein, 9 Sept 1897, *Conrath 645* (holotype: Z; isotype: K).

*ALOE WELWITSCHII* Klopper & Gideon F. Sm., *Phytotaxa* 76: 12. 2013. *Haworthia angolensis* Baker, *Trans. Linn. Soc. London, Bot.* 1: 263. 1878. *Chortolirion angolense* (Baker) A. Berger in *Engler, Pflanzenr.* IV. 38 (Heft 33): 73. 1908. [non *Aloe angolensis* Baker, *Trans. Linn. Soc. London, Bot.* 1: 263. 1878].—TYPE: Angola: Huilla, Nov 1859, *Welwitsch 3756* (holotype: BM).

6. *ASTROLOBA* Uitewaal, *Succulenta* (Amsterdam) 5: 53. 1947.—TYPE: *Astroloba pentagona* (Ait.) Uitewaal (= *Astroloba spiralis* (L.) Uitewaal).

*Aloe* section *Imbricatae* Salm-Dyck, *Aloes Mesembr.* 1: sect. 1. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe spiralis* L. (= *Astroloba spiralis* (L.) Uitewaal).

*Aloe* section *Foliolosae* Salm-Dyck, *Aloes Mesembr.* 1: sect. 2. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe foliolosa* Haw. (= *Astroloba foliolosa* (Haw.) Uitewaal).

Dwarf, caulescent herbs, clump-forming. Leaves spirally inserted, imbricate, leathery or hard, deltoid-pungent, smooth or tuberculate, usually eccentrically keeled beneath, margins smooth or denticulate. 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 connate in lower half. Anthers included. Style straight, included.

A small genus of six species, mainly from winter rainfall, southern and southwestern South Africa.

#### 6.1. Section *ASTROLOBA*

Flowers smaller, brownish or whitish, tepals erect or apically spreading.

A section of five species with small flowers adapted to pollination by insects.

[*Astroloba bullulata* (Jacq.) Uitewaal, *A. congesta* (Salm-Dyck) Uitewaal, *Astroloba corrugata* N. L. Mey. & Gideon F. Sm., *Astroloba foliolosa* (Haw.) Uitewaal, *Astroloba herrei* Uitewaal, *Astroloba spiralis* (L.) Uitewaal].

6.2. Section *Poellnitzia* (Uitewaal) Boatwr. & J. C. Manning, stat. nov. *Poellnitzia* Uitewaal, *Succulenta* (Leeuwarden) 22: 61. 1940.—TYPE: *Poellnitzia rubriflora* (L. Bolus) Uitewaal (= *Astroloba rubriflora* (L. Bolus) Gideon F. Sm. & J. C. Manning).

Flowers larger, reddish, tepals apically connivent.

A monotypic section with flowers adapted for sunbird pollination. [*A. rubriflora* (L. Bolus) Gideon F. Sm. & J. C. Manning].

7. *Aristaloe* Boatwr. & J. C. Manning, gen. nov.—TYPE: *Aristaloe aristata* (Haw.) Boatwr. & J. C. Manning.

*Aloe* series *Aristatae* A. Berger, *Bot. Jahrb. Syst.* 36: 46. 1905, syn. nov. *Aloe* section *Aristatae* (A. Berger) Glen & D. S. Hardy, *Fl. Southern Africa* 5(1, 1): 31. 2000.—TYPE: *Aloe aristata* Haw. (= *Aristaloe aristata* (Haw.) Boatwr. & J. C. Manning).

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

A monotypic genus from montane, southeastern South Africa. [*Aristaloe aristata* (Haw.) Boatwr. & J. C. Manning].

*Aristaloe aristata* (Haw.) Boatwr. & J. C. Manning, comb. nov. *Aloe aristata* Haw., *Philos. Mag. J.* 66: 280. 1825. *Tulista aristata* (Haw.) G. D. Rowley, *Alsterworthia Int.* 10: 5. 2013.—TYPE: South Africa: near Steynsburg, *Reynolds 1024* (neotype, designated by Glen and Hardy (2000): PRE!).

8. *Gonialoe* (Baker) Boatwr. & J. C. Manning, stat. nov. *Aloe* subgenus *Gonialoe* Baker, *J. Linn. Soc., Bot.* 18: 155. 1880.—TYPE: *Gonialoe variegata* (L.) Boatwr. & J. C. Manning.

*Aloe* section *Serrulatae* Salm-Dyck, *Aloes Mesembr.* 3: 20. 1840, syn. nov.—TYPE: *Aloe variegata* L. (= *Gonialoe variegata* (L.) Boatwr. & J. C. Manning).

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

A small genus of three species from arid South Africa and Namibia. [*Gonialoe dinteri* (A. Berger) Boatwr. & J. C. Manning, *G. sladeniana* (Pole-Evans) Boatwr. & J. C. Manning, *G. variegata* (L.) Boatwr. & J. C. Manning].

*Gonialoe dinteri* (A. Berger) Boatwr. & J. C. Manning, comb. nov. *Aloe dinteri* A. Berger in *Dinter, Neue Pfl. Deutsch-Südwest-Afr.*: 14. 1914.—TYPE: Namibia: Outjoi, *Dinter 2791a* (holotype: SAM!).

*Gonialoe sladeniana* (Pole-Evans) Boatwr. & J. C. Manning, comb. nov. *Aloe sladeniana* Pole-Evans, *Ann. Bolus Herb.* 3: 13. 1920.—TYPE: Namibia, *Pearson PSME9000* (holotype: PRE).

*Gonialoe variegata* (L.) Boatwr. & J. C. Manning, comb. nov. *Aloe variegata* L., *Sp. Pl.*: 321. 1753.—Iconotype: "*Aloe Afric. humilis, foliis ex albo & viride variegatis*" in Commelin, *Horti med. amstelod.*: 47, t. 47. 1706.

9. *TULISTA* Raf., *Autikon botanikon*: 137. 1840.—TYPE: *Tulista margaritifera* (L.) Raf. (= *Tulista pumila* (L.) G. D. Rowley).

*Haworthia* section *Albicantes* Haw., Saxifrag. enum. 2: 52. 1821, syn. nov. *Aloe* section *Albicantes* (Haw.) Salm-Dyck, Aloes Mesembr. 1: sect. 5. 1836.—TYPE: *Haworthia albicans* Haw. (= *Tulista marginata* (Lam.) G. D. Rowley).

*Haworthia* section *Margaritiferae* Haw., Saxifrag. enum. 2: 53. 1821, syn. nov. *Aloe* section *Margaritiferae* (Salm-Dyck) Haw., Aloes Mesembr. 1: sect. 6. 1836.—TYPE: Lectotype, designated here: *Haworthia margaritifera* (L.) Haw. (= *Tulista pumila* (L.) G. D. Rowley).

*Haworthia* subgenus *Robustipedunculatae* (Uitewaal) M. B. Bayer [as *Robustipedunculatae* Uitewaal ex M. B. Bayer], *Haworthia* Handbook: 14. 1976., syn. nov. *Haworthia* [unranked] *Robustipedunculatae* Uitewaal, Succulenta (Amsterdam): 51. 1947.—TYPE: Lectotype, designated by Bayer (1976): *Haworthia margaritifera* (L.) Haw. (= *Tulista pumila* (L.) G. D. Rowley).

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

A genus of four species from winter rainfall, southwestern South Africa. [*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].

**Note**—Scott's (1978) lectotypification of *Aloe pumila* L. var. *margaritifera* L. renders it homotypic with *Aloe pumila* L., which as the autonym has statutory priority (Jarvis 2007). Breuer and Metzger (1997) correctly treated the species under the name *H. margaritifera* since the combination *H. pumila* (L.) Duval is an illegitimate later homonym of *H. pumila* (Ait.) Haw.

**Tulista minima** (Ait.) Boatwr. & J. C. Manning, comb. nov. *Aloe margaritifera* Burm. f. var. *minima* Ait., Hort. kew. 1: 468. 1789. *Haworthia minima* (Ait.) Haw., Syn. pl. succ.: 92. 1812. —TYPE: illustration in Dillenius, Hort. eltham.: t. 16, f. 18. 1732, (lectotype, designated by Scott 1985).

10. **HAWORTHIOPSIS** G. D. Rowley, *Alsterworthia* Int. 10: 4. 2013.—TYPE: *Haworthiopsis coarctata* (Haw.) G. D. Rowley.

*Aloe* section *Parviflorae* Haw., Trans. Linn. Soc. London 7: 6. 1804, syn. nov. *Aloe* subgenus *Parviflorae* (Haw.) Salm-Dyck, Aloes Mesembr. 1: Tabula synoptica Sectionum. 1836.—TYPE: Lectotype, designated here: *Aloe viscosa* L. (= *Haworthiopsis viscosa* (L.) G. D. Rowley). [We select the species listed first in the section by Haworth (1804)].

*Haworthia* section *Trifariae* Haw., Saxifrag. enum. 2: 49. 1821, syn. nov.—TYPE: Lectotype, designated here: *Haworthia viscosa* (L.) Haw. (= *Haworthiopsis viscosa* (L.) G. D. Rowley).

*Haworthia* section *Luridae* Haw., Saxifrag. enum. 2: 50. 1821, syn. nov. *Aloe* section *Luridae* (Haw.) Salm-Dyck, Aloes Mesembr. 1: sect. 7. 1836.—TYPE: Lectotype, designated

here: *Haworthia scabra* Haw. (= *Haworthiopsis scabra* (Haw.) G. D. Rowley).

*Aloe* section *Triquetrae* Salm-Dyck, Aloes Mesembr. 1: sect. 3. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe cordifolia* (Haw.) Schult. f. (= *Haworthiopsis viscosa* (L.) G. D. Rowley). [We select the species listed first in the section by Salm-Dyck (1836)].

*Aloe* section *Tortuosae* Salm-Dyck, Aloes Mesembr. 1: sect. 4. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe tortuosa* Haw. (= *Haworthiopsis viscosa* (L.) G. D. Rowley). [We select the species listed first in the section by Salm-Dyck (1836)].

*Aloe* section *Tessellatae* Salm-Dyck, Aloes Mesembr. 1: sect. 8. 1836, syn. nov.—TYPE: Lectotype, designated here: *Aloe tessellata* (Haw.) Schult. f. (= *Haworthiopsis tessellata* (Haw.) Boatwr. & J. C. Manning).

*Haworthia* section *Hexangulares* Uitewaal, Succulenta (Amsterdam) 5: 51. 1947, syn. nov. *Haworthia* subgenus *Hexangulares* (Uitewaal) M. B. Bayer [as Uitewaal ex M. B. Bayer], *Haworthia* Handbook: 14. 1976.—TYPE: Lectotype, designated by Bayer (1976): *Haworthia coarctata* Haw. (= *Haworthiopsis coarctata* (Haw.) G. D. Rowley).

Dwarf, acaulescent or caulescent herbs. Leaves rosulate or spirally inserted, smooth or with white subtuberculate to subsperescent 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, obclavate and tapering (substipitate) to the pedicel, brownish or whitish, outer and inner tepals connate at base, both whorls adherent. Anthers included. Style straight, included.

A genus of 18 species restricted to winter rainfall, southwestern South Africa.

[*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].

**Note**—Rowley (2013) made combinations for *Haworthia viscosa* (L.) Haw. in both *Haworthiopsis* and *Tulista*, we presume in error. We treat the species here based on its placement in *Haworthia* subg. *Hexangulares* by Bayer (1999).

**Haworthiopsis koelmaniorum** (Oberm. & Hardy) Boatwr. & J. C. Manning, comb. nov. *Haworthia koelmaniorum* [as *koelmaniora*] Oberm. & Hardy, Fl. Pl. Afr.: t. 1502. 1967. *Tulista koelmaniorum* (Oberm. & Hardy) G. D. Rowley, *Alsterworthia* Int. 10: 5. 2013.—TYPE: South Africa: Groblersdal, *Hardy & Mauve* 2267 (holotype: PRE).

**Haworthiopsis pungens** (M. B. Bayer) Boatwr. & J. C. Manning, comb. nov. *Haworthia pungens* M. B. Bayer,



Haworthia Revisited: 188. 1999. *Tulista pungens* (M. B. Bayer) G. D. Rowley, *Alsterworthia* Int. 10: 6. 2013.—TYPE: South Africa: Joubertina, *Bruyns 7090* (holotype: BOL).

**Haworthiopsis tessellata** (Haw.) Boatwr. & J. C. Manning, comb. nov. *Haworthia tessellata* Haw., *Philos. Mag. J.* 44: 300. 1824.—TYPE: illustration [later published in *Cact. Succ. J.* (Los Angeles) 50: 75. 1978], (lectotype, designated by Scott (1978): K).

11. GASTERIA Duval, *Pl. succ. horto Alencon.*: 6. 1809. *Aloe* section *Gasteria* [as *Gasteriae*] (Duval) Salm-Dyck, *Aloes Mesembr.* 1: sect. 29. 1836—TYPE: lectotype, designated by Maire, *Flore de l'Afrique du nord* 5: 71. 1958. *Gasteria angustifolia* (Ait.) Duval. (= *Gasteria disticha* (L.) Haw.).

*Aloe* section *Curviflorae* Haw., *Trans. Linn. Soc. London* 7: 12. 1804. —TYPE: Lectotype, designated here: *Aloe verrucosa* Mill. [= *Gasteria carinata* Mill.] Duval [The species listed first by Haworth is selected as lectotype].

*Gasteria* section *Breviflorae* Haw., *Saxifrag. enum.* 2: 47. 1821., nom. nud.

*Gasteria* section *Longiflorae* Haw., *Saxifrag. enum.* 2: 47. 1821., nom. nud.

*Gasteria* section *Mediocres* Haw., *Saxifrag. enum.* 2: 47. 1821., nom. nud.

Acaulescent or caulescent herbs. Leaves rosulate or distichous, smooth, rugulose, pubescent, 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 connate. Anthers included. Style arcuate, included.

A genus of 23 species endemic to South Africa, mainly the southern and eastern parts [see Van Jaarsveld (2007) for species].

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APPENDIX 1. Taxa, location, collector, collection number, (herbarium acronym), and GenBank accession numbers for material used in the molecular phylogenetic analyses. GenBank accession numbers are listed in the following order: *trnL* intron, *trnH-psbA*, ITS1, *rbcl*, and *matK*. Missing sequences are indicated with a dash in the relevant position. DNA sequences generated from this study are indicated by \*; taxa with multiple accessions relate to different individuals, with GenBank accessions listed in sequence. Collector abbreviations: Barnabas H. Daru (BHD); Olivier Maurin (OM); Renaud Lahave (RL). Specimens are from South Africa unless otherwise noted.

**Aloe section Aloe:** *A. arenicola* Reynolds. Western Cape, OM 3018 (JRAU), JX630328\*, JQ024863, JQ025268, JQ024487, JQ024111. *A. pearsonii* Schönland. Northern Cape, Namibia, OM 2955 (JRAU), JX630325\*, JQ024868, JQ025269, JQ024526, JQ024154. *A. perfoliata* L. (GENERITYPE), Eastern and Western Cape, BHD 391, OM 2819 (JRAU), JX630322\*, —, JQ025315, JQ024527, JQ024155. **Aloe section Aloidendron:** *A. barberae* Dyer. Eastern Cape, KwaZulu-Natal, Mpumalanga, Swaziland, BHD 192 (JRAU), JX630188\*, JQ024864, JQ025262, JQ024489, JQ024113. *A. emimens* Reynolds & P. R. O. Bally. Northern Somalia, BHD 474 (JRAU), JX630329\*, JQ039258, JQ025369, JQ669552, JQ669521. **Aloe section Anguialoe:** *A. alooides* (Bolus) Druten. Mpumalanga, BHD 476 (JRAU), JX630286\*, JQ039243, JQ025325, JQ669544, JQ669515. *A. spicata* L. f. KwaZulu-Natal, Limpopo, Mpumalanga, Swaziland, OM 1522 (JRAU), JX630301\*, JQ039282, JQ025290, —, —. *A. vryheidensis* Groenew. KwaZulu-Natal, Limpopo, Mpumalanga, BHD 467 (JRAU), JX630279\*, JQ039288, JQ025308, JQ669561, —. **Aloe section Arborescentes:** *A. arborescens* Mill. Eastern and Western Cape, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, North-West, Botswana, Swaziland, BHD 420 (JRAU), JX630265\*, JQ039246, JQ025326, JQ024486, JQ024110. **Aloe section Aristatae:** *A. aristata* Haw. Eastern and Western Cape, Free State, KwaZulu-Natal, Limpopo, BHD 459 (JRAU) BG Heidelberg BG Jena, JX630272\*, JQ039247, JQ025312/AY323651/AY323652, AJ512319/AY323634, AJ511407/AY323713. **Aloe section Asperifoliae:** *A. dewinteri* Giess ex H. Borman & Hardy. Namibia, BHD 386 (JRAU), JX630249\*, JQ039254, JQ025303, JQ024500, JQ024125. *A. hereroensis* Engl. Free State, Northern Cape, Namibia, BHD 388 (JRAU), JX630251\*, JQ039266, JQ025305, JQ024514, JQ024140. **Aloe section Chabaudia:** *A. chabaudii* Schönland. KwaZulu-Natal, Limpopo, Mpumalanga, Botswana, Swaziland, OM 1625 (JRAU), JX630303\*, JQ039249, JQ025299, JQ669548; JQ669518. **Aloe section Dracoaloe:** *A. dichotoma* Masson. Northern Cape, Namibia, OM 2953 (JRAU), JX630323\*, —, JQ025368, JQ024501, JQ024126. *A. dichotoma* Masson subsp. *ramosissima* (Pillans) Zonn. Namibia, OM 2954 (JRAU), JX630324\*, JQ039256, JQ025367, JQ024503, JQ024128. *A. pillansii* L. Guthrie, Northern Cape, Namibia, BHD 390 (JRAU), JX630252\*, JQ039255, JQ025372, JQ024502, JQ024127. **Aloe section Echinatae:** *A. melanacantha* A. Berger. Northern and Western Cape,

BHD 462 (JRAU), JX630274\*, JQ039271, JQ025267, JQ669554, JQ669524. *A. pictifolia* D. S. Hardy, Eastern Cape, BHD 381 (JRAU), JX630248\*, JQ039277, JQ025324, JQ024530, JQ024158. **Aloe section Haemanthifoliae:** *A. haemanthifolia* Marloth & A. Berger. Western Cape, BHD 484 (JRAU), KC985129\*, KC960554\*, KC880129\*, KC960551\*, KC960548\*. **Aloe section Kumara:** *A. plicatilis* (L.) Burm. f. Western Cape, BHD 193 (JRAU), BG Heidelberg, Germany 9286, JX630189\*, JQ039278, JQ025373/AY323662, JQ024531/AY323613, JQ024159/AY323693. **Aloe section Latebracteatae:** *A. lutescens* Groenew. Limpopo, RL 1193 (JRAU), JX630330\*, JQ039270, JQ025348, JQ669553, JQ669523. **Aloe section Leptoaloe:** *A. albida* (Stapf) Reynolds. Mpumalanga, Swaziland, BHD 475 (JRAU), —, JQ039242, JQ025366, JQ669543, JQ669514. *A. challisii* van Jaarsv. & A. E. van Wyk. Mpumalanga, BHD 471 (JRAU), JX630283\*, JQ039250, JQ025355, JQ669549, JQ669519. *A. chortolirioides* A. Berger. Limpopo, Mpumalanga, Swaziland, BHD 477 (JRAU), JX630287\*, JQ039251, JQ025374, JQ669550, —. *A. ecklonis* Salm-Dyck, Eastern Cape, Free State, KwaZulu-Natal, Limpopo, Mpumalanga, BHD 465 (JRAU), JX630277\*, JQ039257, JQ025307, JQ669551, JQ669520. *A. fouriei* D. S. Hardy & Glen. Limpopo, Mpumalanga, BHD 469 (JRAU), JX630281\*, JQ039261, JQ025358, —, JQ669522. **Aloe kniphofioides** Baker. Eastern Cape, KwaZulu-Natal, Mpumalanga, BHD 481 (JRAU), KC985128\*, KC960553\*, KC880128\*, KC960550\*, —. *A. nubigena* Groenew. Limpopo, Mpumalanga, BHD 353 (JRAU), JX630239\*, JQ039274, JQ025356, JQ669556, JQ669526. *A. saundersiae* (Reynolds) Reynolds. KwaZulu-Natal, BHD 463 (JRAU), JX630275\*, JQ039281, JQ025345, JQ669558, JQ669529. *A. verecunda* Pole-Evans. Gauteng, Limpopo, Mpumalanga, BHD 444 (JRAU), JX630271\*, JQ039286, JQ025346, JQ669559, JQ669530. *A. vossii* Reynolds. Limpopo, BHD 464 (JRAU), JX630276\*, JQ039287, JQ025347, JQ669560, JQ669531. **Aloe section Macrifoliae:** *A. ciliaris* Haw. Eastern and Western Cape, BHD 431 (JRAU), JX630267\*, JQ024866, JQ025292, JQ024496, JQ024121. *A. commixta* A. Berger. Western Cape, BHD 405 (JRAU), JX630258\*, JQ039252, JQ025329, JQ024497, JQ024122. *A. gracilis* Haw. Eastern and Western Cape, BHD 399 (JRAU), JX630255\*, JQ039263, JQ025330, JQ024510, JQ024136. *A. striatula* Haw. Eastern Cape, Limpopo, BHD 191 (JRAU), JX630187\*, JQ024872, JQ025291, JQ024538, JQ024166. *A. tenuior* Haw. Eastern and Western Cape, KwaZulu-Natal, Mpumalanga, BHD 393 & 415 (JRAU), JX630254\*, JQ039284, JQ025331, JQ024541, JQ024169. **Aloe section Pachydendron:** *A. angelica* Pole-Evans, Limpopo, OM 2960 (JRAU), JX630327\*, JQ039244, JQ025310, —, JQ024109. *A. excelsa* A. Berger. Limpopo, Botswana, OM 1621 (JRAU), JX630302\*, JQ039259, JQ025301, —, —. *A. ferox* Mill. Eastern and Western Cape, KwaZulu-Natal, Limpopo, BHD 407 (JRAU), JX630259\*, JQ039260, JQ025327, —, —. *A. petricola* Pole-Evans. Limpopo, Mpumalanga, OM 2959 (JRAU), JX630326\*, JQ039276, JQ025300, JQ024529, JQ024157. *A. rupestris* Baker. KwaZulu-Natal, Swaziland, BHD 468 (JRAU), JX630280\*, JQ039280, JQ025317, JQ669557, JQ669528. *A. thraskii* Baker. KwaZulu-Natal, BHD 411 (JRAU), JX630261\*, JQ039285, JQ025319, JQ024542, JQ024170. **Aloe section Paniculatae:** *A. buhrii* Lavranos. Northern Cape, BHD 402 (JRAU), JX630257\*, JQ024865, JQ025263, JQ024494, JQ024118. *A. kouebokveldensis* van Jaarsv. & A. B. Low. Western Cape, BHD 378 (JRAU), JX630245\*, JQ024867, JQ025264, JQ024518, JQ024144. *A. reynoldsi* Letty, Eastern Cape, BHD 379 (JRAU), JX630246\*, JQ024869, JQ025265, JQ024532, JQ024160; *A. striata* Haw., Eastern and Western Cape, BHD 400 (JRAU), JX630256\*, JQ024870, JQ025260, JQ024534, JQ024162. *A. striata* Haw. subsp. *karasbergensis* (Pillans) Glen & D. S. Hardy. Northern Cape, BHD 408 (JRAU), JX630260\*, JQ039283, JQ025306, JQ024536, JQ024164. *A. striata* Haw. subsp. *komaggasensis* (Kritz. & van Jaarsv.) Glen & D. S. Hardy. Northern Cape, BHD 417 (JRAU), —, JQ024871, JQ025261, JQ024537, JQ024165. **Aloe section Pictae:** *A. greatheadii* Schönland var. *davyana* (Schönland) Glen & D. S. Hardy. Free State, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, North-West, Swaziland, BHD 380 (JRAU), JX630247\*, JQ039264, JQ025304, JQ024512, JQ024138. **Aloe section Proliferae:** *A. brevifolia* Mill. Western Cape, BHD 460 (JRAU), JX630273\*, JQ039248, JQ025314, JQ669547, JQ669517. **Aloe section Purpurascetes:** *A. microstigma* Salm-Dyck. Northern and Western Cape, Namibia, BHD 392 (JRAU), JX630253\*, JQ039272, JQ025323, JQ024525, JQ024152. *A. succotrina* All. Western Cape, BHD 424 (JRAU), JX630266\*, JQ024873, JQ025266, JQ024539, JQ024167. **Aloe section Rhodacanthae:** *A. comosa* Marloth & A. Berger. Western Cape, BHD 385 (JRAU), —, JQ039253, JQ025328, JQ024499, JQ024124. *A. glauca* Mill. Northern and Western Cape, BHD 419 (JRAU), JX630264\*, JQ039262, JQ025313, JQ024508, JQ024134. *A. lineata* (Aiton) Haw. Eastern and Western Cape, BHD 416 (JRAU), JX630263\*, JQ039267, JQ025320, JQ024520, JQ024147. *A. lineata* (Aiton) Haw. var. *muirii* (Marloth) Reynolds. Eastern and Western Cape, BHD 412 & 387 (JRAU), JX630262\*/JX630250\*, JQ039269,

- JQ025321/JQ025322, JQ024521/JQ024522, JQ024148/JQ024149. *Aloe* section *Serrulatae*: *A. variegata* L. South Africa, Namibia, *BHD* 398 (JRAU), KC985127\*, KC960552\*, KC880127\*, KC960549\*, KC960547\*.
- Not placed to section: Madagascan species:** *A. anivooranoensis* (Rauh & Hebbing) L. E. Newton & G. D. Rowley. North-Eastern Madagascar, *BHD* 473 (JRAU), JX630285\*, JQ039245, JQ025371, JQ669545, JQ669516. *A. haworthioides* Baker. Central Madagascar, *BHD* 190 (JRAU), JX630186\*, JQ039265, JQ025357, JQ024513, JQ024139. *A. propagulifera* (Rauh & Razaf.) L. E. Newton & G. D. Rowley. Central to Eastern Madagascar, *BHD* 472 (JRAU), JX630284\*, JQ039279, JQ025359, JQ669546, JQ669527. **Mainland African species:** *Aloe murchii* Christian. Zimbabwe, Mozambique (Chimanimani Mountains), *BHD* 470 (JRAU), JX630282\*, JQ039273, JQ025302, JQ669555, JQ669525. *Astroloba*: *A. corrugata* N. L. Mey. & Gideon F. Sm. Western Cape, *BHD* 219 (JRAU), JX630201\*, JQ039290, JQ025350, JQ024545, JQ024173. *A. foliolosa* (Haw.) Uitewaal. Eastern Cape, *BHD* 228 (JRAU), JX630207\*, JQ039291, JQ025351, JQ024547, JQ024175. *A. herrei* Uitewaal. Western Cape, *BHD* 225 (JRAU), JX630206\*, JQ039292, JQ025349, JQ024548, JQ024176. *A. rubriflora* (L. Bolus) Gideon F. Sm. & J. C. Manning. Western Cape, *BHD* 229 (JRAU), JX630208\*, JQ039293, JQ025297, JQ024549, JQ024177. *Chortolirion*: *C. angolense* (Baker) A. Berger. Eastern and Northern Cape, Free State, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, North West, Botswana, Namibia, Swaziland, *BHD* 466 (JRAU), JX630278\*, JQ039295, JQ025344, JQ669569, JQ669535. *Gasteria* section *Gasteria*: *G. disticha* (L.) Haw. Western Cape, *OM* 2778 (JRAU), JX630307\*, JQ024879, JQ025278, JQ024560, JQ024187. *G. doreniae* van Jaarsv. & A. E. van Wyk. Eastern Cape, *OM* 2793 (JRAU), JX630320\*, JQ024880, JQ025279, JQ024561, JQ024188. *G. glomerata* van Jaarsv. Eastern Cape, *OM* 2772 (JRAU), JX630304\*, JQ024884, JQ025283, JQ024566, JQ024193. *G. obliqua* (Aiton) Duval. Eastern Cape, *OM* 2788 (JRAU), JX630315\*, JQ024886, JQ025274, JQ024569, JQ024196. *G. pillansii* Kensis var. *ernesti-ruschii* (Dinter & Poelln.) van Jaarsv. Northern Cape, Namibia, *OM* 2779 (JRAU), JX630308\*, —, JQ025285, JQ024570, JQ024197. *G. pillansii* Kensis var. *pillansii*, Northern Cape, *OM* 2781 (JRAU), JX630310\*, JQ024874, JQ025284, JQ024553, JQ024180. *G. rawlinsonii* Oberm. Eastern Cape, *OM* 2775 (JRAU), JX630306\*, JQ024889, JQ025288, JQ024573, JQ024200. *Gasteria* section *Longiflorae*: *G. acinacifolia* (J. Jacq.) Haw. Eastern Cape, *OM* 2790 (JRAU), JX630317\*, JQ024875, JQ025271, JQ024554, JQ024181. *G. batesiana* G. D. Rowley var. *dolomitica* van Jaarsv. & Van Wyk. Mpumalanga, *OM* 2777 (JRAU), —, JQ024876, JQ025273, JQ024555, JQ024182. *G. carinata* (Mill.) Duval var. *carinata*. Western Cape, *OM* 2780 (JRAU), JX630309\*, JQ039297, JQ025275, JQ669562, JQ669537. *G. carinata* (Mill.) Duval var. *retusa* van Jaarsv. Western Cape, *OM* 2798 (JRAU), JX630321\*, JQ024877, JQ025276, JQ024556, JQ024183. *G. croucheri* (Hook. f.) Baker. Eastern Cape, KwaZulu-Natal, *OM* 2773 & 2791 (JRAU), JX630318\*, JQ024878, JQ025277, JQ024559/JQ024558, JQ024186. *G. ellaphiae* van Jaarsv. Eastern Cape, *OM* 2782 (JRAU), JX630311\*, JQ024881, JQ025280, JQ024562, JQ024189. *G. excelsa* Baker. Eastern Cape, *OM* 2789 (JRAU), JX630316\*, JQ024882, JQ025281, JQ024564, JQ024191. *G. glauca* van Jaarsv. Eastern Cape, *OM* 2771 (JRAU), —, JQ024883, JQ025282, JQ024565, JQ024192. *G. nitida* Haw. var. *armstrongii* (Schönland) van Jaarsv. Eastern Cape, *OM* 2792 (JRAU), JX630319\*, JQ024885, JQ025272, JQ024567, JQ024194. *G. polita* van Jaarsv. Western Cape, *OM* 2784 (JRAU), JX630312\*, JQ024887, JQ025286, JQ024571, JQ024198. *G. pulchra* (Aiton) Haw. Eastern Cape, *OM* 2785 (JRAU), JX630313\*, JQ024888, JQ025287, JQ024572, JQ024199. *G. tukhelensis* van Jaarsv. KwaZulu-Natal, *OM* 2774 (JRAU), JX630305\*, JQ024890, JQ025289, JQ024574, JQ024201. *G. vlokii* van Jaarsv. Western Cape, *OM* 2786 (JRAU), JX630314\*, JQ039298, JQ025298, JQ024575, JQ024202. *Haworthia* subgenus *Haworthia*: *H. angustifolia* Haw. Eastern Cape, *BHD* 234 (JRAU), JX630211\*, JQ039299, —, JQ024593, JQ024219. *H. arachnoidea* (L.) Duval. Western Cape, *BHD* 29 & 30 (JRAU), JX630221\*, JQ024891/JQ024892, —, JQ024601/JQ024602, JQ024226. *H. bayeri* J. D. Venter & S. A. Hammer. Eastern and Western Cape, *BHD* 110 (JRAU), JX630180\*, JQ039301, JQ025360, JQ024615, JQ024239. *H. blackburniae* W. F. Barker. Western Cape, *BHD* 198 (JRAU), JX630191\*, JQ024893, JQ025226, JQ024616, JQ024240. *H. blackburniae* W. F. Barker var. *derustensis* M. B. Bayer. Western Cape, *BHD* 243 (JRAU), JX630213\*, JQ039302, JQ025361, JQ024617, JQ024241. *H. blackburniae* W. F. Barker var. *graminifolia* (G. G. Sm.) M. B. Bayer. Western Cape, *BHD* 201 (JRAU), JX630194\*, JQ039303, JQ025362, JQ024618, JQ024242. *H. chloracantha* Haw. Western Cape, *BHD* 75 (JRAU), JX630291\*, JQ039305, JQ025363, JQ024625, JQ024249. *H. cooperi* Baker. Eastern Cape, *BHD* 133 (JRAU), JX630183\*, JQ024895, JQ025227, JQ024631, JQ024255. *H. cooperi* Baker var. *doldii* M. B. Bayer. Eastern Cape, *BHD* 209 (JRAU), JX630198\*, JQ024896, JQ025228, JQ024634, JQ024258. *H. cymbiformis* (Haw.) Duval. Eastern Cape, *BHD* 322 (JRAU), JX630225\*, JQ024898, JQ025229, JQ024645, JQ024269. *H. cymbiformis* (Haw.) Duval var. *ramosa* (G. G. Sm.) M. B. Bayer. Eastern Cape, *BHD* 321 (JRAU), JX630224\*, JQ024897, JQ025231, JQ024644, JQ024268. *H. cymbiformis* (Haw.) Duval var. *setulifera* (Poelln.) M. B. Bayer. Eastern Cape, *BHD* 320 & 325 (JRAU), JX630223\*/JX630226\*, JQ024899/JQ024900, JQ025230/JQ025232, JQ024648/JQ024649, JQ024272/JQ024273. *H. decipiens* Poelln. Eastern and Western Cape, *BHD* 132 (JRAU), JX630182\*, JQ024901, JQ025233, JQ024652, JQ024276. *H. decipiens* Poelln. var. *pringlei* (C. L. Scott) M. B. Bayer. Eastern Cape, *BHD* 196 (JRAU), JX630190\*, JQ024902, JQ025250, JQ024654, JQ024278. *H. decipiens* Poelln. var. *virella* M. B. Bayer. *BHD* 328 (JRAU), JX630228\*, JQ024903, JQ025234, JQ024656, JQ024280. *H. emelyae* Poelln. Western Cape, *BHD* 105 (JRAU), JX630179\*, JQ024904, JQ025236, JQ024661, JQ024285. *H. emelyae* Poelln. var. *comptoniana* (G. G. Sm.) J. D. Venter & S. A. Hammer. Eastern Cape, *BHD* 220 (JRAU), JX630202\*, JQ039307, JQ025364, JQ024663, JQ024287. *H. floribunda* Poelln. Western Cape, *BHD* 77 (JRAU), JX630292\*, JQ024906, JQ025251, JQ024666, JQ024290. *H. herbacea* (Mill.) Stearn. Western Cape, *BHD* 237 (JRAU), —, —, —, JQ024685, JQ024307. *H. herbacea* (Mill.) Stearn var. *flaccida* M. B. Bayer. Western Cape, *BHD* 333 (JRAU), JX630230\*, JQ024907, JQ025252, JQ024686, JQ024308. *H. herbacea* (Mill.) Stearn var. *paynei* (Poelln.) M. B. Bayer. Western Cape, *BHD* 373 (JRAU), JX630243\*, JQ024908, JQ025254, JQ024687, JQ024309. *H. lockwoodii* Archibald. Western Cape, *BHD* 213 (JRAU), JX630200\*, —, JQ025378, JQ024711, JQ024336. *H. maculata* (Poelln.) M. B. Bayer. Western Cape, *BHD* 203 (JRAU), JX630195\*, JQ024911, JQ025237, JQ024715, JQ024340. *H. magnifica* Poelln. var. *dekenahii* (G. G. Sm.) M. B. Bayer. Western Cape, *BHD* D92 (JRAU), JX630294\*, JQ024912, JQ025238, JQ024716, JQ024341. *H. marumiana* Uitewaal var. *archeri* (W. F. Barker ex M. B. Bayer) M. B. Bayer. Northern and Western Cape, *BHD* 235 (JRAU), JX630212\*, JQ024913, JQ025248, JQ024727, JQ024352. *H. marxii* Gildeh. Western Cape, *BHD* 339 (JRAU), JX630234\*, JQ024914, JQ025249, JQ024728, JQ024353. *H. mirabilis* (Haw.) Haw. Western Cape, *BHD* 32 (JRAU), JX630222\*, JQ039317, JQ025365, JQ024650, JQ024274. *H. mirabilis* (Haw.) Haw. var. *calcareia* M. B. Bayer. Western Cape, *BHD* 232 (JRAU), JX630210\*, JQ024916, JQ025246, JQ024771, JQ024397. *H. mirabilis* (Haw.) Haw. var. *paradoxa* (Poelln.) M. B. Bayer. Western Cape, *BHD* 44 (JRAU), JX630270\*, JQ024915, JQ025254, JQ024749, JQ024373. *H. mirabilis* (Haw.) Haw. var. *triebneriana* (Poelln.) M. B. Bayer. Western Cape, *BHD* 20 (JRAU), JX630192\*, JQ024917, —, JQ024773, JQ024399. *H. monticola* Fourc. var. *asema* M. B. Bayer. Western Cape, *BHD* 251 (JRAU), JX630216\*, JQ024918, JQ025255, JQ024780, JQ024405. *H. mucronata* var. *bijliana* (Poelln.) ined. Western Cape, *BHD* 350 (JRAU), JX630238\*, JQ024919, JQ025239, JQ024782, JQ024407. *H. mucronata* Haw. var. *habdomadis* (Poelln.) M. B. Bayer. Western Cape, *BHD* 347 (JRAU), JX630236\*, —, JQ025379, JQ024784, JQ024409. *H. mucronata* Haw. var. *morrisiae* (Poelln.) Poelln. Western Cape, *BHD* 349 (JRAU), JX630237\*, JQ024920, JQ025240, JQ024785, JQ024410. *H. mucronata* Haw. var. *rycroftiana* (M. B. Bayer) M. B. Bayer. Western Cape, *BHD* 345 (JRAU), JX630235\*, JQ024921, JQ025241, JQ024787, JQ024412. *H. mutica* Haw. Western Cape, *BHD* 102 (JRAU), JX630178\*, JQ024922, JQ025242, JQ024797, JQ024421. *H. mutica* Haw. var. *nigra* M. B. Bayer. Western Cape, *BHD* 72 (JRAU), JX630290\*, JQ024923, JQ025243, JQ024798, JQ024422. *H. outeniquensis* M. B. Bayer. Western Cape, *BHD* 356 (JRAU), —, JQ024924, JQ025256, JQ024807, JQ024431. *H. pulchella* M. B. Bayer var. *globifera* M. B. Bayer. Western Cape, *BHD* 206 (JRAU), JX630197\*, JQ024925, JQ025257, JQ024813, JQ024437. *H. pygmaea* Poelln. Western Cape, *BHD* 358 (JRAU), JX630240\*, JQ039320, JQ025333, JQ024816, JQ024440. *H. reticulata* (Haw.) Haw. Western Cape, *BHD* 117 (JRAU), JX630181\*, JQ024927, JQ025244, JQ024819, JQ024443. *H. retusa* (L.) Duval, *BHD* 27 & 120 (JRAU), JX630220\*, JQ024928, JQ025245, JQ024832, JQ024456/JQ024455. *H. semiviva* (Poelln.) M. B. Bayer. Northern and Western Cape, *BHD* 360 (JRAU), JX630242\*, JQ024929, JQ025247, JQ024844, JQ024467. *H. springboklakensis* C. L. Scott. Eastern Cape, *BHD* 362 (JRAU), —, —, —, JQ024847, JQ024470. *H. truncata* Schönland. Western Cape, *BHD* 210 (JRAU), JX630199\*, —, —, JQ024848, JQ024471. *H. variegata* L. Bolus. Western Cape, *BHD* 367 (JRAU), —, JQ039324, JQ025376, JQ024850, JQ024473. *H. vlokii* M. B. Bayer. Western Cape, *BHD* 249 (JRAU), JX630215\*, JQ024930, JQ025258, JQ024858, JQ024481. *H. wittebergensis* W. F. Barker. Western Cape, *BHD* 200 (JRAU), JX630193\*, JQ024931, JQ025259, JQ024859, JQ024482. *H. zantneriana* Poelln. Eastern Cape, *BHD* 230 (JRAU), JX630209\*, JQ039326, JQ025370, JQ024860, JQ024483. *Haworthia* subgenus *Hexangulares*: *H. attenuata* Haw. Eastern Cape, *BHD* 253 (JRAU), JX630217\*, JQ039300, JQ025311, JQ024610, JQ024234. *H. bruynsii* M. B. Bayer. Eastern Cape, *BHD* 374 (JRAU), JX630244\*, JQ039304, JQ025334, JQ024622, JQ024246. *H. coarctata* Haw. Eastern Cape, *BHD* 327 (JRAU), —,

JQ024894, JQ025296, JQ024629, JQ024253. *H. coarctata* Haw. var. *adelaidensis* (Poelln.) M. B. Bayer. Eastern Cape, *BHD* 326 (JRAU), JX630227\*, JQ039306, JQ025335, JQ024630, JQ024254. *H. fasciata* (Willd.) Haw. Eastern Cape, *BHD* 330 (JRAU), JX630229\*, JQ024905, JQ025270, JQ024664, JQ024288. *H. glauca* Baker. Eastern Cape, *BHD* 61 (JRAU), JX630289\*, JQ039308, JQ025336, JQ024673, JQ024295. *H. koelmaniorum* Oberm. & D. S. Hardy var. *mcmurtryi* (C. L. Scott) M. B. Bayer. Mpumalanga, *BHD* 336 & 337 (JRAU), JX630232\*/JX630233\*, JQ024909/JQ024910, JQ025293/JQ025294, JQ024690/JQ024689, JQ024312/JQ024311. *H. limifolia* Marloth. KwaZulu-Natal, Mpumalanga, *BHD* 159 & 175 (JRAU), JX630184\*/JX630185\*, JQ039311/JQ039312, JQ025341/JQ025342, JQ024697/JQ024693, JQ024321/JQ024316. *H. limifolia* Marloth var. *ubomboensis* (I. Verd.) G. G. Sm. Swaziland, *BHD* 221 (JRAU), JX630203\*, JQ039313, JQ025343, JQ024710, JQ024335. *H. longiana* Poelln. Eastern Cape, *BHD* 48 & 49 (JRAU), JX630288\*, JQ039314, JQ025316, JQ024714, JQ024339. *H. nigra* (Haw.) Baker. Eastern and Western Cape, *BHD* 224 (JRAU), JX630205\*, JQ039318, JQ025352, JQ024799, JQ024423. *H. reinwardtii* (Salm-Dyck) Haw. Eastern Cape, *BHD* 254 (JRAU), JX630218\*, JQ039321, JQ025332, JQ024817, JQ024441. *H. reinwardtii* (Salm-Dyck) Haw. var. *brevicula* G. G. Sm. Eastern Cape, *BHD* 359 (JRAU), JX630241\*, JQ024926, JQ025295, JQ024818, JQ024442. *H. sordida* Haw. Eastern Cape, *BHD* 205 (JRAU), JX630196\*, JQ039322, JQ025354, JQ024845, JQ024468. *H. venosa* (Lam.) Haw., Western Cape, *BHD* 246 (JRAU), JX630214\*, JQ039325, JQ025309, JQ024852, JQ024474. *H. venosa* (Lam.) Haw. subsp. *granulata* (Marloth) M. B. Bayer. Northern and Western Cape, *BHD* 88 (JRAU), JX630293\*, —, JQ025377, JQ024853, JQ024475. *Haworthia* subgenus *Robustipendunculatae*: *H. kingiana* Poelln. Western Cape, *BHD* 335 & 435 (JRAU), JX630231\*/JX630268\*, JQ039309/JQ039310, JQ025339/JQ025340,

JQ024688/—, JQ024310/—. *H. marginata* (Lam.) Stearn. Western Cape, *BHD* 26 & 439 (JRAU), JX630219\*/JX630269\*, JQ039315/JQ039316, JQ025338/ JQ025337, JQ024719/—, JQ024344/—. *H. pumila* (L.) Duval. Western Cape, *BHD* 222 (JRAU), JX630204\*, JQ039319, JQ025353, JQ024815, JQ024439. **OUTGROUP TAXA:** *Anthericum* L.: *A. liliago* L. Europe, Turkey, *Chase* 515 (K), —, —, —, JQ669567, JQ669532. *Asphodeline* Rchb.: *A. lutea* (L.) Rchb. South-eastern Europe to Turkey, *UCI Arb.* 3440, JX630297\*, JQ039289, —, JQ669566, JQ669533. *Bulbine* Wolf: *B. fistulosa* Chiov. Eritrea, *Chase* 3941 (K), JX630298\*, JQ039327, —, —, JQ669538. *B. frutescens* (L.) Willd. Eastern, Northern and Western Cape, Free State, Gauteng, KwaZulu-Natal, Limpopo, Namibia, Swaziland, *Van Wyk* 4115 (JRAU), —, JQ039294, AY323650, AJ512323, AJ511414. *B. semibarbata* (R. Br.) Haw. Australia, except Northern Territory, *K. Dixon s.n.* (KPBG), —, —, —, JQ669568, JQ669534. *Eremurus* M. Bieb.: *E. spectabilis* M. Bieb. Israel, Lebanon, North Caucasus, South European Russia, Transcaucasia, Armenia, Georgia, Asiatic Turkey, Ukraine, *Chase* 490 (K), JX630300\*, JQ039296, —, JQ669570, JQ669536. *Kniphofia* Moench: *K. galpinii* Baker KwaZulu-Natal, Mpumalanga, Swaziland, *IPMB* 040340 (HEID), —, —, —, AJ512329, AJ511423. *K. uvaria* (L.) Oken. Northern and Western Cape, *IPMB* 040342 (HEID), —, —, —, AJ512330, AJ511425. *Tecophilaea* Bert. ex Colla: *T. cyanocrocus* Leyb. Chile, *Chase* 447 (K), JX630299\*, —, —, —, JQ669539. *Xanthorrhoea* Sm.: *X. resinosa* Pers. Australia, *Chase* 192 (NCU), —, —, U23993, HM640546, HM640663. *X.* sp. (stemless), Western Australia, *Brummitt* 21391, JX630295\*, JQ039328, —, JQ669563, JQ669540. *X.* sp. (with trunk), Western Australia, *Brummitt*, *George & Oliver* 21376, JX630296\*, JQ039329, —, JQ669564, JQ669541. *Zephyra* D. Don: *Z. elegans* D. Don. Chile, *Chase* 1575 (K), —, —, —, JQ669565, JQ669542.