

A systematic account of
Haemanthus
(Amaryllidaceae: Haemantheae)

D.A. Snijman





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A peer-reviewed publication of the
South African National Biodiversity Institute



Pretoria
2025

*S*TRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of the Kirstenbosch Botanic Gardens*, which the South African National Biodiversity Institute (SANBI) inherited from its predecessor organisations.

The plant genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and two acaulescent species, known as crane flowers or bird-of-paradise flowers. The logo of SANBI is partly based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of SANBI to champion the exploration, conservation, sustainable use, appreciation and enjoyment of South Africa's exceptionally rich biodiversity for all people.

Editor:	Nicole Meyer
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Front cover:	<i>Haemanthus pubescens</i> (photographer: John Manning)
Inside front and back covers:	<i>Haemanthus sanguineus</i> (photographer: John Manning)
Photographs:	John Manning and Colin Paterson-Jones
Distribution maps:	Michelle Smith and Elizma Fouché

Recommended citations:

SNIJMAN, D.A. 2025. A systematic account of *Haemanthus* (Amaryllidaceae: Haemantheae). *Strelitzia* 48. South African National Biodiversity Institute, Pretoria.

SNIJMAN, D.A., MAGEE, A.R., CONRAD, F., MANUEL, R. & BOATWRIGHT, J.S. 2025. Molecular phylogenetics of *Haemanthus* (Amaryllidaceae: Haemantheae). In: D.A. Snijman, A systematic account of *Haemanthus* (Amaryllidaceae: Haemantheae). *Strelitzia* 48: 170–183. South African National Biodiversity Institute, Pretoria.

ISBN: 978-1-928224-69-3

Obtainable from: SANBI Bookshop, 2 Cussonia Ave., Brummeria, Pretoria, 0184 South Africa

E-mail: sanbibookshop@sanbi.org.za

Website: www.sanbi.org

Printed by: Shereno Printers, 10 Atlas Road, Dunswart, Boksburg, South Africa; website: www.shereno.co.za

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Abstract



Haemanthus is a genus of 25 species endemic to southern Africa. Morphologically it is the most diverse member of the sub-Saharan African and Arabian-peninsula Haemantheae, the only tribe within family Amaryllidaceae that has baccate fruits. All species of *Haemanthus* are perennial bulbous plants, characterised by tunicate bulbs, mostly paired, fleshy to leathery, often pubescent, opposite leaves, a brush-type inflorescence of many, relatively small flowers, surrounded by several, variously coloured spathe bracts, and a base chromosome number $x = 8$. Molecular and morphological evidence, including the arrangement of bulb tunics, flowering phenology and seed pigmentation, supports a new classification in which two subgenera are recognised. Subg. *Serena* (7 spp.), which is widespread within the summer-rainfall region of southern Africa, mainly in temperate grasslands and subtropical thicket, is recognised by ovoid bulbs with few, uniseriate tunics, synanthous or near-synanthous leaves, and green or ivory-white, non-dormant seeds. Within subg. *Serena*, plants bear inflorescences comprising thin-textured, pink, pale pink or white, spreading or erect spathe bracts, and matching-coloured flowers with a smooth perigone tube. Subg. *Haemanthus* (18 spp.), which is species-rich within the semi-arid winter-rainfall region of Namibia, Northern Cape and Western Cape, is distinguishable by obclavate or pyriform bulbs with many, uniseriate or biseriate tunics, hysteroanthous leaves, and wine-red or brownish red, non-dormant seeds containing anthocyanins. Species within subg. *Haemanthus* have inflorescences in which the spathe bracts vary from membranous to leathery or fleshy, and the colour ranges from white to cream-coloured, pink or bright red, with the spathe bracts and flowers in the latter typically held erect. Most red-flowered species possess a specialised perigone tube that is shallowly grooved below the tepal sinuses and gibbose below each tepal, increasing support for the upright tepals. Several species that are adapted to semi-arid habitats have specialised foliage, notably the prostrate-leaved habit, psammophorous or bristly leaf surfaces within *H. nortieri* and *H. humanii*, respectively, and sinuate leaf edges within *H. crispus* and *H. namaquensis*. This account covers the taxonomy, morphology, flowering, fruiting and seeding biology within the genus, as well as its evolution. Keys to the 28 taxa recognised within *Haemanthus* are provided. Each species is described in full, with complete synonymy, notes on ecology and distribution maps. All but one taxon are illustrated in colour. To establish conformity in the application of taxonomic rank within the genus, the populations that until now were treated as subspecies within *H. pubescens* are elevated to species rank as *H. arenicola* and *H. leipoldtii*.



Acknowledgements



I am most grateful to botanical artists Fay Anderson, Vicki Thomas and Elbe Joubert for generously permitting their paintings to be included in this work. Sue Goldswain kindly gave permission to use the paintings and drawings of her late mother, Ellaphie Ward-Hilhorst; the editor of *Curtis's Botanical Magazine* granted permission to use the painting by Elbe Joubert; and SANBI allowed the use of the painting by the late Cythna Letty. John Manning kindly contributed photographs, as did the Trust of the late Colin Paterson-Jones. Michelle Smith helped considerably by preparing the maps and Tasha Lyner with the DNA extraction. I am extremely grateful to the Mapula Trust for the generous sponsorship towards the publication, and to Sandra Turck, Elizma Fouché and Nicole Meyer for their support with the design, technical editing and production of this account. For the new insights that I gained from her phylogenetic studies on Haemantheae, my sincere appreciation goes to Ferozah Conrad. Lastly, I am greatly indebted to Elizabeth Parker and John Manning for their companionship and help in bringing this work to fruition.

Nomenclatural novelties published in this volume

Haemanthus subg. **Serena** (Raf.) Snijman, stat. nov.

Haemanthus arenicola (Snijman) Snijman, stat. nov.

Haemanthus leipoldtii (Snijman) Snijman, stat. nov.

Introduction



Just one year after the Dutch East India Company established its vast trading network that linked Europe with the East in 1602, Gouarus de Keyser dug up some bulbs of what we now know as *Haemanthus* and shipped them from the refreshment station, later known as the Cape of Good Hope, to his brother, Jacobus de Keyser, a plant lover and wealthy merchant of Wiesbaden. It is impossible to know whether or not he was driven by an economic imperative, but even today it is not difficult to imagine what De Keyser must have felt when newly faced with the wealth of plants surrounding Table Mountain. His particular choice, consequently, says much about how strikingly different and appealing these bulbous plants must have appeared to him. As anticipated, his consignment aroused similar interest in Europe, where the bulbs soon found homes among other rare and exotic plants on display within the grand gardens of the time.

Despite possible hopes for economic returns, the bulbs failed to gain the popularity that other Cape plants were able to attain. Their unusual inflorescences and flowering habits, however, continued to attract some interest, and in 1687 Paul Hermann, botanist at the service of the Dutch East India Company, conceived of the name *Haemanthus*. Derived from the Greek *haima*, blood, and *anthos*, flower, it is an apt descriptor of the plant's startling scarlet flowers, which create brilliant splashes of colour against the Cape's dry autumn landscape.

Even a cursory look at the various common names that have been applied to species like *H. coccineus* and *H. sanguineus* confirms the sense of curiosity that people retain for these plants. Names range from April-fool, which is evocative of surprise on first seeing their red inflorescences appear, devoid of leaves, in autumn, to paintbrush and *velskoenblaar*, both suitably descriptive albeit more predictable choices, to other local names such as *umathunga* and *uzaneke*, for *H. albiflos* and *H. deformis*, which refer to yet another aspect of *Haemanthus*, namely their importance as traditional medicine.

The genus, as it is understood today, is found exclusively within southern Africa, where it is the most morphologically diverse member of the sub-Saharan African and Arabian-peninsula Haemantheae, the only tribe within family Amaryllidaceae in which the fruits are berries. Like its sister genus *Scadoxus* Raf., *Haemanthus* has a characteristic brush-type inflorescence of many, relatively small flowers, surrounded by several, mostly colourful spathe bracts. *Haemanthus*, however, is distinguished within Haemantheae in having few, fleshy or leathery, mostly paired and often pubescent, opposite leaves, and a base chromosome number of $x = 8$.

In this systematic account of *Haemanthus*, 25 species are recognised within two newly recognised subgenera, *Haemanthus* and *Serena*. Drawing on a thorough knowledge of the plants in the field, this work brings together new insights derived from morphological data that were previously lacking, most notably on the group's large, non-dormant seeds, and from phylogenetic studies that are based on nuclear ribosomal and plastid data (Conrad et al. 2006; Conrad 2008). Much of the information

on the habits and habitats of the plants is enriched by the large body of literature on southern African plant ecology.

This study reveals that the key morphological features of the bulbs and seeds that are present within *Haemanthus* are either unique within the genus or are unusual within the tribe. In combination they are inferred to have promoted the adaptive shifts in flowering phenology that have enabled the lineage to radiate across southern Africa in response to the divergent rainfall regimes that have developed within the east and the west of the subcontinent.

Material and methods



Field studies of *Haemanthus* were undertaken throughout the winter-rainfall region of southern Africa, whereas the summer-rainfall taxa were largely studied as living collections at Kirstenbosch National Botanical Garden, Cape Town. All taxa were seen in their natural habitats, apart from *H. avasimontanus* and *H. pauculifolius*.

To obtain complete herbarium specimens, bulbs collected in habitat were grown at Kirstenbosch National Botanical Garden for their matching leaves, flowers and fruits. To record the qualitative characters differentiating taxa, herbarium records were supplemented with photographs of the bulbs and notes on the colour, markings, texture and orientation of the leaves, the spathe bracts and flowers. Fresh flowers were mounted on gummed card to ensure that floral measurements remained representative of the living plants. Likewise, the colour illustrations portray as closely as possible the typical in situ appearance of the plants. Vouchers for the paintings are preserved in NBG and PRE. Terminology follows Stearn (1980).

The data on climate and vegetation provided for each taxon are from Mucina and Rutherford (2006) and Dayaram et al. (2019), and the geographical referencing system used is from Leistner and Morris (1976). All type specimens were examined, including additional material from B, BM, BOL, E, GRA, K, MO, NBG, PRE, SAM, STE and WIND (herbarium acronyms according to Thiers [2022]). The nomenclature follows Turland et al. (2018). Vouchers for the respective taxa used in the molecular phylogenetic studies of Conrad et al. (2006) and Conrad (2008) are included in Appendix 1 (pp. 184–190).

Distribution maps were prepared using herbarium records within BOL, NBG, NH, PRE and SAM, as well as from confirmed observations (though not necessarily Research Grade rated) on iNaturalist (as on 12 Aug. 2022).

Given the diagnostic importance of recalcitrant seeds in delimiting taxa (Snijman & Linder 1996), seed pigmentation within *Haemanthus* was plotted on the strict consensus tree generated in the molecular phylogenetic study by Conrad (2008). The respective seed characters that support the major dichotomy resolved within the genus are thus taken to be diagnostic at subgeneric rank.

The molecular phylogenetic analysis of tribe Haemantheae by Conrad et al. (2006) and Conrad (2008) included 19 and 24 taxa of *Haemanthus*, respectively, and used four plastid DNA regions (*rpoB-trnC* intergenic spacer, *trnL-F* intron, *rps16* intron and *psbA-trnH* intergenic spacer) and one nuclear region (ITS). Using Parsimony analysis, Conrad (2008) generated a strict consensus tree,

based on combined nuclear and plastid data, that resolved a strongly supported dichotomy within *Haemanthus*, a result that closely resembled the topology generated by ITS nuclear data alone. The topology is supported by a Maximum Likelihood tree generated by Madzivire (2021) using ITS, mitochondrial *nad1i477* and *trnL-F* sequence data of 26 *H. pumilio* samples and the 24 previously used *Haemanthus* taxa, with *Scadoxus* as the outgroup. Conrad's (2008) topology is likewise corroborated by the Bayesian and Maximum Parsimony analyses of 25 *Haemanthus* taxa contributed here in collaboration with co-authors Magee et al. (see Addendum pp. 170–183), based on ITS, *rps16* and *trnL-F* sequences, and using representatives of *Scadoxus*, subtribes Gethyllidinae and Cliviinae, plus *Cyrtanthus sanguineus* Hook.f., *Calostemma purpureum* R.Br. and *Pancratium illyricum* L. as outgroups (Figure 1). Other phylogenetic studies of Haemantheae (Meerow & Clayton 2004; Bay-Smidt et al. 2011; Rønsted et al. 2012) that resolved a slightly different result for *H. montanus* were based on fewer gene regions and less than half the number of accepted taxa.

As yet, the reproductive biology of *Haemanthus* is largely unknown, apart from that of *H. pumilio* (Markötter 1936; Madzivire 2021). Thus, the taxonomic circumscriptions in this work draw heavily on patterns of morphological cohesiveness among populations relative to differences from others. This largely matches the phylogenetic species concept, defined as the smallest aggregation of populations diagnosable by a unique combination of character states in comparable individuals (Nixon & Wheeler 1990). The recognition of subspecies follows the criteria recommended by Stuessy (1990). In so doing it is assumed that the observed morphological patterns are indicative of underlying genetic and reproductive relationships among species and subspecies, and as such, this treatment presents a hypothesis for reassessment in future studies.

Appendix 2 (pp. 191–193) gives the identities of taxa that were originally described within *Haemanthus* but are currently excluded from the genus.

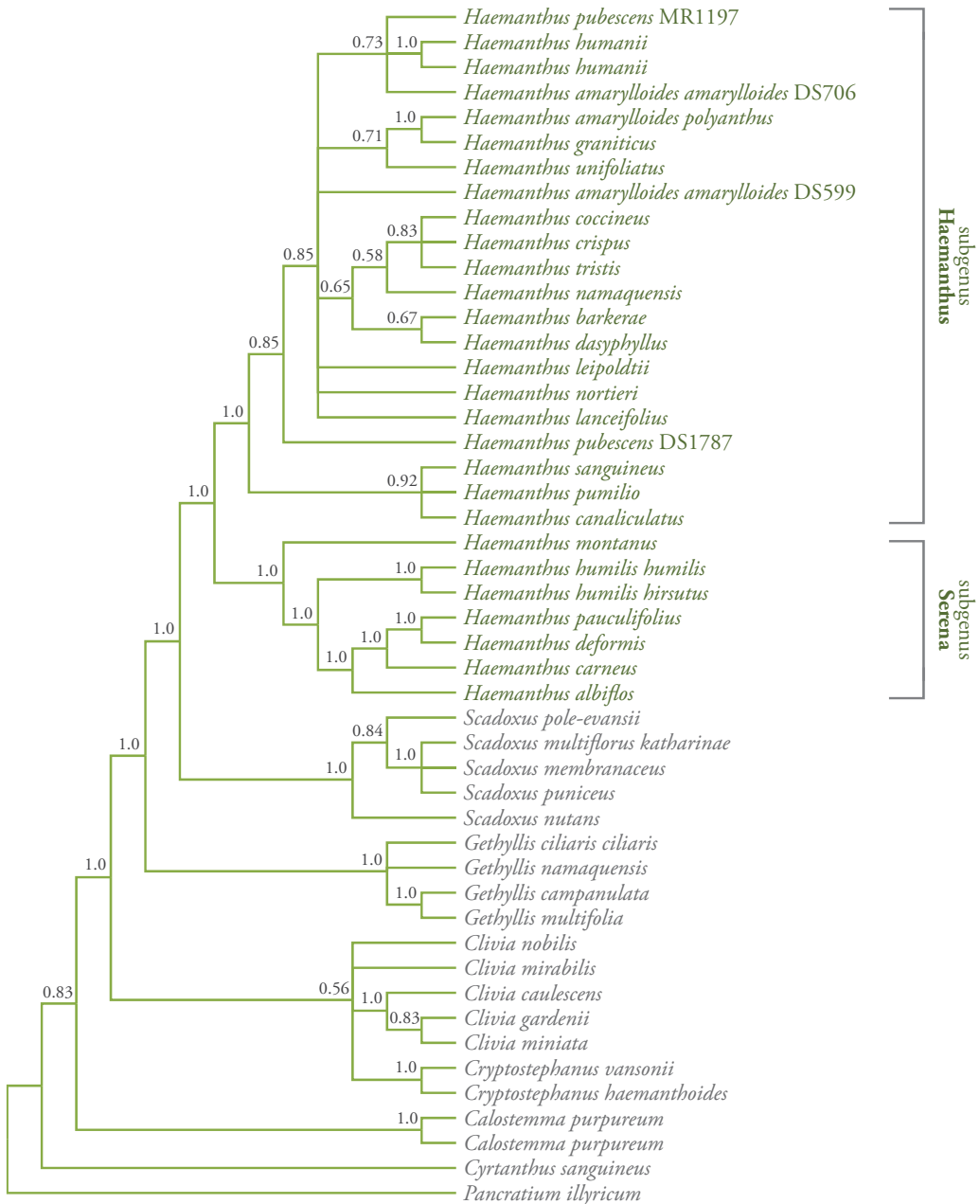


Figure 1A. Phylogenetic relationships within *Haemanthus* and tribe Haemantheae. Majority Rule Consensus tree from Bayesian analysis of nrITS and the two plastid markers, *rps16* and *trnL-F*. Posterior probability values > 0.5 are indicated above the branches (see Addendum pp. 170–183).

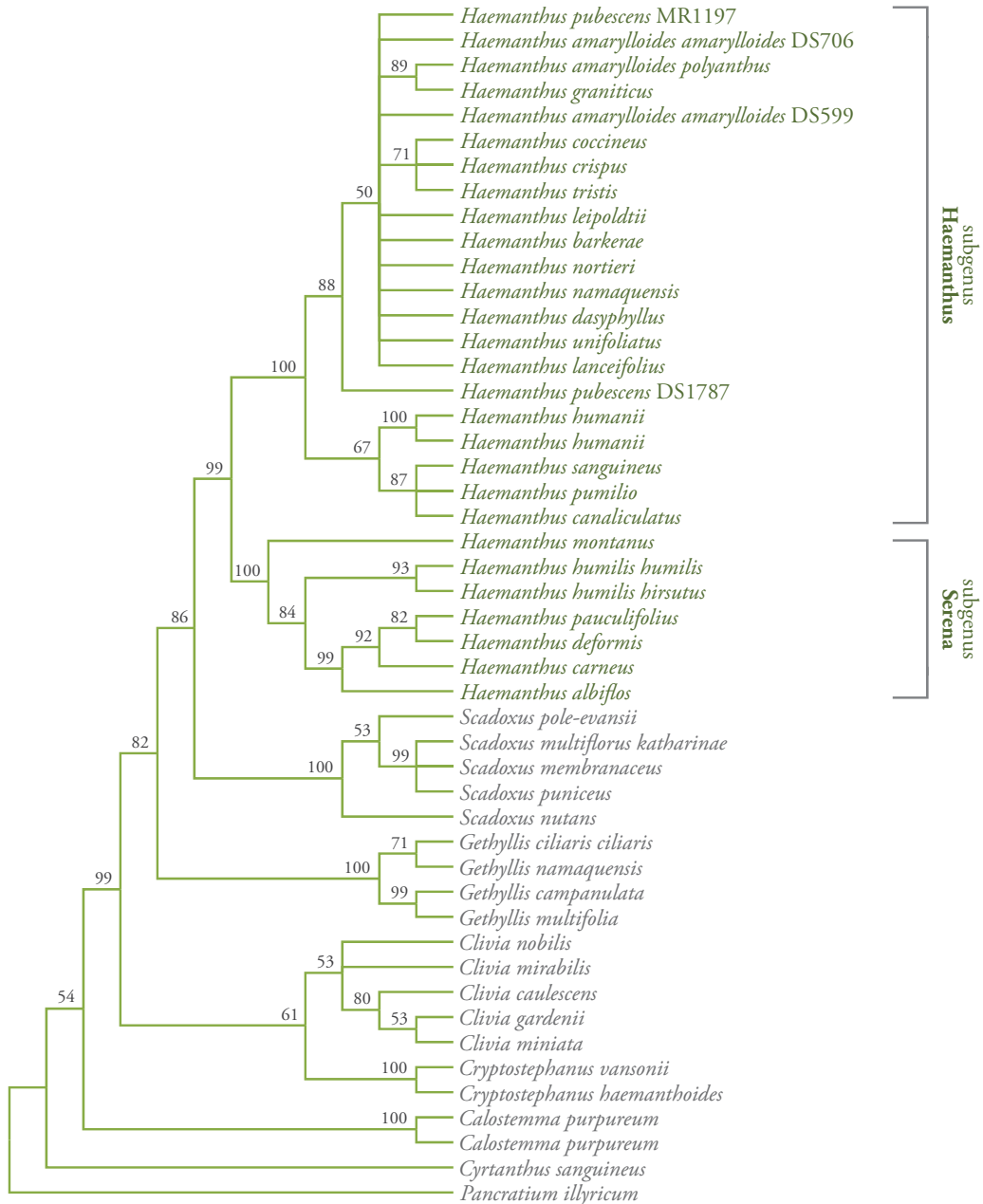


Figure 1B. Phylogenetic relationships within *Haemanthus* and tribe Haemantheae. Strict Consensus tree of the 650 equally most parsimonious trees with a length of 760 steps, based on the Maximum Parsimony analysis of nrITS and the two plastid markers, *rps16* and *trnL-F*. Bootstrap support values > 50% are indicated above the branches (see Addendum pp. 170–183).

Taxonomic history



Past circumscriptions

The earliest known reference to what we know as *Haemanthus* is by the Flemish botanist De l'Obel (1605), who provided descriptions of two plants under the phrase names *Narcissus Africanus sive* [or] *Narcissus exoticus* and *Narcissus Aphricanus folio rotundiore*. Although the accompanying illustrations are highly fanciful depictions, the names most likely refer to what have come to be known as the two most widespread species in the Greater Cape Floristic Region, *H. coccineus* and *H. sanguineus*. De l'Obel was unstinting in his appreciation of these new discoveries and he deemed them to be among the rarest and most elegant of exotic delights for any gardener (Gunn & Codd 1981).

New phrase names for the plants continued to be proposed for what were probably the same species in several later publications of the 17th century (Ferrari 1633; Van Stapel 1644; Colonna 1651; Morison 1680), but these finally gave way to the name *Haemanthus*, published by Hermann in 1687. The name, meaning blood-flower, which was chosen for the red-flowered species, was quickly adopted and the plants were soon being referred to in the form of the binomial, *Haemanthus africanus* (Tournefort 1700; Commelin 1701; Boerhaave 1720).

In 1753, when the first edition of Linnaeus' *Species plantarum* appeared, *H. coccineus* was among the earliest species to be formally recognised, and thus replaced the name *H. africanus*. Linnaeus also included within the genus another species, *H. puniceus* L. from the eastern coastal regions of South Africa, the Guinea-Congolian Region, Tanzania and Ethiopia (Bjørnstad & Friis 1974). In doing so, he initiated a long tradition of uniting the strictly southern African species of *Haemanthus* with other, predominantly tropical and subtropical African species.

Thereafter, few additions were made until 1797, when Jacquin's beautifully illustrated volumes of *Plantarum rariorum horti caesarei Schoenbrunnensis* (1797, 1804) added 12 new *Haemanthus* species. Herbert (1837) followed suit with his major contribution that added descriptions of seven new species, mostly from the collections of Masson and Burchell.

Rafinesque (1838) chose to divide *Haemanthus* into four new genera, delimited by the colour and length of the spathe bracts and the shape of the perigone tube. Rafinesque's genera, *Leucodesmis* Raf., *Perithema* Raf. and *Serena* Raf., later came to be included within *Haemanthus* subg. *Haemanthus*, whereas *Scadoxus* Raf., which accommodated the subtropical species thus far placed in *Haemanthus*, remained overlooked at subgeneric rank (Bjørnstad & Friis 1972).

Salisbury (1866) subsequently chose to divide *Haemanthus* into four additional genera: *Diacles* Salisb., *Melicho* Salisb., *Gyaxis* Salisb. and *Nerissa* Salisb. The former two, together with *Haemanthus*, were characterised by compressed, imbricate bulbs and non-sheathing leaves, whereas the two latter

were diagnosed by an ovate bulb and sheathing, petiolate leaves. Genera within the two groups were further distinguished by the shape and degree of dominance of the spathe bracts. Despite listing the species that belonged within his genera, Salisbury's (1866) combinations fail to constitute valid publication (Turland et al. 2018: Art. 35.2, Ex. 6).

The first comprehensive taxonomic treatment of *Haemanthus* was by Baker (1888, 1896), who added several more species, based principally upon collections from the previously unexplored interior regions of southern Africa. Baker (1888, 1896) largely followed Salisbury's classification, but he reduced Salisbury's genera to subgenera. When combining *Haemanthus* and *Diacles* at subgeneric rank, however, he named the taxon subg. *Diacles* Baker, rather than by the autonym subg. *Haemanthus*. The subtropical group in turn were accommodated within subg. *Nerissa* (Salisb.) Baker. Although now outdated, Baker's accounts of *Haemanthus* were extremely valuable in bringing together all available knowledge of the genus and in providing keys for the identification of species.

Several decades later Bjørnstad and Friis (1972) revised the infrageneric classification of *Haemanthus*. They recognised just two subgenera: subg. *Haemanthus*, which included sections *Haemanthus* and *Melicho* (Salisb.) Pax & K.Hoffm.; and subgenus *Nerissa* (Salisb.) Baker, which included sections *Nerissa*, *Gyaxis* (Salisb.) Pax & K.Hoffm., *Demeusea* (De Wild. & T.Durand) Pax & K.Hoffm., *Choananthus* (Rendle) I.Bjørnstad & Friis, and *Gamolepis* I.Bjørnstad & Friis. Shortly thereafter Müller-Doblies and Müller-Doblies (1975) provided additional morphological evidence in support of raising these two subgenera to distinct genera and thereby they drew attention to the priority of the name *Scadoxus* for the subtropical group. Friis and Nordal (1976) put the revised classification into effect and made the necessary nomenclatural changes, thus refining the morphological coherence of each genus within subtribe Haemanthinae (Meerow & Clayton 2004).

As presently circumscribed, *Haemanthus sensu stricto* (s.s.) is restricted to southern Africa and includes only species with true bulbs, distichous fleshy or leathery leaves, and the base chromosome number $x = 8$. The genus *Scadoxus*, in contrast, includes species with bulbous and rhizomatous root stocks, soft net-veined leaves with a distinct midrib and pseudo-petiole, and the base chromosome number $x = 9$. *Scadoxus* occurs predominantly in tropical and subtropical Africa, but it extends into southern Africa along the equable east coast to the vicinity of Bredasdorp on the Agulhas plain, Western Cape. The prevailing difficulties that prevented Friis and Nordal gaining access to South African herbarium material at that time, unfortunately hindered a thorough revision of *Haemanthus* s.s. Thus, in their review only nine *Haemanthus* species and species complexes were recognised (Friis & Nordal 1976).

In contrast, Snijman's (1984) revision of *Haemanthus*, based largely on the study of wild plants in habitat, recognised 21 species and eight subspecies, of which seven taxa were newly described. Moreover, through matching several previously published plates of taxonomic importance with modern herbarium material, nomenclatural stability was brought to the group. Similarly, the colour illustrations by artists, Ellaphie Ward-Hilhorst and Fay Anderson, provided definitive portraits of most of the species recognised in the revision.

More recently, Snijman and Van Wyk (1993) described one additional species, and Duncan et al. (2016) contributed a fully illustrated, generalised account of the genus, as circumscribed by Snijman (1984) and Snijman and Van Wyk (1993). The surprising discovery in 2018 of a population of highly distinctive plants in Namaqualand, unlike any taxon thus far known, led to one more species being described in 2022 (Duncan & Joubert 2022).

Newly applied circumscriptions

In their classification of *Haemanthus* (as subg. *Haemanthus*), Bjørnstad and Friis (1972) recognised two sections based on the orientation of the spathe bracts: dominating and ascending for sect. *Haemanthus* versus not dominating and early descending for sect. *Melicho*. In their later studies, however, they noted that the *Haemanthus albiflos* complex appeared to be intermediate between the two sections and thereby concluded that their earlier classification was too rigid. They recognised the possibility of grouping the species within three sections, but they finally avoided subdivision of the genus entirely, pending further study (Friis & Nordal 1976).

Using the previously overlooked character states of the leaf habit and the newly available cytological data (Vosa & Snijman 1984), Snijman (1984) recognised four informal groups within *Haemanthus*: one group of evergreen plants, and three groups of deciduous plants, of which one was characterised by synanthous leaves, another by hysternanthous leaves, and the last was defined by hysternanthous or rarely synanthous leaves and a derived karyotype.

More recently, greater clarity on the infrageneric relationships within *Haemanthus* has emerged from the molecular phylogenetic studies of Conrad (2008), Madzivire (2021) and in collaboration with co-authors Magee et al. (see Addendum pp. 170–183), based on nuclear ribosomal and plastid DNA sequences. Consequently, two subgenera are recognised that correspond with the two well-supported major clades within the lineage (Figure 1). Named subg. *Serena* (Raf.) Snijman and subg. *Haemanthus*, these taxa are diagnosed by differing states in bulb tunic arrangement (equally uniseriate versus unequally tiered in horizontal or oblique rows); flowering and leafing phenology (synanthous versus hysternanthous); and seed pigmentation (green or white versus wine-red), respectively (Table 1). Whereas the orientation of spathe bracts is diagnostic for individual species or small groups of species, this character has little value at subgeneric rank. Snijman's (1984) weighting of karyotype morphology for infrageneric groupings is also not supported.

Species delimitations in the majority of species are clear-cut and the species are relatively easily distinguished by several independent characters. The remaining species, however, are more complex and their treatment unavoidably continues to be subjective. For species with several regional races but equally many intermediates, such as within *H. coccineus* and *H. sanguineus*, the full morphological amplitude within each species is discussed, but no infraspecific taxa are recognised. Where closely related but morphologically distinct forms have differing distribution ranges with minor geographic overlap and some intermediate populations, they are given subspecific rank, as within *H. amarylloides* and *H. humilis*. Snijman (1984), however, also treated as subspecies within *H. pubescens*, three

Table 1. Subgeneric classification of *Haemanthus* L.

Subg. <i>Serena</i> (Raf.) Snijman	
1. <i>H. montanus</i> Baker	5. <i>H. albiflos</i> Jacq.
2. <i>H. avasimontanus</i> Dinter	6. <i>H. deformis</i> Hook.f.
3. <i>H. carneus</i> Ker Gawl.	7. <i>H. pauculifolius</i> Snijman & A.E.van Wyk
4. <i>H. humilis</i> Jacq.	
4a. subsp. <i>humilis</i>	
4b. subsp. <i>hirsutus</i> (Baker) Snijman	
Subg. <i>Haemanthus</i>	
8. <i>H. amarylloides</i> Jacq.	16. <i>H. crispus</i> Snijman
8a. subsp. <i>amarylloides</i>	17. <i>H. coccineus</i> L.
8b. subsp. <i>polyanthus</i> Snijman	18. <i>H. dasyphyllus</i> Snijman
8c. subsp. <i>toximontanus</i> Snijman	19. <i>H. unifolius</i> Snijman
9. <i>H. graniticus</i> Snijman	20. <i>H. arenicola</i> (Snijman) Snijman
10. <i>H. nortieri</i> Isaac	21. <i>H. leipoldtii</i> (Snijman) Snijman
11. <i>H. barkerae</i> Snijman	22. <i>H. pubescens</i> L.f.
12. <i>H. tristis</i> Snijman	23. <i>H. sanguineus</i> Jacq.
13. <i>H. lanceifolius</i> Jacq.	24. <i>H. canaliculatus</i> Levyns
14. <i>H. humanii</i> G.D.Duncan	25. <i>H. pumilio</i> Jacq.
15. <i>H. namaquensis</i> R.A.Dyer	

geographically and vegetatively discrete groups of populations that occupy similar sandy habitats and have inflorescences with prominent, bright red spathe bracts, which typically exceed the flowers. In the interest of reaching taxonomic conformity with respect to the application of morpho-geographic patterns within the genus, the original classification of *H. pubescens* has been reassessed (see pp. 136–140) and the two taxa previously treated as subspecies within *H. pubescens* are elevated here to species, as *H. arenicola* and *H. leipoldtii*, each being distinguished by differences in their bulbs and leaves. This brings the total number of species recognised within *Haemanthus* to 25.

Morphology



Bulb

Haemanthus, like most other Amaryllidaceae s.s. (i.e., excluding Agapanthaceae and Alliaceae), are bulbous perennials. The bulbs within *Haemanthus* are invariably tunicate, mostly medium to large in size, and they are anchored in the ground by numerous thick contractile roots that pull them to a depth that is optimal for the bulb's growth and storage. This large investment in the bulb is of critical importance for the survival of the plants, especially for the species that occupy regions of unreliable rainfall where the plants need to survive short-term drought and then respond rapidly when moisture conditions improve (Dafni et al. 1981; Rees 1984).

The bulb tunics, each derived from the sheathing thick base of a foliage leaf, accumulate slowly over several years to give the mature bulb its particular form, which varies from narrowly to broadly ovoid, obclavate or pyriform. Moreover, the bulbs vary as to how the tunics are arranged, with the resultant patterns being diagnostic of the subgenera (Figure 2).

The bulbs within species of subg. *Serena*, located predominantly within southern Africa's summer-rainfall region (Table 1), are considered to be the least specialised in the genus. Relatively few, evenly thick fleshy tunics, usually amounting to less than six pairs, persist in the mature state. They are concentrically arranged and either attain the same height or are slightly unequal and tiered, giving the bulb a somewhat smooth, ovoid form. Invariably the bulbs are slightly compressed in the direction of the distichous leaf arrangement. They remain close to the soil surface and, although slightly narrowed distally, they are not contracted into a slender neck (Figure 2). The outermost tunics are often pale brown and papery, whereas the inner fleshy, storage tunics often become pinkish, as in *H. humilis*, *H. carneus* and *H. montanus*, or green and photosynthetic, as in *H. albiflos*, *H. deformis* and *H. pauculifolius*, when exposed to light.

The bulbs within species of subg. *Haemanthus*, centred in the winter-rainfall region (Table 1), vary from obclavate to pyriform or rarely ovoid and, in contrast to the bulbs within subg. *Serena*, they possess features that are more specialised. Apart from the small, shallow bulbs within *H. humanii*, the majority of bulbs are deeply buried and they give rise to roots up to ± 1.2 metres long. When mature, the bulbs have numerous tunics, typically at least eight pairs, although in old plants, such as those of *H. arenicola* that inhabit the semi-arid sandy plains of northern Namaqualand, this number increases to 13 or more tunic pairs. In general, large bulbs provide the benefits of increased carbohydrate, mineral ion and water storage capacity, which in turn promotes their ability to occupy edaphically specialised or semi-arid habitats (Ruiters 1995; Procheş et al. 2006). Within subg. *Haemanthus* the species that occupy dry habitats also retain the protective brown leathery remnants of old tunics, either over the entire bulb or on the tunic edges only.

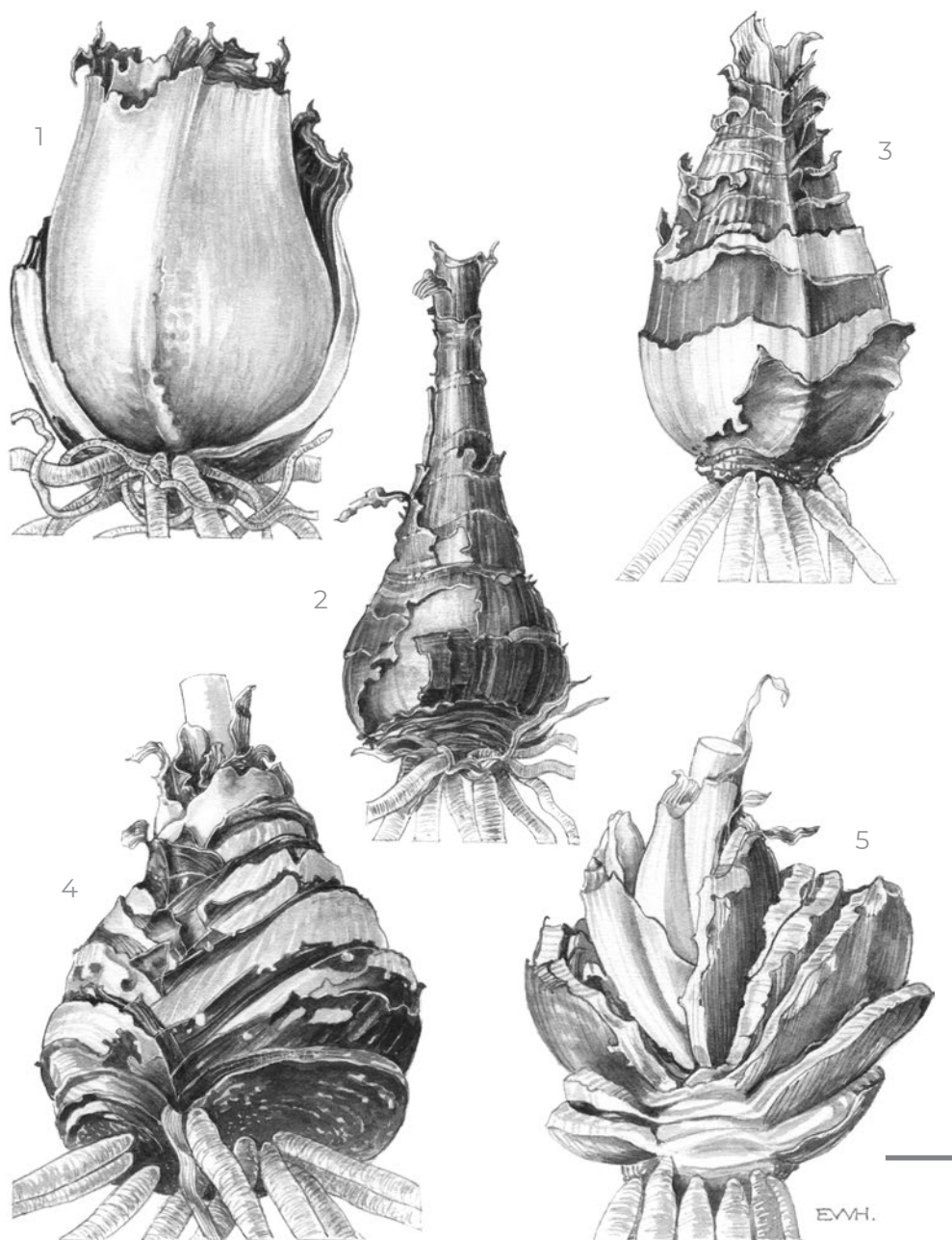


Figure 2. Bulb morphology within subgenera *Serena* (1) and *Haemanthus* (2–5). 1, *H. humilis* subsp. *hirsutus*, outer tunic partially removed to show equal inner tunics, Van Jaarsveld 1834 (NBG); 2, *H. barkerae*, Snijman 132 (NBG); 3, *H. unifolius*, Snijman 181 (NBG); 4, *H. coccineus*, Snijman 87a (NBG); 5, *H. canaliculatus*, Van Essen s.n. (NBG). Artist: Ellaphie Ward-Hilhorst. Scale bar: 1 = 10 mm; 2, 3, 5 = 12 mm; 4 = 16 mm.

Bulb size within subg. *Haemanthus* is notably associated with patterns of tunic arrangement. Species with relatively small bulbs have tunics that die back horizontally, forming a single, mostly tiered series of concentric, parallel-edged layers, as in *H. barkerae*, *H. crispus*, *H. nortieri*, *H. tristis* and *H. unifolius* (Figure 2). The bulbs within *H. barkerae*, *H. crispus* and *H. tristis* are mostly round in cross section and they have a well-developed slender neck, associated with narrow foliage leaves, and a deeply buried habit. Those of *H. nortieri* and *H. unifolius*, both unifoliate species, are compressed in the plane of the erect leaf blades.

Contrastingly, species with larger bulbs within subg. *Haemanthus* have tunics that die down obliquely to form two series of downward slanting tunics that are longer and thicker on the leaf-blade portion of the sheath, as within *H. coccineus* and *H. canaliculatus* (Figure 2), as well as most of the remaining species within the subgenus. Within *H. canaliculatus*, *H. namaquensis* and *H. pubescens* the tunics are so thick that they are loosely packed and appear scale-like due to the extreme one-sided reduction of the sheath close to the base. Invariably the bulbs that have two-ranked tunics are flattened cross-wise to the distichously arranged leaves. In effect, the unequal reduction in tunic height appears to promote the bulb's outward expansion, which leads to an increase in bulb size and storage capacity. Nonetheless, the bulbs within *Haemanthus* never match those within genera such as *Boophone* Herb. and *Crossyne* Salisb. (tribe Amaryllideae), which attain considerably larger size, aided by the presence of extensible fibres within the bulb tunics (Snijman & Linder 1996; Meerow et al. 1999).

For most species within *Haemanthus*, the bulbs can be induced to form offsets under cultivation (Duncan et al. 2016) and to a lesser extent by means of tissue culture. However, in the latter, contamination of the explants is high (Rabe & Van Staden 1999). In nature, the species most likely to form bulblets are *H. albiflos*, *H. canaliculatus*, *H. crispus*, *H. humilis*, *H. namaquensis*, *H. pauculifolius* and *H. pubescens*.

Leaves

The leaves, which are the main organs of photosynthesis, vary remarkably within the genus as to number, orientation, shape, texture, markings and indumentum. Consequently, they provide an array of diagnostic characters. Most species bear two leaves per year at maturity, although three may occasionally appear, but never consistently so. Reduction to a solitary leaf is characteristic of just three species, *H. pauculifolius*, *H. nortieri* and *H. unifolius*. The former belongs within subg. *Serena* and the two latter fall within subg. *Haemanthus*, hence the unifoliate habit is inferred to have evolved at least twice within the genus. Despite the majority of plants within each of these three species being unifoliate, plants with two leaves can occasionally be found.

As is typical of the geophytic habit, most species are deciduous, except three species. The evergreen *H. albiflos* and *H. deformis*, which inhabit the frost-free mesic eastern seaboard, may have up to four or six leaves throughout the year, and the closely allied *H. pauculifolius*, which favours drier, shady, more inland subtropical habitats, has only one green leaf annually, although the leaves of the previous and current season may briefly coincide.

Unusual leaf orientation is a striking feature of some species. Most notable is the prostrate leaf syndrome (Esler et al. 1999; Manning et al. 2002), which in *Haemanthus* is characterised by mostly two, flattened leaves pressed firmly to the ground, as in *H. amarylloides* subsp. *toximontanus*, *H. humanii*, *H. deformis* and the lowland forms of *H. sanguineus* (Figure 3). This strategy has been interpreted as a means to avoid herbivory or competition from neighbours, to create a carbon dioxide-rich environment below the leaves, or to regulate evapotranspiration (Esler et al. 1999; Cramer et al., 2007).

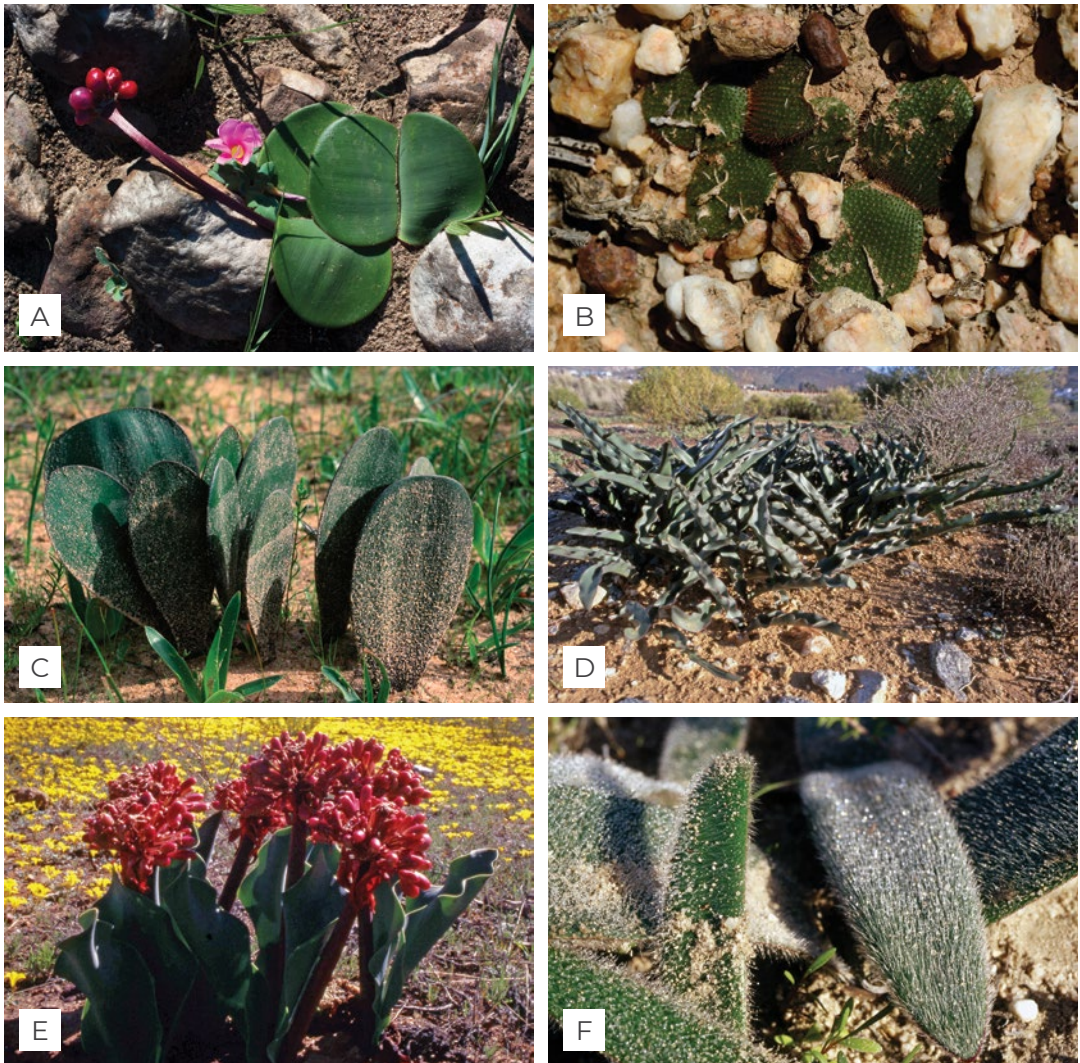


Figure 3. Specialised foliage within subg. *Haemanthus*. A, *H. sanguineus*; B, *H. humanii*; C, *H. nortieri*; D, *H. crispus*; E, *H. namaquensis*; F, *H. pubescens*. Photographs: A, C, E, F, Colin Paterson-Jones; B, D, John Manning.

Other novelties are the stiffly erect, solitary leaves of the winter-growing *H. nortieri* (Figure 3C) and *H. unifolius*. In these species the reduction in leaf number is possibly offset by the leaf's upright habit, which may enhance the interception of solar radiation during the cool winter months when energy for growth is low. The orientation of leaves within most other species of the genus, however, is variable and is influenced by local habitat conditions.

Broad elliptic to oblong-shaped leaves characterise the few widespread species, whereas the majority of species have strap-shaped leaves that vary from moderately broad, ± 15 –50 mm wide, to narrow, ± 5 –15 mm. *Haemanthus crispus* from Namaqualand and the adjacent dry areas in Western Cape has conspicuously undulate leaf edges (Figure 3D), a characteristic shared with several other geophytic species within various monocotyledonous families within the region. Procheş et al. (2006) hypothesised that the leaf undulations provide an enlarged photosynthetic surface area as an adaptation to the low-energy growth conditions of the winter-wet climate of Namaqualand and the northwestern region of Western Cape. Vogel and Müller-Doblies (2011), however, proposed that the leaf undulations are an adaptation to trap dew and fog in areas of low rainfall. The only other species that has undulate leaf edges is *H. namaquensis* from southern Namibia, western Richtersveld and northern Namaqualand, but the extent and degree of the undulations are markedly variable (Figure 3E).

Leaf texture ranges from succulent to leathery, and the colour varies from bright shiny green, dark or pale green to glaucous green. Leaf markings are absent in all species within subg. *Serena*, whereas barring and speckling in contrasting reddish brown or dark green colours is present in 10 species within subg. *Haemanthus*, although lacking in *H. amarylloides*, *H. nortieri* and *H. tristis*. This feature is shared with *Scadoxus*, which has speckling exclusively on the leaf sheaths. The leaf surface is smooth apart from the rough adaxial surfaces arising from the possession of minute papillae within *H. humanii*, *H. lanceifolius*, *H. nortieri*, occasionally in *H. humilis* subsp. *humilis*, and most lowland forms of *H. sanguineus*.

The leaves of *H. nortieri* are unique in being sticky to the touch and, consequently, grains of wind-blown sand become firmly fixed to the leaf blade (Figure 3C). Psammophorous leaves are presumed to have evolved primarily as an adaptation to habitats that are heavily impacted by wind abrasion, although in areas with more moderate wind runs the phenomenon may also influence the plant's water- or thermal energy-budgets (Jürgens 1996). Preliminary studies suggest that the viscous secretion consists mainly of polysaccharides (Neinhuis et al. 1996).

Although pubescence is uncommon within Amaryllidaceae s.s. (Meerow & Snijman 1998), the leaves, and often the scapes, of approximately half the taxa within *Haemanthus* are pubescent, a feature shared with the closely related *Gethyllis* L. The hairs are mostly uniseriate, thin-walled and white, varying from long and soft to short and firm (Figure 3B & 3F). The pubescence may be present on both or one or other leaf surface and often it is confined to the leaf margins. *Haemanthus lanceifolius* and most forms of *H. sanguineus* are exceptional in having leaves that are fringed with recurved, reddish, multiseriate, often branched trichomes, whereas the adaxial leaf surface of *H. humanii* is unique in bearing longitudinally arranged rows of straight, slanting to suberect, reddish brown trichomes

(Figure 3B). In the latter the apparently uniseriate trichomes have remarkably thick, minutely colliculate outer walls and each is inserted on a multicellular translucent papilla.

Inflorescence

Each year a solitary inflorescence is produced in which the flower head of several, reduced helicoid cymes, surrounded by several spathe bracts, is inserted distally on a fleshy scape. The scape, which is slightly compressed laterally, is mostly concolorous, ranging from green, pink, wine-red to bright red. Within subg. *Haemanthus*, however, the scape within several species is attractively maculate, most notably *H. coccineus*. The scape is mostly glabrous, but within hairy-leaved species the scape is also usually pubescent, typically of soft, white, spreading hairs, whereas within the sticky-leaved *H. nortieri* and glabrous-leaved *H. amarylloides* subsp. *polyanthus*, the scape is unusually rough to the touch due to a covering of minute, recurved hairs or papillae.

Unlike most Amaryllidaceae *s.s.* that have only two spathe bracts per inflorescence, *Haemanthus* and its sister, *Scadoxus*, are unique within Haemantheae in having at least four spathe bracts. These enclose the flower head in bud, then either fade and deflex during flowering or remain upright and closely surround the mature flower head. This variation in habit, together with the variation in number, texture and colour of the spathe bracts, provides useful diagnostic characters, especially for distinguishing taxa within subg. *Haemanthus*. The widely spreading, early fading, typically pale-coloured spathe bracts, considered here to be the least specialised within the genus, are typical of *H. avasimontanus*, *H. carneus*, *H. humilis* and *H. montanus* within subg. *Serena*, as well as *H. amarylloides*, *H. barkeriae*, *H. lanceifolius*, *H. pumilio* and *H. tristis* within subg. *Haemanthus* (Figure 4). The more specialised state of firm, upright bracts is associated with a more diverse array of colours. White, often green-veined or fully green spathe bracts characterise *H. albiflos*, *H. deformis* and *H. pauculifolius* within subg. *Serena*, whereas bright red or rarely pink spathe bracts are typical of the majority of species within subg. *Haemanthus*. Those of *H. canaliculatus*, *H. dasyphyllus*, *H. graniticus*, *H. sanguineus*, *H. nortieri* and *H. unifolius* are leathery in texture, which contrasts with the stiff, fleshy spathe bracts typical of *H. arenicola*, *H. coccineus*, *H. crispus*, *H. leipoldtii* and *H. pubescens* (Figure 4). Particularly striking spathe bracts that overtop the flower cluster characterise *H. arenicola* (Figure 5A) and *H. leipoldtii*.

Linear bracteoles that subtend the individual flowers vary from being markedly long and conspicuous within taxa that possess spreading inflorescences to short and cryptic within species that have suberect inflorescences. The flowers within *H. carneus* and *H. montanus* have especially long (up to 15 mm), filiform bracteoles that are tipped with a tuft of elongated balloon-shaped cells.

Flowers

The flower head contains numerous ($\pm$ 10–150), relatively small, actinomorphic flowers in which the pedicel is shorter or slightly longer than the perigone. The flowers, like those of *Scadoxus*, are markedly reduced in size compared with other genera within Haemantheae. *Haemanthus carneus* is

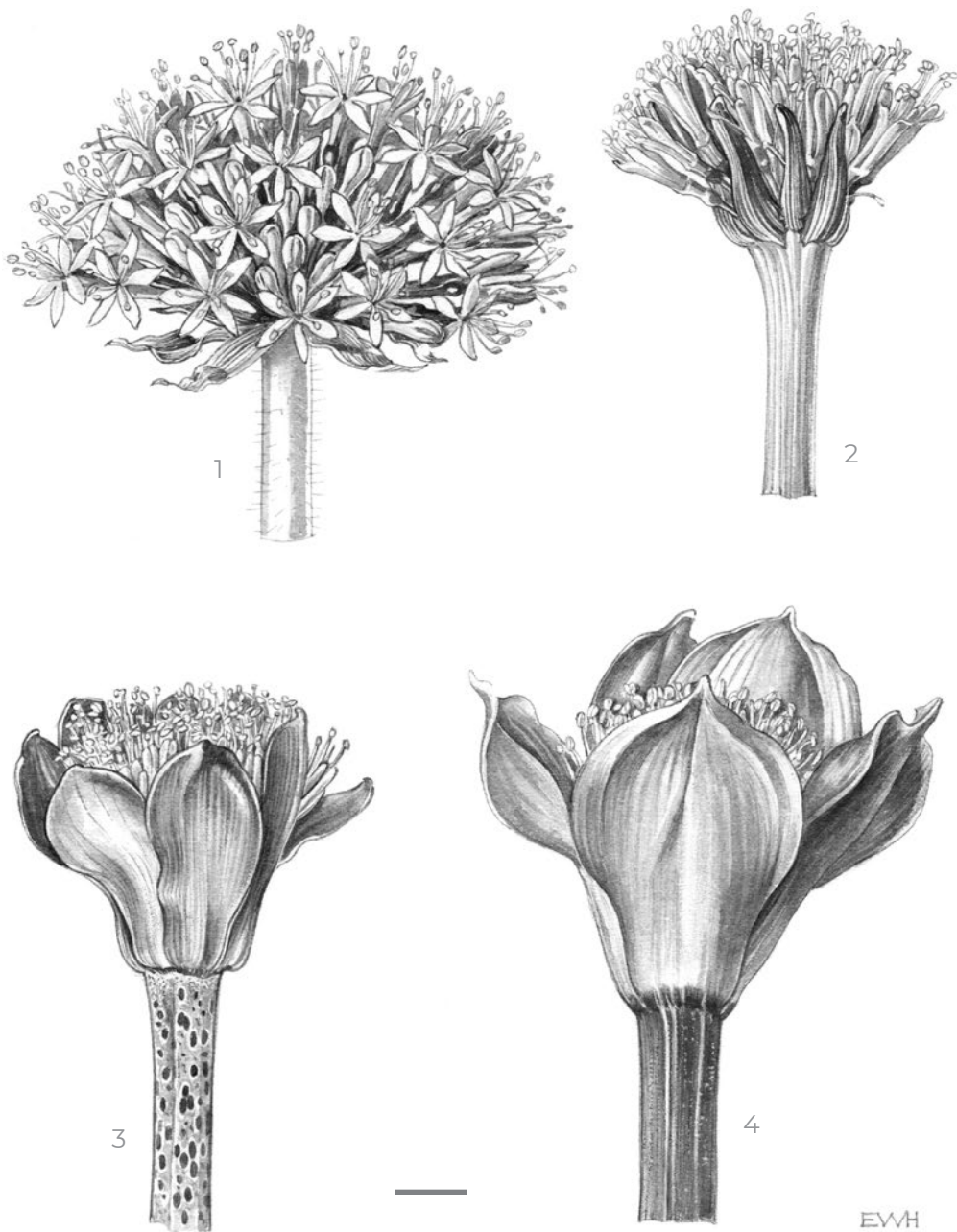


Figure 4. Inflorescence morphology within subgenera *Serena* (1) and *Haemanthus* (2–4). 1, *H. humilis* subsp. *humilis*, OFS 32/68 (NBG); 2, *H. amarylloides* subsp. *toximontanus*, W. Olivier 1193 (NBG); 3, *H. coccineus*, Snijman 87a (NBG); 4, *H. pubescens*, NBG 28/80 (NBG). Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–3 = 10 mm; 4 = 8.5 mm.



Figure 5. Edaphically differentiated habitats of species within subg. *Haemanthus*. A, *H. arenicola* in deep aeolian sand; B, *H. humanii* amongst quartz pebbles; C, *H. barkerae* in dolerite-derived clay; D, *H. canaliculatus* in fire-prone peaty vleis; E, *H. pumilio* on fire-prone alluvial flats. Photographs: A, C, D, E, Colin Paterson-Jones; B, John Manning.

exceptional in usually having notably long pedicels relative to the perigone (11–25 versus 11–13 mm long), which give rise to an especially lax, spreading flower head. In contrast, noticeably short pedicels of 0.5–4.0 mm occur within species that have tightly clustered flowers, notably *H. crispus*, *H. pauculifolius* and *H. pubescens*.

The perigone, which is variously funnellform or cylindrical, consists of six equally long tepals that are connate below into a short tube that never exceeds the length of the tepals, except within a few populations of *H. humilis* subsp. *humilis*. Within most species the perigone tube is smooth and gradually widens distally, but within subg. *Haemanthus* most species have a cylindrical or cyathiform tube that is often shallowly grooved below the tepal sinuses and gibbose at the base of each tepal. In the latter, the tepals bend slightly inwards above the perigone tube, and this maintains their close upright alignment. This novelty is restricted mostly to the red-flowered species and is combined with the tepal tips being white and notably swollen. In combination, these features likely provide extra support for visiting nectar-feeding birds. Both the nipped-in shape of the perigone immediately above the tube and the upright orientation of the tepals are diagnostic for *H. arenicola*, *H. coccineus*, *H. crispus*, *H. dasyphyllus*, *H. leipoldtii*, *H. namaquensis*, *H. pubescens* and *H. unifolius*, although within the widespread *H. coccineus* the flowers are somewhat variable; populations from the strictly winter-rainfall region in the west have mainly erect flowers, whereas those from the non-seasonal rainfall region east of $\pm 21^\circ$ E have slightly spreading flowers.

Since floral colour within *Haemanthus* is more diverse than in any other genus within the tribe Haemantheae it is often a useful diagnostic character. All the species within subg. *Serena* have white or pink flowers, whereas only five species within subg. *Haemanthus* are typically pale pink- to white-flowered: *H. amarylloides*, *H. barkeriae*, *H. humanii*, *H. lanceifolius* and *H. pumilio*. Elsewhere within subg. *Haemanthus* shades of red predominate, although some red-flowered species have rare, pink-flowered forms, namely *H. canaliculatus*, *H. crispus*, *H. pubescens* and *H. sanguineus*. Unique within subg. *Haemanthus* is *H. tristis*, which has cream-coloured flowers that age to pale pink.

The subequal, symmetrically arranged stamens that are inserted in the perigone throat are most often exserted beyond the tepals. Especially prominent stamens characterise the flowers of *H. humilis* subsp. *hirsutus* and they contribute to the flower head's attractive powderpuff-like appearance. In contrast, *H. carneus* is unique in having distinctly short stamens that are markedly unequal (three outer < three inner) and confined within the lower half of the perigone. *Haemanthus humanii* is also unique within the genus in having inner filaments that have thick ridges on the adaxial surface that reach up to ± 2.5 mm above the base and terminate in a minute, inwardly curved hook. Throughout the genus the dorsifixed anthers are consistently yellow and contain large ellipsoid, sulcate pollen grains (Bjørnstad & Friis 1972).

The ovary, situated below the perigone, contains one or two pendulous, bitegmic ovules in each of its three locules, and the filiform style, which invariably equals the stamens in length, ends in a minutely trifid stigma. *Haemanthus carneus* is exceptional in having a style half as long as the stamens, and in *H. humanii* the stigma is markedly trifid.

Fruits and seeds

The baccate fruit, which is unique within Amaryllidaceae *s.s.*, is synapomorphic for the entire tribe Haemantheae (Meerow et al., 1999). Within *Haemanthus* the berries are characteristically ovoid to globose and when they are mature the walls frequently become soft and aromatic. The red-flowered species are exceptional in having berries that become copiously mucilaginous before releasing their moisture-rich seeds (Figure 6). Within subg. *Serena* the berries are dull orange to whitish in



Figure 6. Berries within subg. *Haemanthus*. A, *H. coccineus*; B, *H. coccineus*, showing extensible funicle and large seed; C, *H. barkerae*; D, *H. tristis*. Photographs: A, D, John Manning; B, C, Colin Paterson-Jones.

H. humilis, pink in *H. carneus*, and bright red in *H. albiflos*, *H. deformis* and *H. pauculifolius*. Within subg. *Haemanthus* the berries of the typically pink-flowered species are invariably pink and in the red-flowered species they vary from deep wine-red to pinkish white and somewhat translucent, depending on their stage of maturity (Figure 6). Two species, *H. montanus* and *H. tristis*, are remarkable in having thin, dry leathery fruit walls that enclose an especially large seed; a strategy that allocates notably more moisture to the seed than to the berry wall itself. In *H. montanus* the seed is green and slightly wrinkled, and it is released from the berry before germinating (<https://www.inaturalist.org/observations/19178551>), whereas in *H. tristis* the dull brownish red wrinkled berry wall remains intact while the seed germinates. The size and colour of the latter's fruit bears a remarkable resemblance to the droppings of small antelope (Figure 6D).

The number of developed seeds per berry varies from one to six, but the majority of fruits produce only one large ovoid or globose seed. At maturity, the seeds have a high moisture content that enables the green embryo to germinate readily without external water sources, a high-risk but opportunistic strategy that is characteristic of the recalcitrant seed habit. Moreover, the funicle that attaches the seed to the placenta is extensible and often acts as a tether (Figure 6B), retaining the seed close to the disintegrating berry wall (Markötter 1936).

Within subg. *Serena* the mature seeds are either green, as within *H. humilis*, *H. carneus*, *H. avasi-montanus* and *H. montanus*, or ivory-white, as within *H. albiflos*, *H. deformis* and *H. pauculifolius*. This differs from the mature seeds within subg. *Haemanthus* that are consistently reddish brown to wine-red coloured due to the presence of anthocyanins (Markötter 1936).

Cytology

The base chromosome number in Amaryllidaceae s.s. is $x = 11$, whereas in *Haemanthus* it is reduced to $x = 8$. The diploid number of $2n = 16$ is uniform throughout the genus and the total chromosome length of the haploid karyotypes varies little (Vosa & Snijman 1984). Nonetheless, some chromosome rearrangements, including translocations and pericentric inversions, have taken place. Of the 20 taxa studied two karyotype groups were identified, although plants of the dwarf forms of *H. humilis* subsp. *humilis* (previously referred to as *H. strigosus* Herb.) have karyotypes within both groups, indicating population genetic divergence within the taxon. Within the polymorphic *H. humilis* complex, however, such karyotypic variability is not entirely unexpected, especially over the taxon's extensive grassland habitat. *Haemanthus barkerae*, *H. crispus* and *H. namaquensis*, together with the derived karyotypic form of *H. humilis* subsp. *humilis* belong to a small group within which deviations from the typical karyotype are thought to be due to pericentric inversions (Vosa & Snijman 1984). Only four chromosomes account for these cytological rearrangements, one of which resulted in the divergence of *Haemanthus* from its ancestral lineage shared with *Scadoxus*. For the latter, Vosa and Marchi (1980) indicated that the two small telocentric chromosomes in the karyotype of *Scadoxus* are homologous to one large, metacentric chromosome in the complement of *Haemanthus*, a chromosome translocation that resulted in the diploid reduction in chromosome number from $x = 9$ to $x = 8$.

Hybrids

In nature hybrids are not easy to distinguish unless the parents are quite distinct morphologically. The only indication that hybridisation may sometimes occur comes from observations made at a newly burnt site on Simonsberg near Stellenbosch in February 1980, when large numbers of *H. coccineus* and *H. sanguineus* were in flower simultaneously. Although both species normally flower at slightly separate times in the southwestern Western Cape, the differences between these populations had become blurred, suggesting that sporadic crossing occurs when both species are induced to flower simultaneously after a fire, followed by early rain. Elsewhere, under semi-arid conditions, Craib (1998) has described a possible natural hybrid between *H. namaquensis* and *H. unifoliatius* northwest of Steinkopf, Northern Cape.

Surprisingly few garden hybrids have been recorded within *Haemanthus*. Crosses known in the horticultural trade are *H. albiflos* × *H. coccineus* (Hannibal 1948; POWO 2022); *H. albiflos* × *H. sanguineus*; *H. humilis* subsp. *hirsutus* × *H. sanguineus* and *H. coccineus* × *H. humilis* subsp. *hirsutus* (Loubser, pers. comm.).

Geography

Distribution

Southern Africa's current geomorphology is dominated by the Great Escarpment that separates the younger low-lying coastal region from the older central plateau, which slopes downwards from east to west. Adding to this environmental complexity is the influence of the warm Agulhas Current in the Indian Ocean and the cold Benguela Upwelling System in the Atlantic Ocean that respectively generate a strongly summer-rainfall system in the east of the country, and a strongly winter-rainfall system in the west. In the south, the transition between the two rainfall regimes lies along a continuum east and west of $\pm 21^\circ$ E (Procheş et al. 2005). Furthermore, rainfall across the central plateau decreases from east to west and from south to north, and rainfall variability follows a similar trend.

Mean daily minimum temperatures in the region are highest along the coast and they increase equatorwards. Conversely, the escarpment and high-lying areas of the plateau experience the coldest minimum temperatures, with the lowest mean minimum temperatures being found towards the centre of the subcontinent as a result of both continentality and altitude. Consequently, the high-lying areas of the escarpment and the central plateau are especially prone to frost (Desmet & Cowling 1999).

Haemanthus, as it is currently distributed, is widespread over most of South Africa, with a few species in marginal areas of Namibia, Botswana, Eswatini and Lesotho. The genus is notably absent, however, from large parts of the western Nama-Karoo Biome, from southeastern Namibia, through southern Kgalagadi and northern Bushmanland to the Western Upper Karoo, Northern Cape, where rainfall is highly unpredictable and the annual range of temperature is greatest (Schulze & McGee 1978).

The genus is most richly represented in the winter-wet/summer-dry region of southern Africa, extending mainly from southwestern Namibia through Namaqualand, Northern and Western Cape, to the Cape Peninsula, Western Cape. This pattern of diversity is common to many other geophytic taxa such as *Oxalis* L. (Oxalidaceae), *Moraea* Mill. (Iridaceae), *Lachenalia* J.Jacq. ex Murray (Hyacinthaceae) and *Eriospermum* Jacq. ex Willd. (Ruscaceae). *Haemanthus* differs, however, in having species concentrated mostly within Namaqualand, a region with a relatively benign climatic regime, characterised by mild, oceanic and fog-ameliorated conditions, combined with usually predictable, albeit low, winter showers. Moreover, frosts are rarely, if ever, experienced over most of the area (Cowling & Hilton-Taylor 1999).

The highest concentration of *Haemanthus* species is within the region recognised by Hilton-Taylor (1996) as the Namaqualand Rocky Hills Centre of Endemism. This encompasses the wetter, high-lying area stretching from the shaley plateau between Anenous and Spektakel in the vicinity of

Steinkopf and Springbok, to the uplands, dominated by granite-gneiss domes, west of Kamieskroon and Garies, and onto the slopes of the Kamiesberg massif, where one endemic species and three near-endemic taxa within *Haemanthus* are present.

A second centre of diversity is the Knersvlakte, between Bitterfontein and Vanrhynsdorp, Western Cape. This semi-arid, edaphically heterogeneous area incorporates low, rolling quartz-strewn hills, dolomite outcrops, sand corridors from the west, and a network of small seasonal rivers in the south. Three species of *Haemanthus* are endemic here, contributing to the substantial number of local endemics from various dicotyledonous and monocotyledonous families within this centre (Hilton-Taylor 1996; Van Wyk & Smith 2001; Snijman 2013).

Species concentration decreases southwards of Namaqualand into the Fynbos Biome, diminishing to just four species within the southwestern Western Cape, of which two are narrowly endemic to seasonally wet habitats. A noteworthy area of species concentration in the eastern end of the Fynbos Biome is within the vicinity of Gqeberha and Makhandia, Eastern Cape, a region of non-seasonal rainfall within the Albany Centre of Endemism (Van Wyk & Smith 2001). Here several species of *Haemanthus* reach the furthest limits of their distribution ranges from the east and the west, rather than contributing any taxa endemic to the area itself.

Only six, mostly widespread species extend further eastwards into the summer-rainfall region; three within the temperate grasslands of South Africa, Eswatini and Lesotho, and three within mosaic patches of subtropical thicket and woodland along the east coast and just below the northeastern escarpment.

Notable outliers from the main distribution range are *H. avasimontanus* on the high escarpment of central Namibia, a population of *H. montanus* within southeastern Botswana, and an incompletely known taxon on the chain of inselbergs running parallel to the Orange River valley within northern Bushmanland, Northern Cape.

Habitat

Haemanthus occupies a wide range of habitats across southern Africa, from the coast to the high Drakensberg escarpment, reaching elevations of up to 2 350 m a.s.l. Despite its large geographical range, *Haemanthus* appears to be restricted by two specific habitat requirements, sufficient moisture during the growing season and the absence of frost during the development and germination of its non-dormant seeds. In regions where rainfall is low, the plants invariably occupy habitats that retain additional water, either within soils that have extra water-holding capacity or in moist, shaded rock crevices. Given that the group has cold-sensitive, water-rich seeds, the climate of late, often unreliable rain combined with early onset of frost, probably prevents the genus from occupying large parts of the western Nama-Karoo Biome, within Namibia and Northern Cape, as well as the Drakensberg afro-alpine region of the Grassland Biome.

In the winter-rainfall region, soils play a significant role in species distribution, although the effect of soil on species' habitats is apparently less where there is ample rain. Semi-arid Namaqualand, in particular, has an impressive diversity of soil types characterised largely by the presence of soluble salts and certain clay minerals that have an exceptional affinity for water. These properties influence how water is redirected or held and stored at the soil surface and beneath it and they consequently determine how much water is available to plants as a compensation for aridity (Francis et al. 2007). The only *Haemanthus* species that are entirely associated with specific soils are from Namaqualand and northwestern Cape. *Haemanthus arenicola* (Figure 5A) and *H. leipoldtii* are restricted to aeolian sands on the northern and central west coast; *H. humanii* is confined to 'island-like' quartz outcrops (Schmiedel & Jürgens 1999, 2004) in central Namaqualand (Figure 5B); *H. lanceifolius* is almost exclusively found on dolomite outcrops within the Knersvlakte; and *H. barkerae* is limited to the heavy clay soils in dolerite and shales of the Dwyka and Eccu series within the Hantam Karoo and Tanqua Karoo (Figure 5C).

Species that are highly restricted to seasonally wet sites within an otherwise well-drained landscape are *H. canaliculatus* and *H. pumilio*, found in vleis and alluvial flats, respectively, within the nutrient-poor soils of the Fynbos Biome (Figure 5D and 5E). *Haemanthus tristis* is confined to sheet washes and gravel plains within the arid Tanqua Karoo (Figure 6D), and *H. graniticus* grows along seasonal stream banks in upper Namaqualand. Within the summer-rainfall grassland *H. montanus* is mostly confined to periodically waterlogged soils. There is little evidence of sympatry between taxa at any of these wet sites, unlike genera such as *Pauridia* Harv. (Hypoxidaceae) within which two or more species co-occur in moist, open habitats (Snijman 2014).

Shade-loving species are *H. avasimontanus*, found on wet rock ledges in upland central Namibia; *H. albiflos* and *H. deformis*, which occur along the equable east coast; and *H. pauculifolius*, found within deep, frost-free valleys that penetrate the northeastern escarpment.



Ecology

Flowering phenology

Flowering time within *Haemanthus* is a trait that is critical to the plant's success, since it determines the fate of the plants' non-dormant, metabolically active and desiccation-sensitive seeds. Consequently, the tightly coupled flowering and fruiting times correlate with the season that best enables the fleshy seeds to survive and establish seedlings. As in all geophytes, the key that enables an adaptive shift in flowering time to evolve is the storage capacity of the bulb and its physiological ability to apportion stored reserves so that seedling establishment matches the best growing season. Hence in *Haemanthus* the flowering and fruiting patterns for species from the east and west of southern Africa have become finely tuned to that of rainfall seasonality across the country. The pattern, which is bimodal, reflects the large east–west transition from strongly summer- to strongly winter-rainfall regimes that were established by the Late Miocene, ± 10 million years ago (Siesser 1980). In the southern part of the Core Cape Floristic Region itself, this rainfall pattern is less pronounced, but it still shows a significant increase in the proportion of winter rain westwards of $\pm 21^\circ$ E (Procheş et al. 2005).

Species with synanthous or near-synanthous leaves that emerge at or very shortly after the time of flowering are restricted to the predominantly summer-rainfall areas in the east, where the bulbs flower at the onset of the summer-wet season (Figure 7). Plants of *H. humilis* subsp. *hirsutus* and *H. montanus* from the high-lying, mesic grasslands reach peak flowering between November and December, thus allowing new seedlings to benefit from late summer growth before entering early dormancy in the cold, dry winter. In grasslands bordering the dry central Nama-Karoo and northern savanna, plants of *H. humilis* subsp. *humilis* flower later, peaking in late January and February, which allows seedling establishment during the later summer-rain season, from February to April.

In the extreme west, species invariably have a hysteroanthous-leaved habit, in which the inflorescence emerges independently of the leaves in autumn (March to April), just prior to the onset of the low-energy growth conditions of the cool winter-wet season (Figure 7). Under these conditions the autumn-flowering, hysteroanthous-leaved phenology allows a sufficiently long time for seedlings to become established before summer drought sets in after September.

In marked contrast with the brief flowering periods of the deciduous-leaved species, the evergreen species, *H. albiflos*, *H. deformis* and *H. pauculifolius*, show marked phenological flexibility within the frost- and fire-free, non-seasonal rainfall southern and eastern regions with flowering staggered over several months (April to October).

Although rain falls strictly in winter throughout the west, the amount of precipitation varies from north to south. Rain is plentiful and reliable in the southwest, whereas Namaqualand in the



Figure 7. Flowering phenology showing synanthous-leaved habit within subg. *Serena* (A, B) and hysteroanthous-leaved habit within subg. *Haemanthus* (C–F). A, *H. humilis* subsp. *humilis*; B, *H. humilis* subsp. *hirsutus*; C, *H. coccineus*; D, *H. unifolius*; E, *H. crispus*; F, *H. amarylloides* subsp. *polyanthus*. Photographs: A, B, C, Colin Paterson-Jones; D, E, F, John Manning.

northwest is semi-arid. The irregular onset of Namaqualand's early rains results in greater variability in flowering here than elsewhere. If rainfall at the beginning of autumn is widespread, then most species in the higher lying regions of Namaqualand flower simultaneously throughout their ranges. In years in which rainfall is scattered and of short duration, however, only isolated populations within the species' range may flower. These fluctuations in moisture availability, compounded by the plants' limited dispersal ability, may account for the existence of many isolated, slightly divergent populations within Namaqualand; a complex pattern of variation that is often not easily resolved in any formal system of classification.

Observations in the field, as well as under cultivation, suggest that one of the roles of the firm, erect spathe bracts within many hysteroanthous-leaved species of the semi-arid west is that of protection against desiccation. Flowers that are loosely surrounded by membranous spathe bracts soon wither in periods of hot, dry weather, whereas those surrounded by fleshy, erect spathe bracts endure for a slightly longer period. This was particularly evident within the central Namaqualand populations of the sympatric *H. amarylloides* subsp. *polyanthus* and *H. crispus* that possess contrasting spathe bract-types (Figure 7E and 7F). Another species in which fleshy, prominent spathe bracts appear to have high selective value under harsh conditions is *H. arenicola* from the arid sand plains of northern Namaqualand, where precipitation is less than 100 mm annually (Figure 5A).

Although Levyns (1971) referred to *H. canaliculatus* as a true fire lily, neither this nor the other species of *Haemanthus* from fire-prone ecosystems are obligate pyrophytes since they flower independently of fire or smoke under cultivation (Duncan et al. 2016). Fires during the dry summers of the Cape fynbos region nevertheless induce dramatic displays within *H. canaliculatus* after the first rains of the season (Figure 5D). Likewise, in the summer-rainfall grasslands, *H. montanus* benefits from fires in late winter or early spring by flowering early in newly formed open sites, in contrast to *H. humilis* and *H. carneus* that escape grassland fires by occupying protected, rocky habitats.

Pollination

Evidence from pollination studies on three species within subg. *Serena* reveals that the typically white-flowered *H. albiflos* and *H. deformis* are strongly dependent on sunbirds for pollination, whereas the white- to delicate, pink-flowered *H. humilis* subsp. *hirsutus*, although attractive to sunbirds, is co-dependent on insect pollinators, *Philoliche aethiopica* (Thunberg) (Tabanidae) and *Amegilla* Friese, 1997 bees (Butler & Johnson 2023). Floral characters that set these three taxa apart within the subgenus are their stiff, densely packed flower heads in which the individual flowers have perigone tubes typically $\pm 6\text{--}9$ mm long. Given the morphological similarities between *H. pauculifolius*, *H. albiflos* and *H. deformis*, and their comparable habitats, the former is also likely to be ornithophilous. Whether sunbirds are able to access the pale, loosely spreading inflorescences of *H. avasimontanus*, *H. carneus*, *H. humilis* subsp. *humilis* and *H. montanus* still remains uncertain, however, especially as these taxa have smaller pink or white flowers with a short perigone tube, typically less than 4 mm long, that possibly favours short-tongued insects.

As yet, pollination studies on taxa within subg. *Haemanthus* are still largely lacking. Observations, nevertheless, indicate that the nectar-rich flower heads, which provide a food source in autumn when few other plants are in flower, also attract various insects and sunbirds that probably act as pollinators. Near Springbok, northern Namaqualand, both the compact red flower heads of *H. unifolius* and the spreading pink flower heads of *H. amarylloides* subsp. *polyanthus* are visited by solitary anthophorid

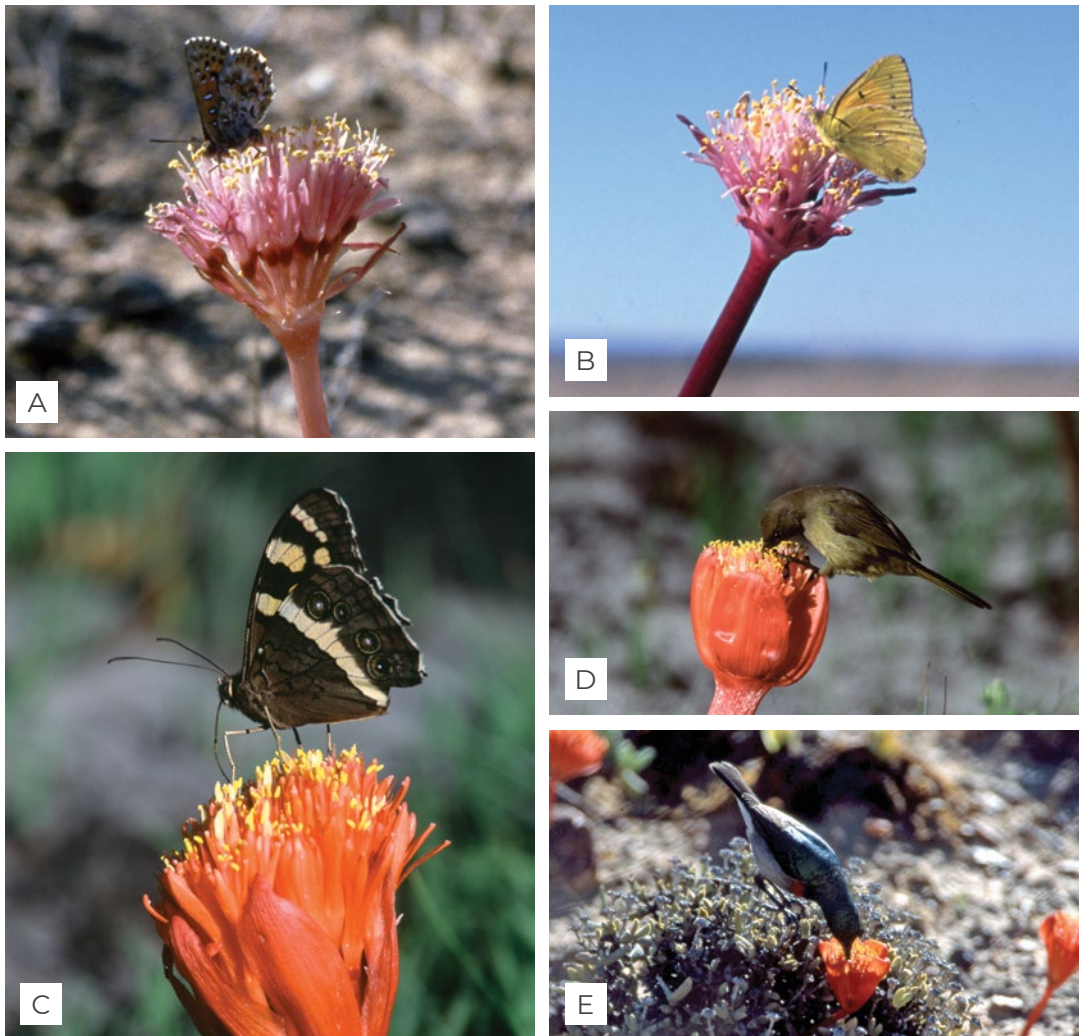


Figure 8. Putative pollinators of species within subg. *Haemanthus*. A, *H. amarylloides* subsp. *amarylloides* and lycaenid butterfly, *Tarucus thespis*; B, *H. barkerae* and pierid butterfly, *Colias electo*; C, *H. sanguineus* and satyrid butterfly, *Aeropetes tulbaghia*; D, *H. sanguineus* and female Southern Double-collared Sunbird; E, *H. crispus* and male Southern Double-collared Sunbird. Photographs: A, Dee Snijman; B, John Manning; C, D, E, Colin Paterson-Jones.

bees and the commonly occurring medium-sized pierid butterfly, *Belenois aurota* (Fabricius) (G. Williamson, pers. comm.), popularly known as the Brown-Veined White. On the Grootvlei uplands in central Namaqualand, the soft-bracted, spreading, pink flower heads of *H. amarylloides* subsp. *amarylloides* are visited by the small lycaenid butterfly, *Tarucus thespis* (Linnaeus), commonly known as the Vivid Dotted Blue, which is widespread in the winter-rainfall region (Figure 8A). Further south on the Bokkeveld escarpment, Northern Cape, and near Stellenbosch, Western Cape, the spreading, pale pink or white flower heads of *H. barkerae* (Figure 8B) and *H. pumilio*, respectively, attract another widespread pierid butterfly, *Colias electo* (Linnaeus), known as the African Clouded Yellow, as well as anthophorid bees, honey bees (*Apis mellifera capensis* Eschscholtz, 1822) and syrphid hoverflies (Markötter 1936; Snijman 1984; Summerville & Van der Walt 1992). Although scanty, such records suggest that the pale-flowered species with soft, membranous, spreading spathe bracts and spreading flowers use a generalist strategy involving small-bodied pollinators.

In contrast, the bright, red-flowered species within subg. *Haemanthus*, which typically have a dense flower cluster surrounded by more or less upright, rigid spathe bracts, appear to take advantage of more specialised pollination systems, as do many other late-summer, red-flowered species within southern Africa. Within the southwestern Western Cape, *H. coccineus*, *H. sanguineus* and *H. canaliculatus* clearly fit the particulars of the satyrid butterfly, *Aeropetes*, and sunbird pollination syndromes described by Johnson and Bond (1994) (Figure 8D and 8E), but whether birds or butterflies are the primary pollinators here is difficult to assess. Within semi-arid Namaqualand and northwestern Western Cape, however, where the Table Mountain Beauty, *Aeropetes tulbaghia* (Linnaeus) is absent, the primary pollinators of the red-flowered species are more likely to be sunbirds, as for *H. crispus* (Figure 8E). Within *H. arenicola*, *H. leipoldtii* and *Boophone haemanthoides* F.M.Leight. subsp. *haemanthoides* (tribe Amaryllideae), however, it is also possible to speculate that the remarkably long, brightly coloured succulent spathe bracts of these west coast taxa perform a dual function; to enable sunbird pollination, as well as to minimise desiccation of the flower head.

From these limited observations it appears likely that different combinations of floral features within *Haemanthus* attract different assemblages of pollinators. Drawing on pollination studies within *Scadoxus* (Butler & Johnson 2020; Butler et al. 2022), it is reasonable to infer a similar scenario for *Haemanthus*, namely that birds, unlike butterflies and bees, cannot easily access nectar from loose, open inflorescences, whereas they can take nectar from inflorescences with stiff spathe bracts and firm pedicels that provide a platform on which birds can perch. Given the variation in putative pollinators from north to south of the winter-rainfall region, it is likely that a further shift in pollinators exists from west to east within the summer-rainfall region of southern Africa. Nevertheless, in the complete absence of pollinators many *Haemanthus* species are known to be partially self-fertile under cultivation (Duncan et al. 2016).

The evidence-based discovery that sunbird pollination within *Haemanthus* is not confined to species within the Cape Floristic Region but occurs across southern Africa in both red- and white-flowered species with stiff flower heads (Butler & Johnson 2023) may indicate that similar patterns could yet emerge within other plant groups. The current estimate, derived from flower morphology within a

wide range of families, that up to 75% of southern Africa's ornithophilous-plant species are confined to the Cape flora (Rebello 1987) may thus require reassessment.

Seed dispersal

When in fruit, the scape of *Haemanthus* elongates and finally bends under the weight of the mature berries, which then detach on the soil surface close to the mother plant. The inner layers of the fruit wall are mucilaginous, often becoming more so with age, as is the funicle that attaches the large, moisture-rich seed to the placenta (Markötter 1936). Mucilage restrains the movement of seeds, either by affixing the seed to the ground, or tethering the seed to the senescing fruit wall by means of the extensible funicle (Figure 6B). For species in summer-dry Namaqualand the presence of mucilage may also be critical in protecting the seed from desiccation until the first winter rains fall. The berries of *H. coccineus*, *H. crispus* and *H. pubescens* produce particularly copious amounts of mucilage (Figure 6A and 6B).

Three species, *H. avasimontanus*, *H. montanus* and *H. tristis*, are remarkable in having thin, somewhat dry leathery fruit walls that tightly envelop an especially large solitary seed, a strategy that allocates more moisture to the seed than to the fruit wall itself. Noteworthy is that these species occupy habitats in which the conditions needed for seedling establishment are particularly unreliable. Thus, the leathery berry and large seed may be adaptations to contend with these ecological constraints.

Marloth (1915) suggests that the berries are biotically dispersed by birds, porcupines and baboons. From field observations, however, it seems likely that the seeds are more often abiotically dispersed to shallow depressions by water runoff, down rocky inclines through gravity, or merely passively by the lengthening and bending of the scape (Markötter 1936; Snijman 1984). In effect this probably maximises the suitability of the niche in which the seed is deposited and in turn increases seedling survival. Apart from some minor chewing of the berries and scapes by rodents, there is little evidence to suggest the seeds would survive the digestive tracts of animals. They may, however, be carried for short distances and randomly dropped by rodents on the way to their nests, as noted by Craib (1998, 2010) for *H. avasimontanus* and *H. namaquensis*.

Not only is desiccation a threat to non-dormant seeds, but the presence of light during dehydration can also be extremely damaging to photosynthetically active tissues (Sherwin & Farrant 1998). Within southern Namibia and Namaqualand the incoming solar radiation in summer (December to February) is higher than that of any other region in southern Africa (Schulze & McGee 1978). Thus, ultraviolet radiation in late summer and autumn could have functioned as a selection pressure here, giving species that are better able to cope with greater amounts of radiation an advantage. All taxa within subg. *Haemanthus* found exclusively in the summer-dry region have brownish red to deep wine-red seeds (Figure 6). It is possible that by preventing the absorption of excess light, the seed's anthocyanins provide critical protection while the seed remains exposed on the soil surface any time from late summer into autumn. In contrast, taxa within subg. *Serena* (Table 1, p. 10) that occupy the summer-wet region, where plants are exposed to lower levels of radiation in summer, have green or ivory-white seeds.

Defences and threats

During the evolutionary history of Amaryllidaceae *s.s.*, both below- and above-ground predation appears to have been curtailed by the accumulation of highly toxic alkaloids. This is a significant advantage in southern Africa where many animals are subterranean foragers, particularly the Cape dune mole-rat (*Bathyrgeus suillus* Schreber, 1782), a large rodent found in sandy lowland soils within the southwestern region of Western Cape, and the widespread porcupine (*Hystrix africaeaustralis* Peters, 1852) which digs extensive foraging pits in its search for food (Smithers 1983).

On the other hand, well before the 18th century, the local inhabitants of the Cape had already learned how to benefit from these poisons by using small extracts of the bulbs and leaves as medicine (Thunberg 1793; Pappe 1857). Since these early beginnings much is now known about the toxic and medicinal constituents in *Haemanthus*. As of 2019, the alkaloid contents of eight *Haemanthus* taxa have been studied, of which *H. coccineus*, *H. humilis*, *H. montanus* and *H. sanguineus* have been assessed as to their relevance in the treatment of cancer and inflammation, as well as for their effect on Alzheimer's disease and depression (Crouch et al. 2005; Bay-Smidt et al. 2011; Masi et al. 2019; Nair & Van Staden 2022).

Concurrent with advances in research into the phytochemistry of *Haemanthus* is an ever-increasing demand in urban areas for their use as traditional medicines. Consequently, the supply of species such as *H. coccineus*, *H. albiflos* and *H. deformis* is being met by a network of commercial gatherers in several provinces, who sell to herb traders and traditional healers in the major cities of South Africa (Williams et al. 2001). The possession of non-dormant seeds, however, makes *Haemanthus* extremely vulnerable to a decline in offspring, due to the plants' inability to build seed stores beyond a few months. Thus, any over-harvesting of bulbs poses a severe threat to the viability of populations, placing them at risk of local extinction.

Conservation status

The conservation status of taxa within *Haemanthus* according to the current updated Red List of South African plants, which is based on the IUCN criteria and categories, version 3.1.1. (IUCN 2012), as well as the criteria and categories that were developed for South Africa's Orange List, namely Critically Rare, Rare and Declining (Victor & Keith 2004; Raimondo et al. 2009), is as follows. Four species are Rare (*H. arenicola*, *H. dasyphyllus*, *H. namaquensis*, *H. paucifolius*); one subspecies is Near Threatened (*H. amarylloides* subsp. *amarylloides*); four species are Vulnerable (*H. deformis*, *H. lanceifolius*, *H. leipoldtii*, *H. tristis*); and five taxa are Endangered (*H. amarylloides* subsp. *toximon-tanus*, *H. canaliculatus*, *H. graniticus*, *H. nortieri*, *H. pumilio*).

Currently the Fynbos Biome contains the highest concentration of South Africa's threatened taxa, followed by the Succulent Karoo Biome (Raimondo & Von Staden 2009). In common with many other geophytic genera, the majority of Red-Listed *Haemanthus* species are from these two biomes.

Only two Red-Listed species, *H. tristis* and *H. pumilio*, are formally protected within conservation areas.

Major threats to species in the Richtersveld and Namaqualand regions of the Succulent Karoo are the extensive mining activities within the lowlands. Whereas terrestrial diamond mining in the past was concentrated almost exclusively within a few kilometres of the coast and major rivers, the current heavy mineral mining operations have extended the degradation of the Namaqualand lowlands further inland. All the major mining activities are surface operations that generate highly mobile sands that bring about secondary degradation of ecological communities over large areas that are not actually mined (Carrick & Krüger 2007). Other human impacts exerted on the ecosystem in the south are the extensive agricultural lands that stretch along the length of the lower Olifants River valley, west of the Cape Fold mountains (Raimondo & Von Staden 2009). Further southwards in the Fynbos Biome, threats to the southwestern lowlands of Western Cape are mainly from intense agricultural, industrial and housing developments, as well as from the rampant spread of alien invasive trees. Adding to these threats are the combined impacts of climate change, as well as poaching to supply the international plant trade. The particular life cycle of *Haemanthus*, which depends on non-dormant seeds for reproduction, makes the plants especially vulnerable to these many threats.



Systematic treatment

Haemanthus L.

Haemanthus L., *Species plantarum*: 325 (1753); *Herb.*: 132 (1837); *Salisbury*: 130 (1866); Bjørnstad & Friis: 190 (1972); Friis & Nordal: 64 (1976); Snijman: 16 (1984). Type: *Haemanthus coccineus* L., lecto., designated by Hitchcock & Green: 147 (1929).

Leucodesmis Raf.: 19 (1838). Type: *Leucodesmis pubescens* (L.f.) Raf. = *H. pubescens* L.f.

Perihemia Raf.: 20 (1838) [as *Perihema*]. Type: *Perihemia coarctata* (Jacq.) Raf. = *H. coccineus* L.

Serena Raf.: 20 (1838). Type: *Serena carnea* (Ker Gawl.) Raf., lecto., designated by Snijman: 17 (1984) = *H. carneus* Ker Gawl.

Diacles Salisb.: 130 (1866), nom. illeg. superfl. pro *Leucodesmis* Raf. (1838). *Haemanthus* subg. *Diacles* Baker: 130 (1888); Baker: 230 (1896). *H.* sect. *Diacles* Pax & K.Hoffm.: 402 (1930). Type: *H. pubescens* L.f.

Melicho Salisb.: 130 (1866). *Haemanthus* subg. *Melicho* (Salisb.) Baker: 63 (1888); Baker: 230 (1896). *H.* sect. *Melicho* (Salisb.) Pax & K.Hoffm. [as *Melchio*]: 401 (1930). Type: *H. amarylloides* Jacq., lecto., designated by Bjørnstad & Friis: 192 (1972). [*Melicho amarylloides* Salisb., combination not validly published (Turland et al. 2018: Art. 35.2)].

Haemanthus sect. *Tristegia* Rchb. ex M.Roem.: 8, 33 (1847). Type: *H. coccineus* L., lecto., designated by Bjørnstad & Friis: 192 (1972).

Haemanthus sect. *Polystegia* Rchb. ex M.Roem.: 8, 38 (1847). Type: *H. coarctatus* Jacq., lecto., designated by Bjørnstad & Friis: 192 (1972) = *H. coccineus* L.

Deciduous or evergreen geophytic herbs, ± 30–400 mm high when flowering. *Bulb* broadly ovoid, obclavate or pyriform, 15–150 mm diam., round in cross section or compressed in plane of distichous leaves or crosswise to distichous leaves; tunics thick and fleshy, equal or unequal, arranged in horizontal layers or distichously in downward slanting layers, cream-coloured, occasionally green or pinkish if exposed; roots perennial, fleshy and contractile, reaching up to ± 1 200 mm long. *Leaves* 1, 2(3) or 4(6), green or dry at flowering, distichous, erect, recurved or prostrate; blades ligulate to lanceolate, elliptical or oblong, longer than broad or rarely broader than long, thick-textured, immaculate or barred and blotched with red and dark green, glabrous or pubescent, rarely viscid. *Scape* slender to stout, solid, slightly compressed laterally, up to 370 mm long, bright red, wine-red, pink or pale green, immaculate or spotted with pink or red, glabrous or pubescent, becoming elongated, decumbent and often furrowed in fruit. *Spathe bracts* 4–13, erect to spreading, lanceolate, oblong-lanceolate, ovate or spatulate, shorter or longer than flowers, membranous, leathery or stiff

and fleshy, red, pink, white or rarely green, rarely pubescent or ciliate. *Inflorescence* a compact or spreading umbel-like cluster, 30–100 mm across. *Flowers* $\pm$ 10–150, erect or spreading, pedicellate; pedicel stiff, rarely lax, shorter to $\pm$ longer than perigone; perigone actinomorphic, cylindrical to funnelform, $\pm$ 6–30 mm long, white, pale or dark pink or red, concolorous or if red, then often white-tipped; tube cylindrical to narrowly infundibuliform, 1–12 mm long, smooth or shallowly 6-grooved; tepals erect or spreading, narrowly oblong or narrowly lanceolate, longer or rarely slightly shorter than tube, if erect, then gibbose at base and thick at tip. *Stamens* inserted at perigone throat, uniseriate, filiform, symmetrical, mostly longer than or rarely half or less as long as tepals; anthers oblong, dorsifixed, versatile, yellow. *Ovary* subglobose, 3-locular, each loculus with a solitary or collateral pair of ovules. *Style* filiform, erect, equalling stamens or rarely half as long; stigma shortly or minutely trifid. *Berry* ovoid to globose; walls usually soft and thinly or copiously pulpy and mucilaginous when ripe, rarely leathery, dull orange, pink, red or whitish and translucent, $\pm$ aromatic. Seeds ovoid, fleshy, green, ivory-white or wine-red. *Chromosome number* $x = 8$ (Vosa & Snijman 1984).

Species 25: southern Africa.



Taxonomic keys

The use of typical analytic keys to identify species of *Haemanthus* is often problematic since users may only have vegetative or floral characters available for the hysteranthous-leaved species. Several keys, therefore, are provided here. Dichotomous keys to species within each subgenus are followed by a synoptic or comparative key that lists the most important morphological features within all the species and allows the user to start at any point and to follow any sequence to identify a particular species.

Note: only mature plants should be examined. Leaf width measurements are taken about midway. Floral measurements pertain to mature flowers at anthesis, and the position of spathe bracts and flowers relate to fully developed inflorescences.

Key to subgenera

- 1a. Bulb broadly ovoid, compressed in plane of leaves; tunics in ≤ 6 pairs, uniseriate, equally long and thick, with edges horizontal; leaves evergreen or deciduous, synanthous or near-synanthous, 1 or 2(3) or 4(6), immaculate; spathe bracts thin-textured, pale pink or white, if erect, then white and green-veined; perigone tube smooth; seeds green or ivory-white subg. *Serena*
- 1b. Bulb obclavate or pyriform, round in cross section or compressed crosswise to leaves; tunics in ≥ 8 pairs, uniseriate and tiered, with edges horizontal, or biseriate and tiered with edges oblique; leaves hysteranthous, 1 or 2(3), abaxial surface often barred and speckled reddish brown or dark green or red-flushed proximally; spathe bracts membranous, leathery or fleshy, white to cream-coloured, pink or red, if erect, then red; perigone tube smooth or shallowly grooved below tepal sinuses and gibbose below each tepal; seeds wine-red or brownish red subg. *Haemanthus*

Dichotomous keys to species

Subg. *Serena*

(based on vegetative and floral characters)

- 1a. Plants evergreen; inflorescence compact, narrowly obovoid to cyathiform; spathe bracts erect; pedicels shorter than perigone:
 - 2a. Leaf mostly solitary; flower head slender, 15–30 mm across; perigone tube 10–13 mm long. 7. *H. pauculifolius*

- 2b. Leaves 2 or more; flower head mostly broad, 25–70 mm across; perigone tube 4–9 mm long:
 - 3a. Leaves spreading to suberect, 25–115 mm wide; scape 50–350 mm long, following current season's leaves; spathe bracts standing slightly apart; perigone 16–23 mm long 5. *H. albiflos*
 - 3b. Leaves appressed to the ground, 70–250 mm wide; scape < 60 mm long, preceding current season's leaves; spathe bracts overlapping; perigone $\pm$ 30 mm long. . . 6. *H. deformis*
- 1b. Plants deciduous; inflorescence spreading, broadly obconical to globose; spathe bracts soon reflexed; pedicels $\pm$ equalling or longer than perigone:
 - 4a. Leaves and scape glabrous, leaves erect:
 - 5a. Spathe bracts 5–8; perigone < 15 mm long 1. *H. montanus*
 - 5b. Spathe bracts 4–5; perigone $\pm$ 20 mm long 2. *H. avasimontanus*
 - 4b. Leaves and scape mostly with some pubescence, leaves suberect, spreading or prostrate:
 - 6a. Stamens unequal, 3 outer < 3 inner, both whorls $\leq$ half as long as tepals at anthesis; style $\pm$ half as long as stamens 3. *H. carneus*
 - 6b. Stamens equal, as long as or longer than tepals at anthesis; style $\pm$ equalling or longer than stamens 4. *H. humilis*

Subg. *Haemanthus*

(based on vegetative characters)

- 1a. Leaves bristly, minutely tomentose or softly hairy, at least on margins (also see *H. crispus*):
 - 2a. Leaf typically solitary 19. *H. unifolius*
 - 2b. Leaves 2(3):
 - 3a. Leaves bristly adaxially 14. *H. humanii*
 - 3b. Leaves glabrous or pubescent adaxially:
 - 4a. Leaves $\pm$ heavily barred or spotted with red or dark green abaxially:
 - 5a. Leaves narrow, mostly $\leq$ 55 mm wide, margins plane. 11. *H. barkerae*
 - 5b. Leaves broad, mostly $\geq$ 85 mm wide, margin often in-rolled 17. *H. coccineus*
 - 4b. Leaves only sparingly spotted with red abaxially:
 - 6a. Leaves $\pm$ twisted or $\pm$ folded 18. *H. dasyphyllus*
 - 6b. Leaves neither twisted nor folded:
 - 7a. Leaves narrow, $\leq$ 40 mm wide, shallowly channelled, edges sparsely hairy abaxially. 20. *H. arenicola*
 - 7b. Leaves narrow to broad, 10–85 mm wide, surface plane, glabrous abaxially:
 - 8a. Leaves glabrous adaxially with fringed margin 21. *H. leipoldtii*
 - 8b. Leaves densely pubescent adaxially 22. *H. pubescens*
 - 1b. Leaves entirely glabrous but if undulate and abaxially ribbed then occasionally shortly pubescent (as in some *H. crispus*):
 - 9a. Leaf 1(2), rough and sticky. 10. *H. nortieri*
 - 9b. Leaves 2(3), smooth or rough, not sticky:
 - 10a. Leaf edges $\pm$ undulate:
 - 11a. Leaves broad, > 45 mm wide 15. *H. namaquensis*

- 11b. Leaves narrow, < 35 mm wide 16. *H. crispus*
- 10b. Leaf edges plane:
 - 12a. Leaf surface rough, at least distally, margins fimbriate to minutely crenulate:
 - 13a. Leaves lightly appressed to the ground. 13. *H. lanceifolius*
 - 13b. Leaves firmly appressed to the ground. 23. *H. sanguineus*
 - 12b. Leaf surface and margins smooth:
 - 14a. Leaves twisted 25. *H. pumilio*
 - 14b. Leaves not twisted:
 - 15a. Leaves deeply channelled, firm-textured 24. *H. canaliculatus*
 - 15b. Leaves ± plane to shallowly channelled, pliable:
 - 16a. Leaves barred or spotted with red or dark green abaxially:
 - 17a. Leaves narrow, mostly ≤ 55 mm wide, margin plane 11. *H. barkerae*
 - 17b. Leaves broad, mostly ≥ 85 mm wide, margin often in-rolled. . 17. *H. coccineus*
 - 16b. Leaves immaculate:
 - 18a. Leaves narrow, 7–16 mm wide, slightly channelled; bulb neck slender
. 12. *H. tristis*
 - 18b. Leaves broad, 10–120 mm wide, plane; bulb without a slender neck:
 - 19a. Leaves spreading to erect; bulbs solitary 8. *H. amarylloides*
 - 19b. Leaves erect; bulbs usually clumped 9. *H. graniticus*

Subg. **Haemanthus**

(based on floral characters)

- 1a. Spathe bracts suberect at anthesis; perigone tube gibbose below each tepal; tepals nipped-in proximally:
 - 2a. Spathe bracts broadest above midway:
 - 3a. Apex of spathe bracts ± blunt, without an acute point:
 - 4a. Spathe bracts stiff and fleshy; scape rarely sparsely hairy 17. *H. coccineus*
 - 4b. Spathe bracts firm but not fleshy; scape often softly hairy 18. *H. dasyphyllus*
 - 3b. Apex of spathe bracts abruptly truncated to a ± acute point:
 - 5a. Spathe bracts rarely exceeding flower head; bulb tunics thin, uniseriate . . . 16. *H. crispus*
 - 5b. Spathe bracts often exceeding flower head by up to ± 20 mm; bulb tunics thick, biseriate 22. *H. pubescens*
 - 2b. Spathe bracts broadest midway or below:
 - 6a. Spathe bracts exceeding flower head by ≥ 20 mm:
 - 7a. Bulbs usually clumped, ± 80 mm diam., ± elliptical in cross section; basal plate elongated 20. *H. arenicola*
 - 7b. Bulb solitary, broadly ovoid, ± 60 mm diam., compressed crosswise to leaves; basal plate ± flat 21. *H. leipoldtii*
 - 6b. Spathe bracts shorter than flower head or exceeding it by < 20 mm:
 - 8a. Scape often softly hairy; flower head 18–50 mm across 19. *H. unifolius*
 - 8b. Scape mostly glabrous; flower head 30–100 mm across:

- 9a. Spathe bracts firm but not fleshy 15. *H. namaquensis*
- 9b. Spathe bracts stiff and fleshy 17. *H. coccineus*
- 1b. Spathe bracts spreading to suberect at anthesis; perigone tube either smooth or slightly swollen below each tepal; tepals not nipped-in proximally:
 - 10a. Inflorescence red:
 - 11a. Scape rough to the touch proximally 10. *H. nortieri*
 - 11b. Scape smooth:
 - 12a. Spathe bracts ± blunt 23. *H. sanguineus*
 - 12b. Spathe bracts acuminate:
 - 13a. Pedicels ± equalling perigone 9. *H. graniticus*
 - 13b. Pedicels shorter than perigone 24. *H. canaliculatus*
 - 10b. Inflorescence pink, white or off-white:
 - 14a. Spathe bracts ± blunt 23. *H. sanguineus*
 - 14b. Spathe bracts acuminate:
 - 15a. Perigone mostly > 12 mm long:
 - 16a. Bulb without a narrow neck 8. *H. amarylloides*
 - 16b. Bulb often with a narrow neck 11. *H. barkerae*
 - 15b. Perigone mostly < 12 mm long:
 - 17a. Tepals spreading up to 30° from vertical at anthesis:
 - 18a. Scape 55–70 mm long; spathe bracts 5, 9–10 mm long; inner filaments thickened proximally 14. *H. humanii*
 - 18b. Scape 45–180 mm long; spathe bracts 4–6, 10–30 mm long; inner filaments unthickened 25. *H. pumilio*
 - 17b. Tepals widely spreading up to ± 45° from vertical at anthesis:
 - 19a. Flowers cream-coloured fading to pink; berries brownish red, walls leathery 12. *H. tristis*
 - 19b. Flowers white to pale pink; berries pale pink, walls fleshy 13. *H. lanceifolius*

Synoptic key to species

Note: taxa in brackets are variable for the particular morphological feature given under that entry. This list is strictly an aid to species identification. It is not equivalent to a list of characters and homologous character states.

1. Growth phenology

- a. Plants evergreen: *H. albiflos*, (rarely *H. canaliculatus*), *H. deformis*, *H. pauculifolius*
- b. Plants deciduous: all remaining taxa, rarely including some of the above

2. Bulb form

- a. Bulb ± globose with an extended narrow neck: (*H. barkerae*), *H. crispus*, *H. tristis*
- b. Bulb ± compressed, either in plane of leaves or crosswise to them, if neck present then short and ± broad: all remaining taxa

3. Bulb tunics

- a. Margins $\pm$ horizontal: *H. albiflos*, *H. avasimontanus*, *H. barkerae*, *H. carneus*, *H. crispus*, *H. deformis*, *H. humanii*, *H. humilis*, *H. montanus*, *H. nortieri*, *H. pauculifolius*, *H. tristis*, *H. unifoliatus*
- b. Margins oblique: *H. amarylloides*, *H. arenicola*, *H. canaliculatus*, *H. coccineus*, *H. dasyphyllus*, *H. graniticus*, *H. lanceifolius*, *H. leipoldtii*, *H. namaquensis*, *H. pubescens*, *H. pumilio*, *H. sanguineus*

4. Leaf number

- a. Leaf typically solitary: *H. nortieri*, *H. pauculifolius*, *H. unifoliatus*
- b. Leaves two: (*H. albiflos*), *H. amarylloides*, (*H. arenicola*), *H. avasimontanus*, *H. barkerae*, (*H. canaliculatus*), *H. carneus*, *H. coccineus*, (*H. crispus*), *H. dasyphyllus*, (*H. deformis*), *H. graniticus*, (*H. humanii*), *H. humilis*, *H. lanceifolius*, *H. leipoldtii*, *H. montanus*, *H. namaquensis*, *H. pubescens*, *H. pumilio*, *H. sanguineus*, *H. tristis*
- c. Leaves more than two: (*H. albiflos*), (rarely *H. arenicola*), (rarely *H. canaliculatus*), (rarely *H. crispus*), (*H. deformis*), (rarely *H. humanii*)

5. Leaf blade

- a. Markedly canaliculate: *H. canaliculatus*, *H. crispus*
- b. Twisted: (*H. dasyphyllus*), *H. montanus*, *H. pumilio*
- c. Neither twisted nor markedly canaliculate: all but the above taxa

6. Leaf surface

- a. Sticky: *H. nortieri*
- b. Long bristly: *H. humanii*
- c. Pubescent with short firm hairs: (*H. barkerae*), (*H. crispus*)
- d. Rough with minute tubercles: *H. lanceifolius*, *H. nortieri*, (*H. sanguineus*)
- e. Glabrous: *H. avasimontanus*, *H. amarylloides*, (*H. barkerae*), *H. canaliculatus*, (*H. coccineus*), (*H. crispus*), *H. graniticus*, *H. montanus*, *H. namaquensis*, *H. pumilio*, (*H. sanguineus*), *H. tristis*
- f. Softly hairy at least on margins: *H. albiflos*, *H. arenicola*, (*H. barkerae*), *H. carneus*, (*H. coccineus*), *H. dasyphyllus*, *H. deformis*, *H. humilis*, *H. leipoldtii*, *H. pubescens*, *H. unifoliatus*

7. Leaf markings

- a. Abaxial surface flushed red proximally: *H. nortieri*, *H. tristis*
- b. Abaxial surface barred or spotted with red or dark green: *H. arenicola*, *H. barkerae*, *H. canaliculatus*, (*H. coccineus*), *H. crispus*, *H. dasyphyllus*, *H. leipoldtii*, *H. pubescens*, *H. pumilio*, *H. unifoliatus*
- c. Unmarked: all remaining taxa rarely including some of the above

8. Leaf edges

- a. Undulate: *H. crispus*, (*H. namaquensis*)
- b. Plane: all but the above taxa

9. Leaf margin

- a. Fimbriate with recurved branched cilia: (*H. lanceifolius*), (*H. sanguineus*)
- b. Fringed with ± short straight pale brown trichomes: *H. humanii*
- c. Softly hairy or smooth: all remaining taxa rarely including the above

10. Flowering phenology

- a. Flowering with leaves or leaves at least emerging: *H. albiflos*, *H. avasimontanus*, (*H. carneus*), *H. deformis*, (*H. humilis*), (*H. montanus*), *H. pauculifolius*
- b. Flowering without leaves: all remaining taxa

11. Scape indumentum

- a. Minutely scabrous: (*H. amarylloides* subsp. *polyanthus*), (*H. lanceifolius*), *H. nortieri*
- b. Hairy: (*H. albiflos*), *H. carneus*, (*H. dasyphyllus*), (*H. deformis*), (*H. humilis*), *H. pauculifolius*, (*H. pubescens*), (*H. unifolius*)
- c. Smooth or glabrous: all remaining taxa including some of the above

12. Spathe bract position

- a. Spreading to ± deflexed: *H. amarylloides*, *H. avasimontanus*, *H. barkerae*, *H. canaliculatus*, *H. carneus*, *H. humilis*, *H. lanceifolius*, *H. montanus*, *H. pumilio*, *H. tristis*
- b. Suberect to erect: *H. albiflos*, *H. arenicola*, *H. coccineus*, *H. crispus*, *H. dasyphyllus*, *H. deformis*, *H. graniticus*, *H. humanii*, *H. leipoldtii*, *H. namaquensis*, *H. nortieri*, *H. pauculifolius*, *H. pubescens*, *H. sanguineus*, *H. unifolius*

13. Spathe bract texture

- a. Stiff and fleshy or waxy: *H. arenicola*, *H. coccineus*, *H. crispus*, *H. leipoldtii*, *H. pubescens*
- b. Leathery: *H. albiflos*, (*H. amarylloides*), *H. barkerae*, *H. canaliculatus*, *H. dasyphyllus*, *H. deformis*, *H. graniticus*, *H. namaquensis*, *H. nortieri*, *H. pauculifolius*, *H. pumilio*, *H. sanguineus*, *H. tristis*, *H. unifolius*
- c. Membranous: *H. avasimontanus*, *H. carneus*, *H. humanii*, *H. humilis*, *H. lanceifolius*, *H. montanus*

14. Spathe bract shape

- a. Broadest above midway: (*H. coccineus*), *H. crispus*, *H. dasyphyllus*, *H. pubescens*
- b. Widest midway or below: all taxa except three of the above

15. Spathe bract apex

- a. Apiculate: *H. pubescens*
- b. Somewhat blunt: (*H. coccineus*), *H. crispus*, *H. dasyphyllus*, *H. deformis*, *H. sanguineus*
- c. Acuminate: all taxa except some of the above

16. Flower colour

- a. Uniformly pink: *H. amarylloides*, *H. barkerae*, *H. carneus*, (*H. humilis*)
- b. White to off-white or cream-coloured often turning pinkish with age: *H. avasimontanus*, *H. humanii*, (*H. humilis*), *H. lanceifolius*, *H. montanus*, *H. pumilio*, *H. tristis*
- c. White, often with green veins, rarely entirely green, never turning pink: *H. albiflos*, *H. deformis*, *H. pauculifolius*
- d. Red: *H. arenicola*, *H. canaliculatus*, *H. coccineus*, (*H. crispus*, rarely pink), *H. dasyphyllus*, *H. graniticus*, *H. leipoldtii*, *H. namaquensis*, *H. nortieri*, (*H. pubescens*, rarely pinkish), (*H. sanguineus*, rarely pink), *H. unifolius*

17. Pedicel versus perigone length at anthesis

- a. Pedicel length $\geq$ perigone length: *H. amarylloides*, *H. avasimontanus*, (*H. barkerae*), *H. carneus*, (*H. graniticus*), *H. humanii*, *H. humilis*, *H. lanceifolius*, *H. montanus*, (*H. namaquensis*), *H. pumilio*, (*H. sanguineus*), *H. tristis*
- b. Pedicel length < perigone length: *H. albiflos*, *H. arenicola*, *H. canaliculatus*, (*H. coccineus*), *H. crispus*, (*H. dasyphyllus*), *H. deformis*, *H. leipoldtii*, *H. nortieri*, *H. pauculifolius*, *H. pubescens*, (*H. unifolius*)

18. Perigone tube

- a. Smooth: *H. albiflos*, *H. avasimontanus*, *H. carneus*, *H. deformis*, *H. humanii*, *H. humilis*, *H. lanceifolius*, *H. montanus*, *H. pauculifolius*, *H. pumilio*, *H. tristis*
- b. Slightly swollen below each tepal but tepals not nipped-in proximally: *H. amarylloides*, *H. barkerae*, *H. canaliculatus*, *H. graniticus*, *H. nortieri*, *H. sanguineus*
- c. Markedly swollen below each tepal and tepals nipped-in proximally: *H. arenicola*, *H. coccineus*, *H. crispus*, *H. dasyphyllus*, *H. leipoldtii*, *H. namaquensis*, *H. pubescens*, *H. unifolius*

19. Tepal position

- a. Erect to suberect: *H. albiflos*, *H. arenicola*, *H. canaliculatus*, *H. coccineus*, *H. crispus*, *H. dasyphyllus*, *H. deformis*, *H. graniticus*, *H. leipoldtii*, *H. namaquensis*, *H. nortieri*, *H. pauculifolius*, *H. pubescens*, *H. sanguineus*, *H. unifolius*
- b. Spreading: *H. amarylloides*, *H. avasimontanus*, (*H. barkerae*), *H. carneus*, *H. humanii*, *H. humilis*, *H. lanceifolius*, *H. montanus*, *H. pumilio*, *H. tristis*

Systematics of Haemanthus



Subg. **Serena** (Raf.) Snijman

Subg. **Serena** (Raf.) Snijman, comb. et stat. nov. *Serena* Raf., *Flora telluriana* 4: 20 (1838). Type: *Serena carnea* (Ker Gawl.) Raf., lecto., designated by Snijman: 17 (1984) = *H. carneus* Ker Gawl.

[*Leucodesmis* sensu Raf.: 19 (1838), excl. type *L. pubescens* (L.f.) Raf.]

[*Diaclis* sensu Salisb.: 130 (1866), excl. type *H. pubescens* L.f.]

Plants deciduous or evergreen. *Bulb* broadly ovoid, compressed in plane of distichous leaves; tunics few, mostly 6, circumference evenly thick, dying back horizontally, $\pm$ equally long or $\pm$ tiered, turning pinkish or green if exposed to light. *Leaves* synanthous or near-synanthous, 1 or 2(3) or 4(6), concolorous and immaculate. *Scape* pink, wine-red or green, immaculate, pubescent or glabrous. *Spathe bracts* spreading and descending early or upright and persistent, shorter than to equalling flowers, thin-textured, pale pink, plain white or white with green veins, rarely plain green, rarely pubescent or ciliate. *Inflorescence* spreading or compact, rarely lax. *Flowers* spreading or clustered and erect; pedicel (1–)5–25(–30) mm long, shorter to longer than perigone, firm or lax; perigone widely or narrowly funnellform, $\pm$ 10–30 mm, pale to dark pink or white, concolorous; tube smooth, widening slightly to throat, 1–12 mm long; tepals longer or rarely slightly shorter than tube, narrowly lanceolate, base and tip not swollen. *Stamens* longer than tepals or rarely up to half as long as tepals. *Style* as long as or rarely only half as long as stamens. *Berry* pale orange, pink or red, walls $\pm$ thin, soft when ripe, rarely leathery. *Seeds* green or ivory-white; embryo green.

Species 7: summer-rainfall and nonseasonal rainfall regions of southern Africa.



1

Haemanthus montanus

Baker

Haemanthus montanus *Baker* in *Flora capensis* 6: 234 (1896); Snijman: 100 (1982). Type: South Africa, Natal [KwaZulu-Natal], in valley of Buffalo River near Charles-town, 5000–6000 ft. [1 524–1 829 m], 8 Dec. 1892, *Medley Wood 4810* (K, holo.; B!, BM!, BOL!, E!, NH!, PRE!, S!, US! iso.).

Plants deciduous, green in summer, up to 500 mm high when flowering. *Bulb* solitary or in clumps, ovoid to pyriform, circular or somewhat compressed in plane of distichous leaves, up to 80 mm diam., tunics ± equal, with horizontal or rarely slightly oblique margins, cream-coloured, outer tunics occasionally dark brown and papery. *Leaves* synanthous or near-synanthous, 2(3), erect, blade narrowly to broadly lorate, 150–250 × 15–50 mm, channelled, often twisted, both surfaces green or glaucous, immaculate or occasionally flushed with red towards base, glabrous, margin smooth, occasionally raised or opaque, apex obtuse to acute. *Scape* up to 400 × 7–12 mm, green to reddish brown, immaculate, glabrous. *Spathe bracts* 5–8, spreading and soon becoming reflexed, shorter or longer than flowers, triangular to lanceolate, 25–40 × 4–13 mm, whitish or pale pink, membranous, tips acute. *Inflorescence* obconical to hemispherical, 40–90 mm across, markedly long-bracteolate. *Flowers* loosely spreading, 30–70 or sometimes more; pedicel 7–20 mm long, brownish green; perigone shortly funnelform, 10–14 mm long, white, often ageing to pink; tube 1–2 mm long, smooth; tepals spreading, lanceolate, 9–13 × 2–3 mm, tips acute. *Stamens* shortly exserted by up to 3 mm; filaments white; anthers 1.5–3.0 mm long, yellow. *Ovary* ± 2 mm diam. *Style* equalling filaments. *Berry* ovoidal, 10–14 mm diam., thin-walled, pale green to brownish or pinkish green. *Seed* solitary, ovoidal, 8–14 mm diam., pale green. *Flowering time*: late October to early January. Figure 9.

Distribution and habitat: The widespread *H. montanus* occupies the eastern high-lying regions of southern Africa, within North West, Gauteng, Mpumalanga and Free State provinces, through the midlands of KwaZulu-Natal, and southwards to Qonce, Eastern Cape, South Africa, with a single population having been recorded in southeastern Botswana (Zimudzi et al. 2008), (Figure 10). The area is mainly flat to rolling country that experiences large temperature differences through the seasons and a high frequency of frost in winter (June to August). Populations of 20 to several hundred individuals occur in open mesic grasslands, either along riverbanks, in poorly drained flats or seasonally dry vleis. The species flowers early, soon after the first rains break the winter drought, which possibly enables the plants to avoid competition for light and pollinators later in the season. The bulbs flower especially abundantly when the surrounding grass cover is restricted

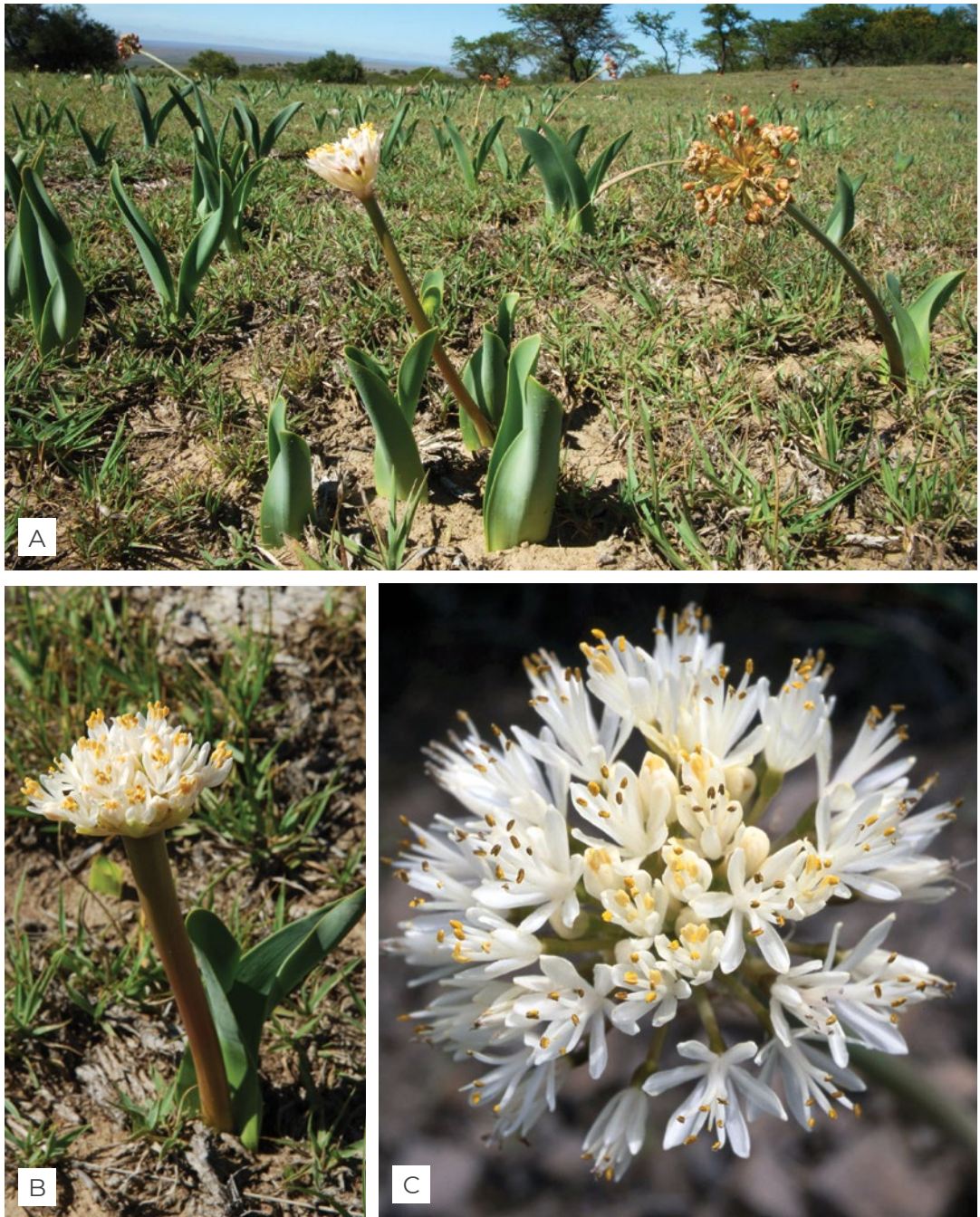


Figure 9. *Haemanthus montanus*. A, in habitat; B, lateral view of inflorescence; C, inflorescence from above. Photographs: A, B, John Manning; C, Colin Paterson-Jones.

by fire, which is frequent in certain parts of the distribution range.

Diagnosis: The species is distinguished by whitish to pale pink membranous spathe bracts that soon reflex and wither, exposing a markedly bracteolate inflorescence of spreading, white flowers that mostly age to pink. The perigone is funnel-shaped, with a short tube, 1–2 mm long and spreading, lanceolate tepals that are 9–13 mm long and relatively broad, 2–3 mm wide. The stamens are short, only exceeding the tepals by up to 3 mm. The leaves, which appear at flowering time or shortly afterwards, are strap-shaped, erect, entirely glabrous and often slightly twisted. The bulb, which is round to slightly compressed in the plane of the leaf blades, has uniformly thick concentric tunics.

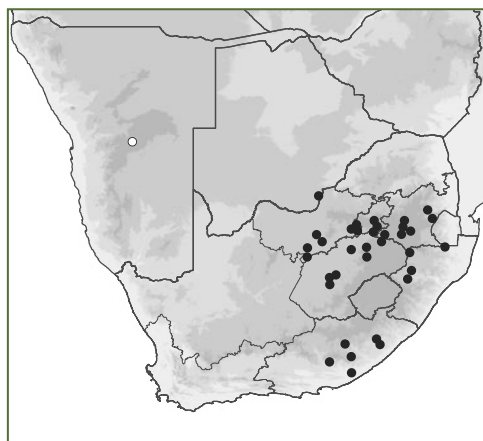


Figure 10. Distribution of *Haemanthus montanus* (●) and *H. avasimontanus* (○).

In contrast to other species, the berry of *H. montanus* is invariably thin walled and the green-pigmented seed is variable in size (McMaster 2011), being especially large (10–14 mm diam.) in populations from the eastern Free State and Highveld. This remarkable increase in seed size may have evolved to allow the establishment of seedlings well in advance of the early winter frosts that occur within this region.

Within subg. *Serena*, *H. montanus* and the central Namibian *H. avasimontanus* are the only entirely glabrous species. *Haemanthus montanus* is distinguished from the latter by its more numerous spathe bracts (5–8 versus 4 or 5), a shorter perigone (10–14 versus 18–22 mm long) and twisted rather than straight leaf blades.

Discussion: In the absence of leaves, *H. montanus* can be distinguished from *H. humilis*, with which it is sympatric, by the glabrous scape and the short perigone tube 1–2 mm long, versus the mostly pubescent scape and longer perigone tube ≥ 2 mm long in the latter. In the vicinity of Somerset East and Makhanda, however, where short-tubed populations of *H. humilis* subsp. *humilis* overlap those of *H. montanus*, the former is smaller in stature, ± 100 mm high, and is late flowering compared with the latter which is 200–300 mm high and early flowering.

Nomenclatural note: *Haemanthus montanus* was first recorded by J.F. Drège, between Gekau and the Bashee River, Eastern Cape, during his expedition to the north in 1832, and thereafter by Zeyher and Burke along the Mooi River in 1841, probably near Potchefstroom (Gunn & Codd 1981). The species has since been widely collected throughout the summer-rainfall grasslands of southern Africa. Baker (1888) introduced confusion as to the identity of the species when he cited a specimen, *Nelson 244* (K) from Bamboesspruit, Eastern Cape under Jacquin's *H. amarylloides*, although he conceded that the specimen probably represented a distinct species. He later described *H. montanus* from the type

specimen collected in KwaZulu-Natal [Natal] but retained additional material with slightly smaller flowers from populations near Bedford and Somerset East, Eastern Cape, within *H. amarylloides* (Baker 1896). These collections were finally included within *H. montanus* when Snijman (1982) revealed that plants from Namaqualand and northwestern Western Cape are the best match with the type of *H. amarylloides* (Jacquin 1804, t. 408).

Specimens examined

SOUTH AFRICA. NORTH WEST. **2627** (Potchefstroom): Mooye River (–CA), *Burke s.n.* (K, SAM); [as ‘Betchuana country’] Mooye River [Mooi River], *Zeyher 1655* (SAM); near Mimosa Park, Potchefstroom (–CB), *Louw 1100* (PRE). **2725** (Bloemhof): Thornhill farm, Wolmaransstad (–BB), *Mainwaring 2794* (PRE); Pringles farm, Christiana (–CC), *Burtt Davy 5539* (PRE).

GAUTENG. **2627** (Potchefstroom): 7 miles [11 km] E of Welverdiend (–AD), *Louw 71* (PRE); Klip River on road from Vereeniging (–DB), *Verdoorn 2343* (PRE). **2628** (Johannesburg): near Premier Paper Mills, Germiston (–AA), *Codd 4470* (K, PRE); Henley-On-Klip (–CA), *Moss s.n.* (K); *Moss* sub NBG 651/41 (NBG). **2629** (Bethal): Vereeniging (–DB), *Leslie 10909* (PRE); 6 km W of Morgenzon on Bethal road (–DC); *Goldblatt 10069* (NBG).

MPUMALANGA. **2530** (Lydenburg): 50 miles [80 km] E of Carolina (–DC), *Reynolds 2143* (PRE). **2628** (Johannesburg): spruit near Val Station (–DD), *Smuts 391* (PRE). **2629** (Bethal): near Vaal River, Standerton (–CD), *Sim 3590* (PRE); 4 miles [6.4 km] W of Morgenzon (–DA), *Mauve 4464* (K); 6 km W of Morgenzon on Bethal road (–DC), *Goldblatt 10069* (NBG). **2630** (Carolina): Steynsdorp [eMlondozi] (–BB), *Dieperink 140* (PRE). **2725** (Bloemhof): Jantjieshoek, 12 miles [19 km] NE of Wakkerstroom (–AC), *Devenish 179* (PRE).

FREE STATE. **2727** (Kroonstad): Heilbron (–BD), *Goosens 521* (PRE); farm Rondavel Noord, W of Kroonstad (–CA), *Scheepers 1752* (PRE); 12.8 miles [20.6 km] from Lindley on road to Heilbron (–DD), *Marais 1092* (K, PRE). **2728** (Frankfort): Villiers (–BA), *Kresfelder s.n.* (PRE). **2826** (Brandfort): farm Peilkop (–CC), *Bourquin 853* (PRE); Glen (–CD), *Heyiule s.n.* (PRE). **2926** (Bloemfontein): 13 miles [20.9 km] N of Bloemfontein (–AA), *Archibald 6129* (GRA).

KWAZULU-NATAL. **2729** (Volkstrust): in valley of Buffalo River, near Charlestown (–DB), *Medley Wood 4810* (BM, E, K, PRE). **2731** (Louwsburg): 25 miles [40 km] NW of Pongola settlement on road to Piet Retief (–BC), *Codd 2105* (PRE). **2829** (Harrismith): near Colenso (–DB), *Mauve 4464* (K, PRE); Estcourt District (–DD), *Green 264* (NH); 5 km from turnoff outside Estcourt towards Weenen, *Van Rensburg 95* (E).

EASTERN CAPE. **3126** (Komani): Komani [Queenstown] (–DD), *Galpin 1676* (GRA, K, PRE); *Everitt s.n.* (PRE); *Koopowitz s.n.* (GRA). **3128** (Umtata): Gcigcira near Baziya (–CB), *Baur 568* (K, SAM); Dutywa [Idutywa], Munyu location (–CD), *Cloete 6501* (NBG); *Evans s.n.* (GRA, PRE 57006). **3226** (Fort Beaufort): Kagaberg (–CA), *MacOwan 2248* (SAM); 4 km from Bedford, just before entering Bushy Pass, *McMaster s.n.* (NBG 158413). **3227** (Stutterheim): 5 miles [8 km] S of Cathcart on the Hogsback road (–AC), *Archibald 6097* (GRA). **3327** (Peddie): Line Drift near King Williamstown [Qonce] (–AA), *Leighton* sub NBG 272/32 (BOL).

Inexact localities: Buffelshoek, Magaliesberg, *Gilfillan 406* (PRE); Bamboesspruit, *Nelson 244* (K); lower Klip River, Moss herb. 26866 (PRE); Klip River valley, *Moss 13806* (BM); Modder River near Bloemfontein, *McNeil s.n.* (K); Kroonstad District, *Pont 523* (PRE); hills between Bedford and Esterhuysens Poort, *MacOwan 2248* (K); between Grahamstown [Makhanda] and Bedford, *Dyer 2324* (K); between Gekau and Bashee Rivers, *Drège 4524* (BM, E, K); between Hogsback and Cathcart, *Barker 2352* (NBG).

Doubtful locality: Oudtshoorn, *Ryder 94* (K).

2

Haemanthus avasimontanus*Dinter*

Haemanthus avasimontanus *Dinter* in Repertorium specierum novarum regni vegetabilis 19: 186 (1923); Sölch: 10 (1969); [as *H. avasimontanus* Dinter: 259 (1931); Snijman: 40 (1984); Duncan et al.: 414 (2016)]. Types: Südwestafrika [Namibia], Tigerfontein bei Auasbergen, 12.2.1923 [inflorescence], *Rusch s.n.* (B 100160886!), lecto., designated here. [The Rusch collection, which is well annotated by K. Dinter, shows characteristics of the inflorescence, the bulb and an emerging young leaf]. Auasgebirge, Südseite des Gebirges bei Tigerfontein (Schäpes farm), 12.II.1923, *Dinter 4465* [leaves] (B!), syntype.

Plants deciduous, green in summer, up to 375 mm high when flowering. *Bulb* solitary or forming clumps, ovoid, 35–45 mm diam., tunics equal, with horizontal edges, outer tunics brown and papery. *Leaves* near-synanthous, 2, suberect, blade lorate, 110–410 × 20–45 mm, shallowly carinate, bright green, glabrous, soft-textured, margin smooth, narrowed to acute apex. *Scape* 150–350 × 4–7 mm, slightly compressed, pale green, glabrous. *Spathe bracts* 4 or 5, upright to somewhat spreading, shorter or as long as flowers, lanceolate, 25–30 × ± 6 mm, greenish or brownish white, membranous, tips acute. *Inflorescence* obconical, 45–60 mm across. *Flowers* 15–20, slightly spreading; pedicel 5–18 mm long; perigone narrowly funnelform, ± 20 mm long, pure white; tube 2–3 mm long, smooth; tepals slightly spreading, linear to lanceolate, ± 17 × 1–2 mm, tips acute. *Stamens* exerted by up to 3 mm; filaments white; anthers 1 mm long, yellow. *Ovary* 2.0–3.5 mm diam., green. *Style* as long as stamens or slightly longer. *Berry* ovoidal, 10–12 mm diam., thin-walled, brownish green. *Seeds* ovoidal, pale green. *Flowering time*: February.

Distribution and habitat: The rare *H. avasimontanus* is known only from central Namibia on the Komas-Hochland mountains northwest and southeast of Windhoek, on Otjihaveraberg and the Auasberge respectively, the latter being among the highest mountain ranges in Namibia (Figure 10). Populations are confined to partially shaded, south-facing rock faces within deeply incised gorges, at elevations of ± 1 600–1 700 m. The bulbs occupy cracks in rocks and patches of friable soil on broad ledges, in places where moisture collects from summer rain. Apart from *H. avasimontanus*, only a few species of ferns, *Oxalis* and *Crassula* occupy these sites. Less frequently, small numbers of bulbs occupy boulder-strewn hillsides among grass and shrubs (Craib 2010). This geographically isolated location on the northwestern edge of the *Haemanthus* distribution range characterises the species as a significant outlier within the genus. It raises questions as to the species' origins and whether it is a

relict of a once unfragmented distribution pattern. Future studies with access to new methods may hopefully provide more insight into its evolutionary history.

Diagnosis: The upright to slightly spreading, membranous spathe bracts that surround the head of white flowers, together with the glabrous, lorate leaves and the bulb with somewhat even tunics, are shared with *H. montanus*, a widespread species in the eastern parts of southern Africa. Several characters, however, separate the two species. *Haemanthus avasimontanus* has few spathe bracts (4 or 5), a longer perigone ± 20 mm long and leaves that are described by Duncan et al. (2016) as straight and shallowly keeled. In contrast, *H. montanus* has more numerous spathe bracts (5–8), a shorter perigone 10–14 mm long and channelled leaves that are usually twisted.

Discussion: *Haemanthus avasimontanus* is represented by very few herbarium records, mainly lodged in the Berlin Herbarium, dating to around 1923. The rediscovery of the species by Craib, Pehlemann and Human in 2009 has added valuable new data on the distribution range and habitat (Craib 2010; Duncan et al. 2016), but in the absence of voucher specimens it still remains one of the least known species in the genus.

Nomenclatural note: Dinter consistently annotated the type specimens of plants he described from the Auasberge with the epithet *avasmontanus*. Nevertheless, the published version in the protologue is *avasimontanus*. There are no compelling grounds for treating this as a correctable error, thus the epithet is retained here as *Haemanthus avasimontanus*, as in *Dipcadi avasimontanus* Dinter and *Crasula avasimontana* Dinter.

3

Haemanthus carneus*Ker Gawl.*

Haemanthus carneus *Ker Gawl.* in Edwards's Botanical Register 6: t. 509 (1821). *Serena carnea* (Ker Gawl.) Raf.: 20 (1838). Type: South Africa, Cape of Good Hope, from nursery of Messrs. Colville [without precise locality or collector], illustration in Edwards's Botanical Register 6: t. 509 (1821), lecto., designated by Friis & Nordal: 70 (1976).

Plants deciduous, green in late summer and rarely into winter, up to 300 mm high when flowering. *Bulb* solitary, ovoid, up to 70 mm diam., $\pm$ compressed towards distichous leaves, tunics $\pm$ equal, circumference uniformly thick, margins horizontally truncate, cream-coloured, outer tunics mostly withered and brown. *Leaves* synanthous or near-synanthous, 2(3), mostly flat on ground, sometimes spreading, blade broadly to narrowly elliptic or ovate, 100–210 $\times$ 35–135 mm, plane, both surfaces immaculate, softly pubescent or glabrous with fringed margins, apex acute or obtuse. *Scape* erect, 60–270 $\times$ 7–12 mm, wine-red or brownish red, immaculate, softly pubescent, rarely subglabrous. *Spathe bracts* 5–7, spreading, soon becoming reflexed, shorter than flowers, narrowly lanceolate, 13–20 $\times$ 2–5 mm wide, membranous, rose-pink with darker veins, tips acute. *Inflorescence* loose, globose, 45–90 mm across, markedly long-bracteolate. *Flowers* 30–120, widely spreading; pedicel 11–25 mm long, brownish red; perigone 11–13 mm long, dark to pale rose-pink; tube 2.5–3.5 mm long, more or less cylindrical, gradually widening upwards; tepals slightly spreading, narrowly oblong to lanceolate, 8.5–10.0 $\times$ 1.5–3.0 mm, tips acute to obtuse. *Stamens* included, less than half as long as tepals at anthesis, unequal, outer 1–3 mm long, inner 3–4 mm long, white to pale pink; anthers small, 1 mm long, yellow. *Ovary* 1–2 mm across, green to reddish brown. *Style* $\pm$ half as long as stamens, 3–7 mm long. *Berry* ovoidal, 12 $\times$ 9 mm, thin-walled, pale green to reddish pink. *Seeds* ovoidal, pale green. *Flowering time*: January to March. Figure 11.

Distribution and habitat: The species is known from isolated sites within southeastern Free State, from the vicinity of Estcourt, KwaZulu-Natal, and from near Somerset East and Makhanda, Eastern Cape (Figure 12). Populations are confined to seasonally dry grassland interspersed with tall shrublands or sparse thornveld, on level plains or slopes at elevations of 300–1 200 m above sea level. Groups of bulbs grow in semi-open grassland habitats, under trees and shrubs, or amongst rock outcrops. In KwaZulu-Natal rain falls strictly in summer, whereas in the Eastern Cape rainfall is bimodal in spring and late summer, with February and March being the maximum rainfall months. Hence, under favourable conditions bulbs from the Somerset East and Makhanda regions

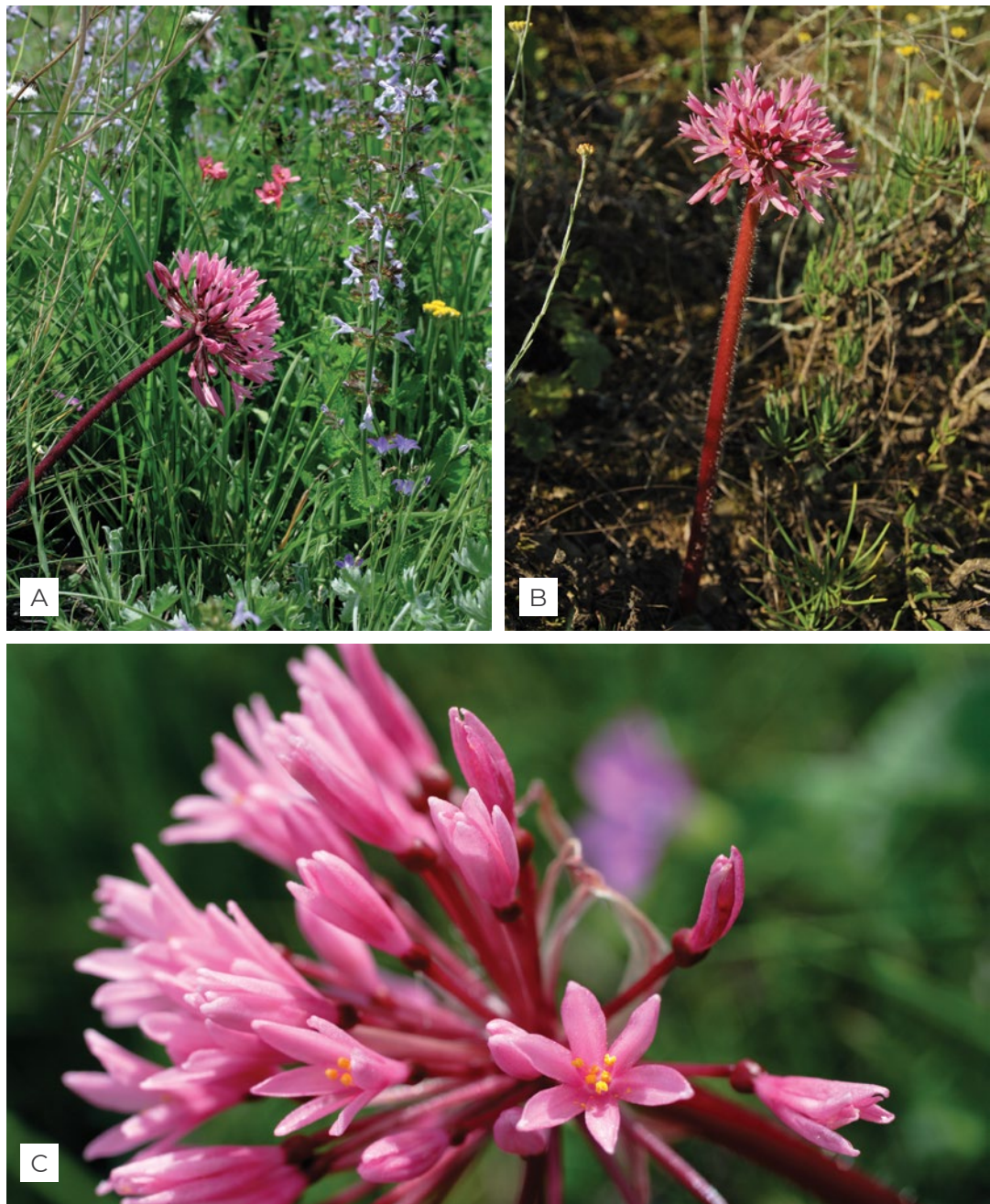


Figure 11. *Haemanthus carneus*. A, in habitat; B, lateral view of inflorescence; C, detail of flower showing unequal inner and outer stamens and inconspicuous style. Photographs: A, C, Colin Paterson-Jones; B, John Manning.

may have leaves throughout winter until spring or early summer.

Although nothing is known of the soils in which the outlying populations were found, the highly fragmented distribution pattern of *H. carneus* may correspond with patches of various shrublands that occupy special geological or topographical situations embedded within the Grassland Biome (see Mucina et al. 2006b, Figure 8.24). A similar disjunction is known for *Cyrtanthus obliquus* (L.f.) Aiton in which the few outliers in KwaZulu-Natal occupy habitats associated with distinct substrates (Scott-Shaw 1999) that link them to the main populations within the Eastern and Western Cape provinces. The scarcity of *H. carneus* within KwaZulu-Natal may suggest that populations here have become critically rare due to competition from neighbouring grassland species as a result of altered grazing pressure and increased frequency of fire.

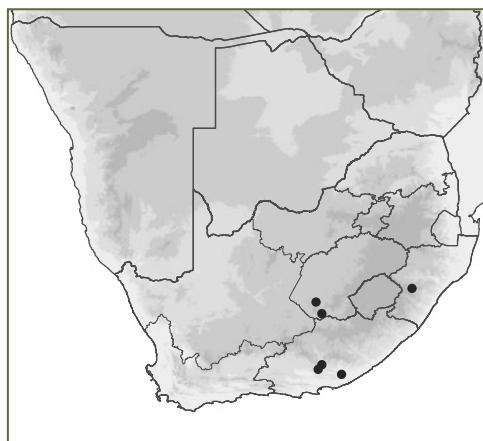


Figure 12. Distribution of *Haemanthus carneus*.

Diagnosis: *Haemanthus carneus* has several unique floral characters that allow easy recognition within the genus. The inflorescence of rose-pink flowers is widely spreading, loose and subglobose, and it is noticeably composed of many, small clusters of flowers in which the pedicels differ in length, clearly revealing its multiple helicoid cymose arrangement, a feature that is cryptic in most other species. The stamens are distinctive in being markedly short and unequal (outer 1–3 mm and inner 3–4 mm long), reaching less than midway up the tepals at anthesis. The style is likewise short, extending less than midway up the stamens.

Vegetatively the species is very like *H. humilis*, which is widespread, mostly in pure grassland. The bulb is usually compressed in the median plane and has somewhat even, horizontally truncate tunics. The prostrate leaves are fleshy, immaculate and range from hairy to glabrous but always with a fringed margin.

Discussion: Following its original description, Baker (1888, 1896) and later Friis and Nordal (1976) amplified *H. carneus* considerably to include a wide range of pink-flowered specimens from the summer-rainfall region of South Africa. A detailed examination of the specimens placed within Friis and Nordal's *H. carneus* complex, however, revealed two discrete groups (Snijman 1984). The smaller group, in which the stamens and style are less than half the length of the tepals, continues to be recognised as *H. carneus*, whereas the larger group that has stamens and style ranging in length from equalling to exceeding the tepals is recognised as the widespread, more variable *H. humilis*. Both species are present within the Grassland Biome, but they occupy different niches, apparently shaped by particular substrates and the frequency of fire.

Specimens examined

SOUTH AFRICA. FREE STATE. **2925** (Jagersfontein): Fauresmith (–CB), *Smith 5604* (PRE). **3025** (Colesberg): Kuilfontein (–BC), *Townshend* [*Townshend*] sub NBG 865/30 (NBG).

KWAZULU-NATAL. **2929** (Underberg): lowlands near Estcourt (–BB), *Schelte* sub NBG 11/42 (NBG).

EASTERN CAPE. **3225** (Somerset East): Somerset East (–DA), *Harries* sub NBG 1170/30 (NBG); *Wisura 1063* (NBG); *West 281* (BOL, GRA); Boschberg mountains (–DA/DC), *Bruce 521* (PRE); *MacOwan 1311* (BOL). **3326** (Makhanda): Pluto Vale, Grahamstown [Makhanda] (–BA), *Wisura 1098* (NBG).

4

Haemanthus humilis*Jacq.*

Haemanthus humilis *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 4: 6, t. 411 (1804). Type: South Africa, Cape of Good Hope [without precise locality or collector], figure in Jacquin: t. 411 (1804), lecto., designated by Snijman: 22 (1984).

See subspecies for further synonymy.

Plants deciduous, green in summer or late autumn, up to 350 mm high when flowering. *Bulb* solitary or in clumps, varying from small to large, mostly ovoid, medianly compressed to $\pm$ round in cross section, up to 80 mm diam., tunics more or less equal with horizontally truncate margins, cream-coloured, sometimes turning dark pink when exposed to light, occasionally with withered brown outer tunics. *Leaves* synanthous or near-synanthous, 2(3), prostrate, spreading or suberect, blade narrowly to broadly elliptic, lanceolate or oblong, 20–300 $\times$ 13–150 mm, flat or slightly channelled at base, immaculate, mostly with some pubescence at least on one surface, rarely entirely glabrous, adaxial surface dark or pale green, sometimes strigose or papillate, abaxial surface pale green, margin ciliate, apex acute or obtuse. *Scape* erect or laterally slanted, 20–300 $\times$ 4–16 mm, varying from pale green to pink or deep maroon, immaculate, usually $\pm$ pubescent, rarely glabrous. *Spathe bracts* (4)5–10, spreading, soon becoming reflexed, shorter than flowers, broadly to narrowly triangular or lanceolate (11–)15–30 $\times$ 2–15 mm, pale to dark pink, membranous, margins sometimes ciliate, tips acute. *Inflorescence* loose or dense, broadly obconical to hemispherical, 25–120 mm across, markedly bracteolate. *Flowers* spreading, 15–120; pedicel 5–30 mm long, green, sometimes flushed with pink; perigone 7–25 mm long, pale pink to rose-pink, or white and fading to pink; tube 1–10(–12) mm long, cylindrical; tepals slightly spreading, narrowly lanceolate, 4–21 $\times$ 1–2 mm, tips acute. *Stamens* equalling tepals or exserted by up to 15 mm; filaments pink or white; anthers 1 mm long, yellow. *Ovary* $\pm$ 2 mm diam., green, sometimes blushed pink. *Style* $\pm$ as long as or longer than filaments. *Berry* ovoidal, 5–10 mm diam., pinkish white to cream or pale orange, pulpy and aromatic when ripe. *Seeds* ovoidal, $\pm$ 5 mm diam., pale green. *Flowering time*: (September–) November to February (–March). Figures 13, 14 and 16.

Distribution and habitat: The species is widespread throughout the interior of southern Africa, only approaching the eastern seaboard in the southeast, within the vicinity of Makhanda, Eastern Cape (Figure 15). Populations are usually small, mostly found on southern slopes, often among rock outcrops (Figure 7). Rainfall varies from strictly summer rain in the northeast to a pattern of late summer and autumn rain in the south and the west. Thus, vegetation in the northern and western

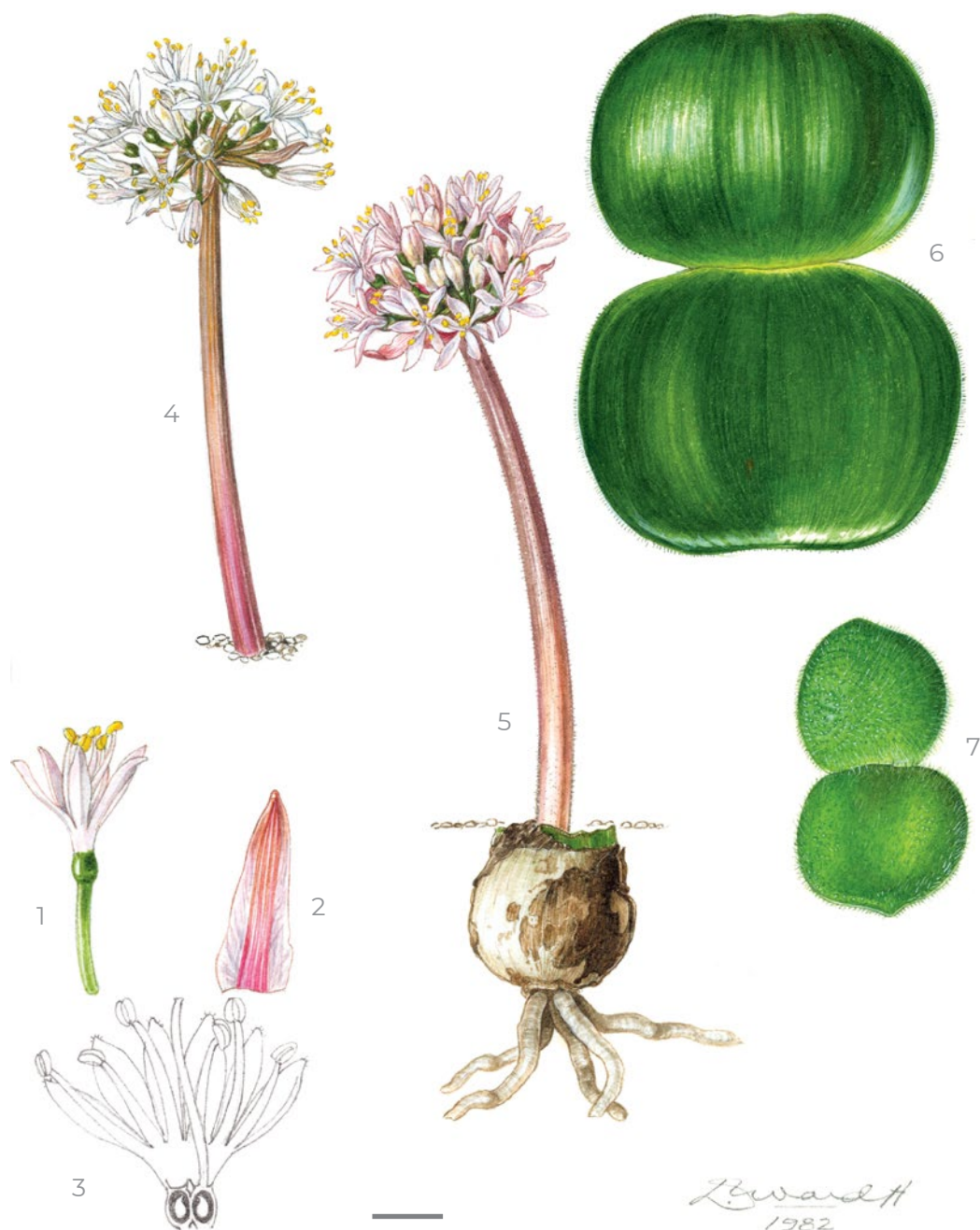


Figure 13. *Haemanthus humilis* subsp. *humilis*. 1, flower; 2, spathe bract; 3, section of flower; 4, inflorescence; 5, bulb, emerging leaves and inflorescence; 6, mature leaves; 7, young leaves. *Batten 591* (NBG), near King William's Town. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 2 = 8 mm; 3 = 5 mm; 4–7 = 15 mm.



Figure 14. *Haemanthus humilis* subsp. *humilis*. 1, inflorescence; 2, flower; 3, flower; 4, spathe bract; 5, bulb and young leaves. OFS 32/68 (NBG), Bloemfontein. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 3, 5 = 12 mm; 2, 4 = 6 mm.

parts of the distribution range, bordering on the Savanna and Nama-Karoo biomes, have maximum growth activity from February to April, whereas vegetation in the temperate northeastern area has maximum growth in January (Mucina et al. 2006b). This pattern closely matches the shifts in flowering and leafing within *H. humilis* populations from the drier interior to the more mesic grasslands below the escarpment in the east. Correlated with this temporal pattern are several floral features that distinguish the two subspecies recognised here.

Diagnosis: The highly polymorphic *H. humilis* is distinguishable vegetatively by its round or medianly compressed bulb that has more or less even, horizontally truncate, concentric tunics. The elliptic-oblong leaves, which vary from synanthous to near-synanthous, are spreading to prostrate, and densely pubescent to almost glabrous. The foliage, however, is always immaculate. When flowering, the species is recognised by the spreading, white to pink, membranous spathe bracts that soon reflex and wither. At anthesis, therefore, the inflorescence is dominated by the white to deep pink flowers in which the stamens either equal the tepals in length or are well exserted. In the latter the flower head resembles a powderpuff.

Discussion: Across its wide distribution range *H. humilis* falls into two main groups based on floral morphology (Snijman 1984). Populations of plants, typical of *H. humilis*, which extend throughout the central interior and reach their southeastern limit in the Eastern Cape, have a short perigone, mostly 7–16 mm long, and stamens that either equal the tepals or exceed them by up to 5 mm. In contrast, populations of plants within the core eastern distribution range, which have a longer perigone, usually 16–26 mm long, and prominent stamens exserted by 5–15 mm, match Baker's (1888, 1896) concept of *H. hirsutus*. There is little overlap in floral features between these two series of populations, except within Gauteng in the north, where populations of the two taxa are sympatric and intermediate plants occur.

The relationship between *H. humilis* subsp. *humilis* and *H. humilis* subsp. *hirsutus* was only weakly supported (bootstrap 61) in the phylogenetic analysis of Haemantheae by Bay-Smidt et al. (2011), based on nuclear ribosomal internal transcribed spacer (ITS) and plastid *trnL-F* regions from plants of unknown provenance. However, the sister-relationship between the two taxa was strongly supported (bootstrap 97) in the analyses by Conrad (2008) and in collaboration with co-authors Magee et al. (Figure 1), based on ITS and four and two plastid regions respectively, and an almost complete sample of vouchered plants of wild provenance. Based on the latter result and the existence of populations morphologically intermediate between these otherwise parapatric taxa, they continue to be recognised here at subspecific rank.

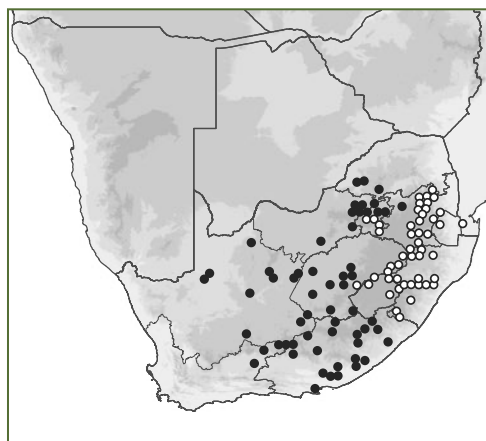


Figure 15. Distribution of *Haemanthus humilis* subsp. *humilis* (●); *H. humilis* subsp. *hirsutus* (○).

Nomenclatural note: In past literature, *H. humilis* remained poorly known to both Baker (1888, 1896) and Friis and Nordal (1976), and it was only with some doubt that the latter authors referred *H. humilis* to their *H. carneus* complex. A comparison by Snijman (1984) of all specimens gathered within the area explored by Jacquin's collectors Boos and Scholl, namely Namaqualand eastwards to the Komgha-Qonce region (Gunn & Codd 1981), showed that collections from along the Kei River, Eastern Cape, namely *Martin* sub NBG 452/38 (NBG), correspond most closely with Jacquin's description of *H. humilis*. The name *H. humilis* thus takes precedence over all other names previously used for the taxon, excluding *H. carneus* s.s., which continues to be treated as a separate species. The characters separating *H. carneus* from *H. humilis* are discussed under the former.

Key to subspecies:

- 1a. Inflorescence loose, hemispherical; spathe bracts 4–7(–10); flowers rose-pink to white; perigone 7–16(–18) mm long, tube 1–6(–7) mm long, tepals 4–10(–14) mm long; stamens equalling the tepals or exerted by up to 5(–8) mm; flowering mostly from late January to February 4a. subsp. *humilis*
- 1b. Inflorescence stiff, widely obconical to hemispherical; spathe bracts 7–10; flowers pale pink to white; perigone (15–)16–26 mm long, tube 5–12 mm long, tepals 10–21 mm long; stamens exerted by 5–15 mm; flowering mostly between November and December 4b. subsp. *hirsutus*

4a. subsp. *humilis*

Haemanthus brevifolius Herb.: 234, t. 30, fig. 3 (1837). Type: South Africa [without definite locality or collector], Hort. Kew, 1800 (BM, holo.).

Haemanthus strigosus Herb.: 234, t. 30, fig. 2 (1837). *Haemanthus carneus* var. *strigosus* (Herb.) Baker: 67 (1888). Type: South Africa [without definite locality], *Masson s.n.* (BM, holo.).

Haemanthus arnotii Baker: 492 (1878a) [as *H. arnottii*]. Type: South Africa [Northern Cape], Colesberg, *Arnot s.n.*, Hort. Kew, 4 Sept. 1879, [K, lecto., designated by Snijman: 27 (1984)].

[*Haemanthus ryderae* Barnes *ms.* Several sheets so annotated in BOL, K, NBG, PRE. *Haemanthus ryderae* var. *glaber* Barnes *ms.* 7 to 8 miles [11.2 to 12.8 km] from Grahamstown [Makhanda] on Peddie road, *Dyer* 2362 (BOL)].

Plants ± 50–350 mm high at flowering. *Leaves* prostrate or recurved, appearing at or shortly after flowering, blade 20–240 × 13–150 mm, flat, adaxial surface dark or pale green, smooth or hairy, hairs sometimes coarse with papillose bases, abaxial surface pale green, glabrous or rarely pubescent. *Scape* 20–300 × 4–9 mm. *Spathe bracts* (4)5–7. *Inflorescence* loose, hemispherical, 25–60(–100) mm across. *Flowers* spreading, 15–80; perigone 7–16(–18) mm long, rose-pink to white and fading to pink; tube 1–6(–7) mm long; tepals (4–)5–10(–14) mm long. *Stamens* equalling tepals or exerted by up to 5(–8) mm. *Flowering time:* January to March with the peak between late January and February. Figures 13 and 14.

Distribution and habitat: Typical *H. humilis* is widespread within the South African interior, predominantly west of $\pm 28^\circ$ E, within the drier areas of all the northern provinces, as well as within Free State, Northern Cape, Western Cape and Eastern Cape (Figure 15). The distribution area straddles thornveld and dry grasslands in which fire is infrequent and of low intensity, mostly at elevations $< 1\,500$ m above sea level. However, populations recorded slightly away from the face of the Eastern Cape escarpment, between Barkly East and Elliot, reach elevations of $\pm 1\,800$ m above sea level. Populations are usually small and most often located in rocky outcrops, predominantly within dolerite and sandstone. Rainfall in the area is strongly seasonal, varying from midsummer in the north to late summer and of increasing uncertainty in the western and southeastern areas. There is a corresponding reduction in plant size and a shift in flowering times within populations located along this north to south gradient.

Diagnosis: *Haemanthus humilis* subsp. *humilis* is distinguished predominantly by the size and proportions of its flowers. The perigone is 7–16(–18) mm long, comprising a tube which ranges in length from 1–6(–7) mm, tepals of 4–10(–14) mm in length, and stamens that equal the tepals or exceed them by up to 5(–8) mm.

Discussion: Populations of *H. humilis* subsp. *humilis* from the North West, Limpopo and Free State provinces, and the wetter areas of Eastern Cape tend to have leaves present at flowering time and they have inflorescences that are generally more robust than elsewhere (Figure 7A). In contrast, populations from the drier western parts, namely the eastern Northern Cape and karroid areas of Eastern Cape, possess smaller inflorescences that usually precede the leaves. Plants from the vicinities of Makhanda, Qonce and Graaff-Reinet, Eastern Cape, and Nelspoort, Western Cape, have developed several xeromorphic characteristics that reflect the severity of the climate in these areas. Here plants may have short scapes (± 30 mm high), particularly small leaves ($\pm 20 \times 7$ mm) and variable karyotypes (Vosa & Snijman 1984). Furthermore, the leaves are sometimes covered with strigose hairs, but this varies both within and among populations. These local forms match Herbert's *H. brevifolius* and *H. strigosus* (Herbert 1837), both treated as synonyms of typical *H. humilis*. The stamens of these diminutive plants barely exceed the perigone, a convergent feature also seen in specimens from the vicinity of Rustenburg, North West, thus differing from plants with exserted stamens that occur elsewhere in the distribution range. Whether floral morphology is correlated with a shift in pollinators across the distribution range is a question for further study.

Specimens examined

SOUTH AFRICA. LIMPOPO. **2427** (Thabazimbi): Matlabas (–AD), *Van Jaarsveld* 3325 [3329] (K, MO, NBG, PRE, S); Krantzberg (–BC), *Dyer & Verdoorn* 4226 (K, PRE). **2428** (Nylstroom): near Warmbaths (–CD), *Codd* 4822 (PRE); *Repton* 808 (PRE).

NORTH WEST. **2527** (Rustenburg): Maricana (–CB), *Pole Evans* 3919 (PRE); Jacksontuin (–DA), *Van Vuuren* 454 (K, PRE); farm Krokodil drift near Brits (–DB), *Obermeyer* in herb. Tvl. 35147 (PRE). **2627** (Potchefstroom): Boskop (–CA), *Louw* 702 (PRE). **2725** (Bloemhof): Wolmaransstad (–BB), *Liebenberg* 3434 (PRE).

GAUTENG. **2527** (Rustenburg): Breedts Nek (–CD), *Dyer & Verdoorn* 3921 (PRE); Hennops River (–DD), *Prosser* 1594 (PRE). **2528** (Pretoria): Pretoria University farm (–CA), *Codd* 5913 (PRE); Pretoria, *Munro* 13782 (PRE);

20 miles [32 km] E of East Lynn (–CD), *Wisura 1216* (NBG); Magaliesberge (–DC), *Dahlstrand 1910* (PRE); *Fouche s.n.* (PRE).

MPUMALANGA. **2529** (Witbank): Doornkop, Middelburg (–CB), *Du Plessis 222* (PRE).

FREE STATE. **2825** (Boshof): Kareepan, Barkly West Division (–CB), *Snyman s.n.* (BOL). **2826** (Brandfort): Tabaksberg summit (–DB), *Van Jaarsveld 1782* (NBG). **2827** (Senekal): Willem Pretorius Wildtuin (–AC), *Muller 858* (PRE); 4 miles [6.4 km] W of Winburg (–CA), *Codd 6359* (PRE). **2925** (Jagersfontein): Fauresmith (–CB), *Henrici 1955* (PRE). **2926** (Bloemfontein): Winter valley, N of Bloemfontein (–AA), *Muller 150* (PRE); Bloemfontein, *OFS 32/68* (NBG); Thabanchu (–BB), *Roberts 2980* (PRE).

NORTHERN CAPE. **2722** (Olifantshoek): top of Verwatersnek, Postmasberg (–BC), *Leistner 1604* (K, PRE). **2820** (Kakamas): Tierberg, Keimoes Nature Reserve (–DB), *Snijman 247* (NBG); Kakamas (–DC), *Fuller 150* (BOL, PRE). **2823** (Griekwastad): Asbestos mountains (–CB), *Marloth s.n.* (PRE); near Campbell, Herbert Division (–DC), *Reynolds s.n.* (K, PRE); Herbert, *Stayner s.n.* (NBG). **2824** (Kimberley): Koppies near Kimberley (–DB), *Power* (BOL 76542); 20 miles [32 km] S of Kimberley (–DC), *Hall* sub NBG 233/53 (NBG). **2922** (Prieska): Prieska (–DA), *Bryant s.n.* (K, PRE); Orange River Crossing, Prieska, *Stayner s.n.* (NBG). **3024** (De Aar): Sea Cow River, farm Klipkraal about 40 km W of Colesberg (–DD), *Murray s.n.* (PRE). **3025** (Colesberg): Colesberg (–CA), *Arnot s.n.* (K). **3026** (Aliwal North): 12 myl [19 km] oos van Bethuli in richting van Aliwal North (–AC), *Werger 189* (K, PRE).

WESTERN CAPE. **3123** (Victoria West): Murraysberg (–DD), *Tyson 463* (GRA); *Tyson s.n.* (BOL). **3223** (Rietbron): Nelspoort, Beaufort West (–AA), *Haynes* sub NBG 46/26 (BOL); *Pearson 1132* (NBG).

EASTERN CAPE. **3026** (Aliwal North): Elandshoek near Aliwal North (–DC), *Bolus* in herb. Austro-Africanæ 226 (BOL). **3027** (Lady Grey): Gatberg (–AD), *Baur 1169* (K). **3028** (Matatiele): Maclear, farm Esperanza ± 24 km NW of Maclear (–CC), *Bester 1574* (NH). **3124** (Hanover): Aasvoelkrantz near New [Nieu] Bethesda (–CD), *Bayer 2355* (NBG); farm Wilgerbos, Compassberg (–DC), *Roux & McMaster 28* (NBG). **3125** (Steynsburg): Middelburg (–AC), *Theron 703* (PRE). **3126** (Komani): Stormberg near Patriots Klip (–AD), *Medley Wood* in herb. Galpin 2379 (BOL, PRE). **3127** (Lady Frere): Bastervoetpad, farm Mount Enterprise, ± 25 km W of Ugie (–BB), *Bester 2015* (NH); Cala Pass (–BC), *Reynolds 1742* (PRE); near Engcobo (–DB), *Bolus* in herb. Austr. Afr. 10328 (BOL, SAM); *Flanagan 2761* (PRE). **3128** (Mthatha): Maclear (–AB), *Martin* sub NBG 451/38 (NBG); Umtata [Mthatha] (–DB), *Pegler 2137* (PRE). **3224** (Graaff-Reinet): Graaff-Reinet (–BC), *Bayer 2349* (NBG); *Bolus 764* (BOL); *Bolus s.n.* (K); *Bowker 33* (K). **3225** (Somerset East): Cradock (–BA), *Brynard 175* (PRE). **3226** (Fort Beaufort): 35 miles [56 km] from Grahamstown [Makhanda] on Fort Beaufort road (–DC), *Dyer 2290* (BOL, K, PRE). **3227** (Stutterheim): Stutterheim (–CB), *Myers* sub NBG 770/29 (BOL); near King William's Town (–CD), *Batten 591* (K, NBG); *Bokelmann s.n.* (K, NBG, PRE); *Brownlee* sub *Marloth 11856* (PRE); along the Kei River near Komgha (–DB), *Flanagan 2251* (PRE); banks of Kei River, *Hiemstra 577* (NBG, PRE); Kei Cutting, *Martin* sub NBG 452/38 (NBG). **3325** (Gqeberha): Kommadagga (–BB), *Bayliss 1244* (NBG); *Bayliss s.n.* (NBG). **3326** (Makhanda): farm Wilgerfontein, between Kommadagga and Alicedale (–AC), *Snijman 471* (NBG); Grahamstown [Makhanda] (–BC), *Black 19* (BOL, PRE); *Bolton s.n.* (K); *Guthrie s.n.* (BOL); 7 to 8 miles [11.2 to 12.8 km] from Grahamstown [Makhanda] on Peddie road, *Dyer 2362* (BOL). **3425** (Skoenmakerskop): Sea View (–AB), *Long 142* (GRA, K).

Inexact localities: Florasfontein, Herbert, *Anderson 719* (SAM); Caledon River, Orange Free State [Free Sate], *Burke 444* (K, SAM); Rhinosterkop, Orange Free State [Free State], *Burke s.n.* (K); Doctors Drift, Aliwal North region, *Gerstner 332* (K, PRE); South Africa, *Masson* in herb. Banks (BM); between Grahamstown [Makhanda] and Fort Beaufort, *Ryder 95* (BOL); Stinkfontein, Kalahari region, *Ryder* sub NBG -/28 (BOL).

4b. subsp. **hirsutus** (*Baker*) *Snijman*

subsp. **hirsutus** (*Baker*) *Snijman* in Journal of South African Botany, suppl. vol. 12: 32 (1984). *Haemanthus hirsutus* Baker in Gardeners' Chronicle, New Series 9: 756 (1878b); Baker: 70 (1888); Baker: 237 (1896). Type: South Africa, Natal [KwaZulu-Natal], near Mooi River, 19 Dec. 1885, *Medley Wood 3443* [K, neo!], designated by Snijman: 32 (1984)].

Haemanthus candidus W.Bull: 3 (1894) [as *H. candidum*]. Type: South Africa, Transvaal [Gauteng], probably not preserved.

Haemanthus nelsonii Baker: 310 (1898). Type: South Africa, Transvaal [Gauteng], Johannesburg, *W. Nelson* sub *Leichtlin s.n.*, Nov. 1897 [K, lecto!], designated by Snijman: 32 (1984)].

Plants up to ± 300 mm high when flowering. *Leaves* recurved to suberect, appearing with inflorescence, blade $150\text{--}300 \times 55\text{--}130$ mm, both surfaces pale green, pubescent or glabrous but usually adaxial surface glabrous and abaxial surface pubescent. *Scape* $150\text{--}300 \times 10\text{--}16$ mm. *Spathe bracts* 7–10, broadly to narrowly triangular or lanceolate, $20\text{--}30 \times 3\text{--}15$ mm. *Inflorescence* stiff, broadly obconical to hemispherical, 50–120 mm across. *Flowers* 25–120; perigone 15–26 mm long, pale pink or white fading to pink; tube (4–)5–12 mm long; tepals 10–17(–21) mm long. *Stamens* exserted by 5–15 mm. *Flowering time*: September to February with the peak between November and December. Figure 16.

Distribution and habitat. *Haemanthus humilis* subsp. *hirsutus* is widespread to the east of $\pm 28^\circ$ E, within the high-lying, mesic grasslands on and to the east of the Great Escarpment, in Mpumalanga, Eswatini, Lesotho, eastern Free State and KwaZulu-Natal, extending westwards onto the Highveld grasslands of the Witwatersrand, Gauteng (Figure 15). Populations occur at elevations mostly $> 1\,500$ m above sea level but below the 2 350 m snowline on the Drakensberg (Hilliard & Burt 1987). Rainfall is strongly seasonal in summer and the winters are dry with a high incidence of frost until September. Fire is frequent, mostly in late winter, and occurs every one to four years (Mucina et al. 2006b). The bulbs typically occupy fire-protected habitats, mainly in humus-filled crevices of rock outcrops and cliffs, predominantly in cave sandstone or basalt, and occasionally in dolerite-derived soils (Figure 7B).

Diagnosis: *Haemanthus humilis* subsp. *hirsutus* is one of the most attractive taxa in the genus. The soft, green leaves which appear at the same time as the inflorescence are usually well-developed when the flowers turn to fruit. The pale pink or white inflorescences are large and dense, usually dominated by flowers in which the perigone is (15–)16–26 mm long, with a tube 4–12 mm long, tepals 10–21 mm long and stamens exserted by 5–15 mm. Unlike typical *H. humilis*, this subspecies is fairly uniform morphologically. No broad pattern of variability is evident but considerable differences in the hairiness of the leaves can be found amongst individuals within a single population.



Figure 16. *Haemanthus humilis* subsp. *hirsutus*. 1, inflorescence and young leaves; 2, flower; 3, spathe bract; 4, bulb. Van Jaarsveld 1834 (NBG), NW of Johannesburg. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–4 = 12 mm.

The leaves may be completely glabrous with only ciliate margins, entirely pubescent, or pubescent on the abaxial surface only.

Nomenclatural note: *Haemanthus hirsutus* was first described by Baker (1878b) from a plant sent from the Transvaal [Gauteng], by Mr C. Mudd, to the nurserymen, Messrs Veitch and Sons in Chelsea, England, where it flowered. A specimen, however, was not preserved. Snijman (1984) selected a neotype from the specimens cited by Baker (1888) that accords well with the original description, namely *Medley Wood 3443* (K) from near Mooi River, KwaZulu-Natal. The type of *H. nelsonii* falls well within the limits of *H. humilis* subsp. *hirsutus*, but the name has been rather loosely applied in the past, and thus many specimens bearing the name *H. nelsonii sensu lato* have been re-identified as *H. humilis* subsp. *humilis* (Snijman 1984).

Specimens examined

SOUTH AFRICA. GAUTENG. **2627** (Potchefstroom): Constantia Kruin hills near Roodepoort (–BB), *Roux 335* (NBG); NW of Johannesburg, *Van Jaarsveld 1834* (NBG). **2628** (Johannesburg): Bryanston (–AA), *Gilliland J35050* (PRE); Johannesburg, *Nelson sub Leichtlin s.n.* (K); Heidelberg (–AD), *Plowes 3173* (PRE); Suikerbosrand (–CB), *Bredenkamp 506* (PRE).

MPUMALANGA. **2430** (Pilgrims Rest): Morgenzon Nature Reserve (–DC), *Kluge 2111* (PRE). **2530** (Lydenburg): De Berg (–AA), *Crouch 756* (NH); farm Kwagershoek near Lydenburg (–AB), *Obermeyer* in herb. Tvl. Mus. *28073* (PRE); between Lydenburg and Schoemanskloof (–AB/AD), *Van Balen s.n.* (PRE); 5 miles [8 km] N of Dullstroom (–AC), *Reynolds 5772* (PRE); between Belfast and Dullstroom, *Harding 7* (PRE); Mount Anderson (–BA), *Smuts & Gillett 2440* (PRE); Belfast (–CA), *Strey 3208* (PRE); *Williams s.n.* (K, MO, PRE); Machadodorp (–CB), *Galpin 12961* (PRE); 1 mile [1.6 km] E of Sewefontein (–CC), *Codd 8089* (BM, K, PRE). **2531** (Komatipoort): Barberton District (–CC), *Thornicroft* in Nat. Herb. *15228* (PRE). **2629** (Bethal): Breyton (–BD), *Steyn* sub NBG *1350/49* (NBG); Spitskop, Ermelo, *Pott-Leendertz 5256* (PRE); Ermelo (–DB), *Burt Davy 2191* (PRE); *Collins s.n.* (PRE); *Scholars 183* (PRE); *Steyn 841* (NBG); *Swart s.n.* (PRE); Nooitgedacht, *Potter 1470* (PRE). **2630** (Carolina): near Carolina (–AA), *Bolus 12367* (BOL, K); Oshoek (–BB), *Devenish 220* (PRE); Mavariestad (–CA), *Pott-Leendertz 5169* (PRE); Amsterdam (–DA), *Van der Merwe 1058* (PRE); Iswepi (–DC), *Sidey s.n.* (K, PRE). **2729** (Volksrust): Volksrust (–BD), *Jenkins* in herb. Tvl. Mus. *10038* (PRE). **2730** (Vryheid): Wakkerstroom (–AC), *Roberts* in herb. Tvl. Mus. *12772* (PRE); Groenvlei, Balele Mountain Lodge (–CA), *Ngwenya 1746* (NH); Fairbreeze farm, Bandalabathwa Hill, Benva (–CC), *Ngwenya 1195* (NH).

FREE STATE. **2828** (Bethlehem): near Elands River at foot of Mont-aux-Sources (–BD/DB), *Flanagan 1830* (BOL); Golden Gate National Park (–DA), *Liebenberg 7313* (K, PRE). **2829** (Harrismith): Harrismith (–AC), *Sankey 307* (K). **2927** (Maseru): farm Sgravenhage, Modderpoort (–AB), *Fawkes* sub NBG *449/37* (NBG).

KWAZULU-NATAL. **2729** (Volksrust): Newcastle District, Ncandu Reserve (–DC), *Ngwenya 1653* (NH); farm Union, Newcastle (–DD), *Guy & Ward 1* (PRE). **2730** (Vryheid): Utrecht (–CB), *Van der Merwe 11* (PRE); Vryheid (–DD), *Galpin 10036* (PRE). **2828** (Bethlehem): Mont-aux-Sources (–DD), *Schweickerdt 792* (PRE). **2829** (Harrismith): Cathedral Peak (–CC), *Killick 1161* (K, PRE). **2830** (Dundee): Draycott Hill, Weenen (–CC), *Acocks 10778* (NH, PRE); Jameson Drift (–DD), *Strey 9312* (K, NH, PRE). **2929** (Underberg): Giants Castle (–AD), *Symons 113* (PRE); *Trauseld 709* (PRE); Tabamhlope (–BA), *Medley Wood ex Wylie 10762* (NH); 10 miles [16 km] SE of Estcourt (–BB), *Dyer 4863* (PRE); farm Farleigh, Estcourt, *Plowes 2385* (NH, PRE); Estcourt, *Werdermann & Oberdieck 1228* (PRE); Impendle District (–DD), *Levett 26* (NH). **2930** (Pietermaritzburg): Estcourt, Griffins Hill (–AA), *Green 285* (NH); Greenwich farm, Rietvlei (–AB), *Fry* in herb. *Galpin 2708* (PRE);

Greytown (–BA), *Handley* sub NBG 161/50 (MO, NBG, PRE); *Ledeboer s.n.* (K, PRE). **3029** (Kokstad): Mount Currie Nature Reserve (–AD), *Abbott 6840* (NH); beyond Kokstad near Mt. Currie (–AD/CB), *Hutchinson 1812* (BOL, K, PRE); Kokstad (–CB), *Sister Mildred 70* (NBG); farm Westlands, Kokstad, *Scott s.n.* (NBG); near Kokstad, *Tyson 1673* (BOL, SAM).

ESWATINI. **2631** (Mbabane): Dalriach (–AC), *Compton 28571* (NBG); Ukutula, *Compton 28479* (NBG). **2632** (Bela Vista): farm Mlawula, Lebombo mountains (–AC), *Culverwell 559* (PRE).

LESOTHO. **2828** (Bethlehem): Leribe (–CC), *Dieterlen 509* (NH, PRE, SAM). **2927** (Maseru): near St. Agnes' Mission, Teyateyaneng (–BB), *Trewren 814* (PRE). **2928** (Marakabei): on road from Thaba-Tseka to Mokhotlong, on hills W of Semena River (–DA), *Harrower 1908* (NBG).

Inexact localities: Tugela valley, *Allison s.n.* (K); Natal [KwaZulu-Natal], *Dunne s.n.* (BM); *Cooper 3231* (K); Upper Moodies, Barberton, *Hayden* in herb. Galpin *1183* (BOL, K, SAM); Weenen Country, Natal [KwaZulu-Natal], *Medley Wood 910* (BM, BOL, MO, SAM); Bushmans River, *Medley Wood 10762* (MO); near Mooi River, *Medley Wood 3443* (K); zwischen Greytown und Newcastle, *Wilms 2298* (BM, K).

5

Haemanthus albiflos*Jacq.*

Haemanthus albiflos *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 1: 31, t. 59 (1797). *Haemanthus virescens* var. *albiflos* (Jacq.) Herb.: 235 (1837) Type: South Africa, Cape of Good Hope, illustration in Jacquin: t. 59 (1797), lecto., designated by Friis & Nordal: 69 (1976).

Haemanthus virescens var. *pubescens* Herb.: 235 (1837) [non *H. pubescens* L.f.]. *Haemanthus albiflos* var. *pubescens* (Herb.) Baker: 68 (1888). Type: South Africa, without precise locality or collector, illustration in Ker Gawler in Edwards's Botanical Register 5: t. 382 (1819), lecto., designated here [a good match with the protologue and cited therein].

Haemanthus virescens Herb.: 235 (1837). Type: South Africa, precise locality not known, neither an illustration nor a collector specified.

Haemanthus virescens var. *intermedius* Herb.: 235 (1837). *Haemanthus intermedius* (Herb.) M.Roem.: 36 (1847). Type: South Africa, without precise locality or collector, illustration in Ker Gawler in Curtis's Botanical Magazine 31: t. 1239 (1809) [1810], lecto., designated here [cited in the protologue].

Haemanthus leucanthus Miq.: 33 (1861). Type: South Africa, Cape Province, without precise locality or collector, cultivated in Hort. Bot. Utrecht, probably lost.

Haemanthus albomaculatus Baker: 202 (1878c). Type: South Africa, without precise locality, ex hort. Henderson s.n. (K, holo!).

Haemanthus albiflos var. *brachyphyllus* Baker: 68 (1888). Type: South Africa, [Eastern Cape], Com-madagga, Somerset division, *Burchell s.n.* [K, lecto.!, designated by Friis & Nordal: 69 (1976)].

Haemanthus albiflos var. *burchellii* Baker: 68 (1888). Type: South Africa, [Eastern Cape], Graaff-Reinet, between Milk River and Platte River, *Burchell 2955* [K, lecto.!, designated by Friis & Nordal: 69 (1976)].

[*Leucodesmis pubescens* sensu Raf.: 19 (1838), non *L. pubescens* (L.f.) Raf.]

[*Haemanthus pubescens* sensu Salisb.: 130 (1866), non *H. pubescens* L.f.]

[*Diaclis ciliaris* Salisb.: 130 (1866), *nom. nud.*, invalid name without description.]

Plants evergreen, up to 375 mm high when flowering. *Bulb* solitary or in clumps, ovoid, up to 80 mm diam., ± round in cross section or compressed towards distichous leaf arrangement; tunics with horizontal edges, equal or slightly tiered, often partially exposed then turning green; outermost tunics occasionally dark brown and papery. *Leaves* 2, 4 or 6, erect, spreading or prostrate, 2 newest leaves preceding

inflorescence, blade oblong or elliptic, (40–)90–400(–500) × 25–115 mm, plane or channelled, both surfaces pale or dark green, immaculate or occasionally white-spotted, glabrous or pubescent sometimes only abaxially or adaxially, margin densely to sparsely ciliate, rarely smooth, apex obtuse or subacute. *Scape* stout or slender, suberect to spreading, 50–350 × 5–14 mm, green, immaculate, glabrous or pubescent. *Spathe bracts* 4–8, erect, held somewhat apart, shorter or rarely ± longer than flowers, broadly triangular-ovate, 18–40 × 6–30 mm, narrowed towards tips, white with green veins, somewhat leathery, fringed with retrorse hairs, rarely smooth. *Inflorescence* compact, narrowly obconical to obovoid, 25–70 mm across. *Flowers* 25–50, erect; pedicel 1–10 mm long, green; perigone narrowly funnelform, 16–23 mm long, white; tube usually ± swollen midway, 4–7 mm long; tepals standing ± apart, narrowly oblong, 10–18 × 1.0–2.5 mm, tips subacute to obtuse. *Stamens* exerted by up to 9 mm; filaments white; anthers 1–2 mm long, yellow to orange. *Ovary* 2–3 mm diam., green. Style as long as stamens. *Berry* ovoid, ± 10 mm diam., fleshy, pale orange or bright red. *Seeds* ovoid, ± 5 mm diam., ivory-white. *Flowering time*: January to October, peaking between April and August. Figure 17.

Distribution and habitat: *Haemanthus albiflos* is widespread along the east coast of South Africa, from slightly inland near Nkandla, KwaZulu-Natal, in the north to Still Bay on the Agulhas plain, Western Cape, in the south and further inland as far as Graaff-Reinet and Komani within the greater Great Fish River basin, Eastern Cape (Figure 18). Populations occupy loose loamy soils, often among rocks, in semi-shade on forest margins or in riverine and coastal scrub, as well as in full sun in thicket, always protected from fire and free of frost. The rainfall in the area is spread throughout the year, varying from approximately 1 100 mm in the north to 500 mm in the south.

Diagnosis: Based on shared vegetative and floral morphology, *H. albiflos* belongs within a small, closely allied group that includes *H. deformis* and *H. pauculifolius*. All three species are easily distinguishable by an evergreen or near-evergreen habit, upright white, green-veined to green, mostly ciliate spathe bracts, and pure white, narrowly funnelform flowers. *Haemanthus albiflos*, the most widespread and variable species within the group, is recognised by triangular-ovate spathe bracts that are consistently narrowed towards the tips. The bracts stand slightly apart, leaving the flowers half exposed distally. This contrasts with the broad, closely overlapping, blunt spathe bracts of *H. deformis* that fully embrace the flowers, and the narrow, oblong-lanceolate spathe bracts in the slender flower heads of *H. pauculifolius*, which overlap for more than half their length. The floral dimensions also differ, with the perigone of *H. albiflos* invariably being the shortest within the group: 16–23 mm for *H. albiflos* versus ± 30 mm for *H. deformis* and 25–35 mm for *H. pauculifolius*. Other features that separate *H. deformis* and *H. pauculifolius* from *H. albiflos* are discussed separately under the former two species.

Discussion: The number, size and hairiness of the leaves varies considerably across the distribution range. In KwaZulu-Natal the leaves usually persist for two or three years so that each bulb has four or six leaves at a time. The leaves are suberect or spreading, obtuse apically and glabrous, but with a fringed margin, either of several rows of hairs or only a few scattered hairs towards the apex.



Figure 17. *Haemanthus albigiflos*. A, habit within sunny habitat; B, habit within shaded riverine habitat; C, mature berries. Photographs: A, John Manning; B, C, Colin Paterson-Jones.

In more open habitats in Eastern and Western Cape, the leaves usually die back more quickly so that each bulb has only one or two leaf pairs at a time, which are spreading to prostrate and usually somewhat acute apically. The leaves show considerable variation in the degree of pubescence, particularly in populations on the coast between Port Alfred and Mossel Bay, and inland from Gqeberha to Graaff-Reinet and Fort Beaufort, largely within the Albany Thicket Biome. Here, local races have been seen with leaves densely pubescent on both surfaces, suggestive of xeric-adapted morphology, or with either the abaxial or adaxial surface entirely or partially pubescent, or with both surfaces glabrous and often only the margin ciliate. Baker (1888, 1896) recognised these forms as distinct varieties. Nevertheless, since the entire range from hairy to glabrous forms exist within a very small area, these varieties are no longer upheld.

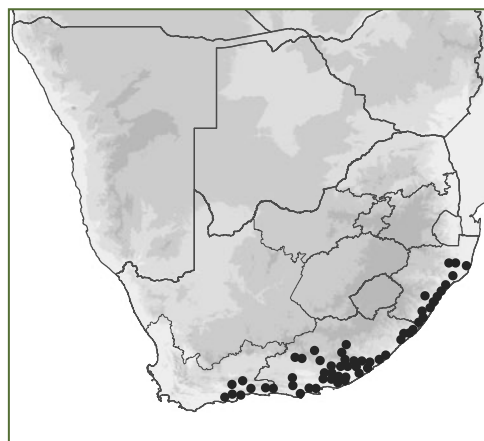


Figure 18. Distribution of *Haemanthus albiflos*.

Another curiously variable character is the occasional presence of white spots on the leaves in specimens gathered in KwaZulu-Natal at Ngoye Forest and between Durban and Port Edward. Baker (1878c) described these plants as *H. albomaculatus* but given the sporadic occurrence of this feature the name is treated as a synonym for *H. albiflos*.

Haemanthus albiflos has a notably long flowering period, from January to October with a peak between April and August. Thus, by occupying equable, frost-free habitats, such as those along the southern and eastern seaboard, *H. albiflos* can benefit from pollinator activity almost year-round.

Nomenclatural note: In several publications (Ker Gawler 1809, 1819; Lindley 1826), plants of *H. albiflos* were misidentified as *H. pubescens* L.f., an error that appears to be due to the comparison of hairy-leaved specimens of *H. albiflos* with a sterile specimen of *H. pubescens* in the Banks herbarium, British Museum (*Masson s.n.*, BM!). Examination of the lectotype of *H. pubescens* (*Thunberg s.n.*, sheet 7927 in Herb. Thunb., UPS!), which has both vegetative and floral parts, leaves no doubt that Ker Gawler's application of the name was incorrect.

Specimens examined

SOUTH AFRICA. KWAZULU-NATAL. **2831** (Nkandla): Hlabisa (–BB), *Feely & Ward 38* (K, PRE); *Harrison s.n.* (K, PRE); Hluhluwe Game Reserve, *Ward 2347* (PRE); Ngoye Forest (–DC), *Crouch 804* (NH); *NBG Expedition 268176* (NBG); *Ross 2125* (K, NH, PRE). **2832** (Mtubatuba): St Lucia system, The Coves (–AD), *Feely & Ward 38* (NH). **2930** (Pietermaritzburg): Pietermaritzburg (–CB), *Carnegie* sub NBG 209/30 (NBG); Isipingo, *Forbes & Obermeyer 53* (NH, PRE); Krantzklouf Nature Reserve (–DD), *Moll 3316* (PRE). **2931** (Stanger): Tugela River Bridge (–AB), *Pole Evans s.n.* (PRE 36934); Umhlali (–AD), *Meeuse s.n.* (PRE); Mount Moreland (–CA), *Medley*

Wood 1006 (K, NH); Salisbury Island (–CC), *Galpin 11865* (PRE); Happy Valley, Durban, *Huntley 20* (MO, NH); near Durban, *Medley Wood 496* (BM, SAM); *Medley Wood 1989* (K, NH); *Thorp* sub NBG 102/37 (NBG); *Warren ex Thorns* sub NBG 517/66 (NBG). **3030** (Port Shepstone): Ifafa (–AD), *Rudatis 665* (BM, PRE); *Rudatis 669* (E, K); Umbogintwini (–BB), *Begley s.n.* (PRE 36921); Nongwana Falls, *Begley s.n.* (PRE 39397); Isipingo Beach, *Gouws* sub NBG 535/64 (NBG); *Ward 914* (PRE); *Warner 914* (PRE); Warner Beach, *Strey 8803* (NH, PRE); 11 km S of Umtamvuna bridge (–CC), *Roux 90* (NBG); Margate coast (–CD), *Cohen s.n.* (NBG). **3130** (Port Edward): Umtamvuna Forest Reserve (–AA), *Strey 9884* (NH, PRE).

EASTERN CAPE. **3126** (Komani): Finchams Nek (–DD), *Galpin 1886* (BOL, GRA, K, PRE). **3129** (Port St. Johns): Magwa Falls (–BC), *Strey 6719* (NH, PRE); Msikabariviermond (–BD), *Venter 1037* (PRE); near Port St. Johns (–DA), *Bayliss BS7067* (K, MO); *Prance s.n.* (NBG). **3224** (Graaff-Reinet): Graaff-Reinet (–BC), *Bolus 85* (BOL, K); *Sister Francis 53* (BOL); between Milk River and Platte River, Graaff-Reinet (–BD), *Burchell 2955* (K); farm Wheatlands, Kendrew (–DB), *Parkes s.n.* (NBG). **3225** (Somerset East): Cradock (–AB), *Muller 696* (PRE); *Rogers s.n.* (MO); Somerset East (–DA), *Marloth 7033* (PRE). **3226** (Fort Beaufort): Katberg Pass (–BC), *Hardick 42* (MO, NBG); just N of farm La Motte (–CC), *Snijman 475* (NBG, PRE); Brambledene, Menziesberg (–DB), *Acoks 1114* (K, PRE); Hogsback Forest Reserve, *Dahlstrand 2935* (GRA, STE); 56 km from Grahamstown [Makhanda] towards Fort Beaufort via Fort Brown (–DC), *Snijman 477* (NBG); Sandile's Kop (–DD), *Giffen s.n.* (PRE). **3227** (Stutterheim): Pirie Forest (–CB), *Martin* sub NBG 393/38 (NBG); Mount Coke (–CD), *Compton 17005* (NBG); King William's Town [Qonce], *Sim 1846* (PRE); Kei road (–DA), *Comins 1551* (PRE); near Komgha (–DB), *Flanagan 1297* (PRE, SAM); Bonza Bay (–DD), *Nichol s.n.* (NBG); Nahoon Valley, *Pamphlett 23* (NBG). **3228** (Butterworth): Mazeppa Bay, Transkei (–BD), *Godfrey s.n.* (BOL); Qoloka Mouth (–CB), *NBG Expedition 334/73* (NBG); Kei Mouth, *Roux 540* (NBG); Kentani, *Pegler 852* (BOL). **3323** (Willowmore): Witels River, Tsitsikamma Coastal National Park (–DC), *Roux 307* (MO, NBG, PRE); Helpmekaar River, *Roux 309* (NBG). **3324** (Steytlerville): farm Marzyl, NE of Steytlerville (–AD), *Paterson s.n.* (NBG); Enkeldoorn track, Baviaanskloof (–CB), *Snijman 330* (NBG). **3325** (Gqeberha): Commadagga (–BB), *Burchell 3348* (K); *Snijman 467* (PRE); *Snijman 468* (NBG); Suurberg Pass (–BD), *Snijman 486* (NBG); Van Staden's Nature Reserve (–CC), *Dahlstrand 3191* (PRE); Uitenhage [Kariega] (–CD), *Zeyher 967* (BM, K); Fairview Golf Course, Port Elizabeth [Gqeberha] (–DC), *Long 963* (GRA, K, PRE); Redhouse, *Paterson 673a* (GRA). **3326** (Makhanda): Riet River, Grahamstown [Makhanda] (–AA), *White 44* (GRA, SAM); Alicedale (–AC), *Cruden 223* (GRA); Coldspring (–AD), *Glass 523* (GRA); 15 miles [24 km] S of Grahamstown [Makhanda], *Stayner s.n.* (NBG); Hopewell, Bathurst (–BD), *Acoks 18380* (PRE); Alexandria (–CB), *Galpin 10796* (PRE); Port Alfred (–DB), *Becker s.n.* (GRA); *Heny s.n.* (GRA, PRE); *Tyson 17546* (PRE); *Tyson s.n.* (GRA, PRE); near Kowie, *Tyson s.n.* (BOL). **3327** (Peddie): Ebb-and-Flow (–AB), *Comins 1507* (PRE); East London (–BB), *Barker* sub NBG 1109/35 (NBG); *Bokelmann s.n.* (NBG); *Carter* sub NBG 91/30 (NBG). **3424** (Humansdorp): Kabeljouws (–BB), *Fourcade 3352* (STE). **3425** (Skoenmakerskop): Sea View, SW of Port Elizabeth [Gqeberha] (–AB), *Snijman 499* (NBG).

WESTERN CAPE. **3321** (Ladismith): Huis River Gorge (–DA), *Bruyns 2223* (NBG). **3322** (Oudtshoorn): Oudtshoorn (–CA), *Deas* sub NBG 221/15 (BOL); Groenkop, Swarttrivier (–DC), *Van Daalen 162* (PRE). **3323** (Willowmore): Deepwalls, Knysna (–CC), *Phillips 18443* (BOL). **3421** (Riversdale): 3.5 km N of Still Bay (–AD), *Burgers 2162* (NBG); Kaffirkuils River near mouth, *Muir 186* (BOL, PRE); Albertinia (–BA), *Muir 2162* (PRE). **3422** (Mossel Bay): W of Great Brak, 0.5 km N of national road (–AA), *Bayer s.n.* (NBG). **3423** (Knysna): Knysna (–AA), *Denman 36* (NBG); Plettenberg Bay (–AB), *Van Jaarsveld 3275* (NBG); *Van Niekerk s.n.* (BOL 26233).

Inexact localities: Pondoland, *Bachmann 293* (K); South Africa, *Ecklon & Zeyher s.n.* (MO); Ifafatal, *Rudatis 1426* (BM, E, K); Bester's Hoek near Somerset East, *Scott Elliot 501* (E); Cape, *Villete s.n.* (K); zwischen Pietermaritzburg und Greytown, *Wilms 2323* (BM, K); Natal [KwaZulu-Natal], *Medley Wood 1935* (E).

6

Haemanthus deformis*Hook.f.*

Haemanthus deformis Hook.f. in Curtis's Botanical Magazine 97: t. 5903 (1871); Baker: 69 (1888); Baker: 236 (1896). Type: South Africa, Natal [KwaZulu-Natal], without precise locality or collector, illustration in Hook.f. in Curtis's Botanical Magazine 97: t. 5903 (1871), lecto., designated by Snijman: 64 (1984), [specimen *McKen s.n.* probably lost *fide* Friis & Nordal: 69 (1976), neither at K nor NH].

Haemanthus baurii Anon: 813 (1885); Baker: 69 (1888); Baker: 236 (1896). Type: South Africa, [Eastern Cape], Griqualand East, Shawbury, close to Tsitsa Falls, *Baur 231* [K, lecto.!, designated by Friis & Nordal: 69 (1976)].

Haemanthus mackenii Baker: 69 (1888); Baker: 237 (1896). Type: South Africa, Natal [KwaZulu-Natal], without precise locality, illustration of a plant received originally from McKen and which flowered for Mr Bull [William Bull] in Nov. 1870 [K, lecto.!, designated by Snijman: 64 (1984); original specimen probably lost *fide* Friis & Nordal: 60 (1976)].

Plants evergreen, up to ± 100 mm when flowering. *Bulb* solitary or in clumps, ovoid, up to 100 mm diam., compressed towards distichous leaf arrangement; tunics $\pm$ evenly thick with horizontal edges, $\pm$ equal in height, if partially exposed, then turning green. *Leaves* 2 or 4, appressed to the ground, persisting mostly for two seasons, older leaf pair contemporaneous with inflorescence, young leaves appearing shortly after, blade broadly oblong, $\pm$ as long as broad or sometimes broader than long, 80–260 $\times$ 70–250 mm, thick and flat, immaculate, entirely glabrous or densely pubescent on abaxial or adaxial surface, margin ciliate, apex blunt. *Scape* erect, arising between leaves of previous season, short, strongly compressed, $< 60 \times 6$ –15 mm, green, glabrous or pubescent. *Spathe bracts* 6 or 7, erect and overlapping, $\pm$ as long as flowers, slightly recurved at tips, oblong to $\pm$ spatulate, 30–60 $\times$ 12–45 mm, apex broad and blunt, white, sometimes with sparse green veining, firm and leathery, margins ciliate. *Inflorescence* compact cyathiform, somewhat compressed, 45–70 mm across. *Flowers* 25–45, erect; pedicel 1–7 mm long, green; perigone narrowly funnelliform, 30–31 mm long, white; tube 7.5–9.0 mm long, widening slightly upwards; tepals suberect, narrowly oblong, 21.0–23.5 $\times$ 1–2 mm, tips subacute to obtuse. *Stamens* exserted by up to 10 mm; filaments white; anthers ± 2 mm long, golden yellow. *Ovary* 2.5–3.0 mm diam., green. *Style* as long as stamens. *Berry* ovoid, ± 15 mm diam., fleshy, orange to bright red. *Seeds* ovoid, ± 5 mm diam., ivory-white. *Flowering time*: May to October. Figure 19.

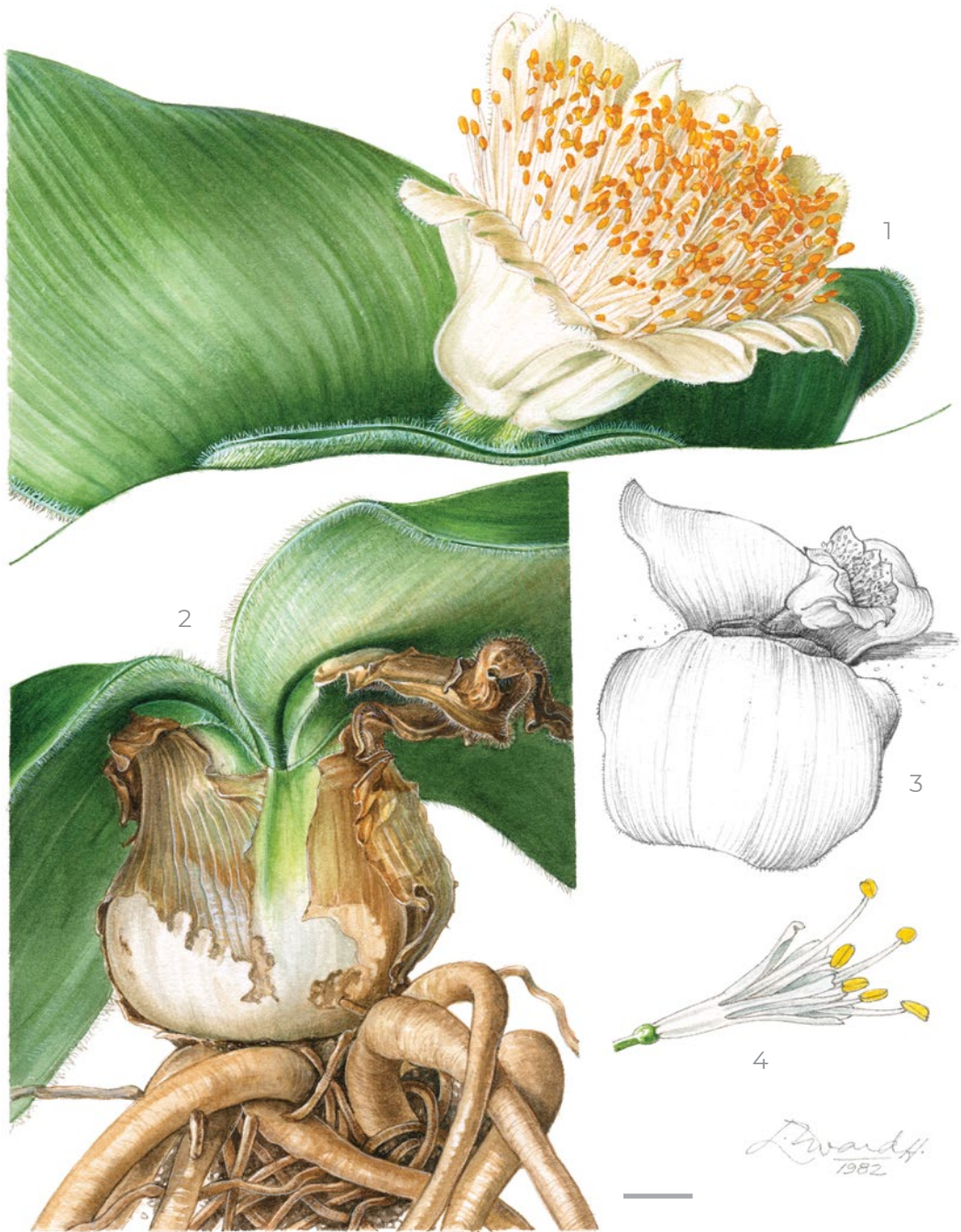


Figure 19. *Haemanthus deformis*. 1, inflorescence and leaves; 2, bulb; 3, habit; 4, flower. Perry 1719 (NBG), near Hela-Hela. Artist: Ellaphie Ward-Hilhorst. Scale bar: habit sketch = 30 mm; bulb and floral details = 12 mm.

Distribution and habitat: Localised populations of *H. deformis* are found in the eastern midlands and coastal forelands of South Africa from the vicinity of Rorke's Drift, KwaZulu-Natal, to the Tsitsa River in northern Eastern Cape, at elevations of 300–1 000 m above sea level (Figure 20). Populations occupy sheltered sites under bushes or on moist rocky banks, often on grassy slopes along broad river valleys where they are periodically exposed to fire.

Diagnosis: *Haemanthus deformis*, together with its close allies *H. albiflos* and *H. pauculifolius*, are the only truly evergreen species in the genus. The habit of *H. deformis* is most unusual, accounting for J.D. Hooker's choice of epithet. The scape is strongly compressed, more so than in any other species of *Haemanthus*, which allows it to push through the tight, narrow gap between the stiff, green leaves of the previous season, finally reaching ± 60 mm above ground. The flower head is especially well protected by 6 or 7, broad, overlapping spathe bracts that are characteristically blunt and eventually apically recurved. The spathe bracts, like the flowers, are white, but the bracts may occasionally have green veins. The current season's leaves appear shortly after anthesis, in a position adjacent to the scape and often after it has withered. The newly emergent leaves are especially thick and fleshy, and become firmly pressed on the ground. When mature the leaves are broadly oblong (70–250 mm wide) and more or less as long as wide. In contrast, the flowering phenology of *H. albiflos* has the newest leaf pair well established before the inflorescence first appears. Thus, the scape characteristically slants outwards below the current season's leaf pair, with the flower head itself held erect.

Discussion: Friis and Nordal (1976) included *H. deformis* in their *H. albiflos* complex on the assumption that specimens bearing this name were merely depauperate forms of *H. albiflos*. Mature bulbs in cultivation at Kirstenbosch National Botanical Garden, however, confirmed that their compact habit remains constant over time. While flowering, the scape remains consistently short, and only lengthens slightly when fruiting. The plants vary considerably in pubescence. Thus, the leaves and scape range from entirely glabrous to densely hairy. From the limited material available no clear trends are evident for this feature.

Bulbs were sent to the Royal Botanic Gardens, Kew, as early as 1869, by McKen of the Botanic Garden Durban and a few years later by Rev. Baur from within Eastern Cape. Both collectors are commemorated in the names *H. mackenii* and *H. baurii*, now treated as synonyms of *H. deformis*.

Specimens examined

SOUTH AFRICA. KWAZULU-NATAL. **2930** (Pietermaritzburg): 2 miles [3.2 km] ENE of Bayne's Drift (–BC), Acocks 13775 (PRE); Noodsberg, Appelbos (–BD), Strey 6029 (PRE); near Hela Hela along road from Ulufafa

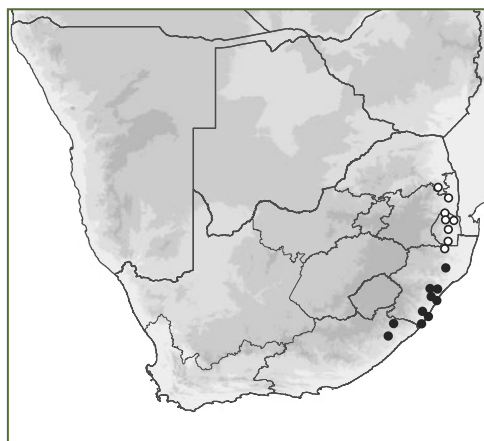


Figure 20. Distribution of *Haemanthus deformis* (●); *H. pauculifolius* (○).

(–CC), *Perry 1719* (NBG); Elsinore farm, Hope Valley Nature Reserve, (–DC), *Sikhakhane 447* (NH, PRE); Mariannhill (–DD), *Marloth 7413* (PRE). **3030** (Port Shepstone): Kunanata, 7 miles [11.2 km] E of Highflats (–AC), *Strey 4416* (NH, PRE); 5 km W of Umzumbi (–CB), *Van Jaarsveld 5733* (NBG); Gundrift (–CC), *Strey 8709* (K, NH, PRE).

EASTERN CAPE. **3028** (Matatiele): Mount Frere (–DD), *Sim 1845* (PRE). **3128** (Mthatha): Shawbury, close to Tsitsa Falls (–BB/BD), *Baur 231* (K).

Dubious locality: Nama’land, Richtersveld, *SUG 3700* (BOL).

7

Haemanthus pauculifolius*Snijman & A.E. van Wyk*

Haemanthus pauculifolius *Snijman & A.E. van Wyk* in South African Journal of Botany 59(2): 247 (1993). Type: South Africa, Transvaal [Mpumalanga], Blyderivierspoort Nature Reserve, Swadini area, kloof just N of the confluence of the Ohrigstad and Blyde Rivers, 24 May 1989, W.S. Matthews 624 (NBG, holo.!, K!, MO!, PRE!, iso.).

Plants evergreen, up to 150 mm high when flowering. *Bulb* solitary or clustered, frequently forming bulblets, ovoid, $\pm$ exposed above ground, up to 47 mm diam., somewhat compressed; tunics fleshy, green when exposed, becoming papery and dark brown when old. *Leaf* mostly solitary except when the new leaf of current season and ageing leaf of previous season overlap briefly in late autumn, recurved, blade narrowly lanceolate, $70\text{--}325 \times 25\text{--}35$ mm, somewhat canaliculate, pale green, immaculate, velutinous on both surfaces, margin densely ciliate. *Scape* adjacent to adaxial surface of new leaf, suberect, compressed, $50\text{--}190 \times 5\text{--}7$ mm, pale green, immaculate, covered with white patent hairs. *Spathe bracts* 4 or 5, erect, closely overlapping for at least half their length, slightly shorter than flowers, oblong-lanceolate, $25\text{--}35 \times 5\text{--}13$ mm, firm, leathery, pale green, edged with white, pubescent or smooth abaxially, $\pm$ fringed with retrorse hairs. *Inflorescence* compact, compressed, 15–30 mm wide. *Flowers* 8–19, erect; pedicels 1–3 mm long; perigone narrowly funnelform, 25–35 mm long, pure white; tube narrow, 10–13 mm long; tepals suberect, narrowly lanceolate, $17\text{--}20 \times 3\text{--}4$ mm. *Stamens* exerted by up to 7 mm; filaments white; anthers 2.5 mm long, yellow. *Ovary* 2–3 mm across, green. *Style* $\pm$ as long as stamens. *Berry* spheroidal, 10–15 mm diam., fleshy, orange to bright red. *Seeds* ovoid, $\pm 8 \times 10$ mm, ivory-white, lustrous. *Flowering time*: late May until July. Figure 21.

Distribution and habitat: *Haemanthus pauculifolius* is endemic to the species-rich montane region encompassing the Limpopo-Mpumalanga-Eswatini Escarpment (Clark et al. 2022). Localised populations are known mainly from steep rocky gorges along deeply incised valleys that stretch from Blyderivierspoort to the Barberton mountainlands of Mpumalanga and western Eswatini, southwards to the Pongola River in northwestern KwaZulu-Natal (Figure 20). When first described in 1993, *H. pauculifolius* was thought to be endemic to Mpumalanga, but recent records confirm that the species is much more widely distributed.

Populations vary in size from a few hundred bulbs to dense colonies of several thousand plants, which are no doubt largely clonal due to the ready production of bulblets. In summer the habitats are hot and relatively dry, with somewhat cooler dry conditions in winter. The bulbs grow in humus-rich



Figure 21. *Haemanthus paucifolius*. 1, bulb, leaf and infructescence with immature berries; 2, 3, inflorescences; 4, mature berries; 5, detail of flower. Van Wyk 8703 (NBG), Blyderivierspoort Nature Reserve. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–4 = 12 mm; 5 = 6 mm.

soil, in shade and semi-shade under weakly developed gallery bush or arid bushveld, in the transition between kloof forest and open rock ledges, where they are protected from fire and frost. The associated plant community at the type locality is heterogeneous and has a marked succulent component, including species of *Aloe* L. (Asphodelaceae), *Euphorbia* L. (Euphorbiaceae), *Pachypodium* Lindl. (Apocynaceae), *Portulacaria* Jacq. (Didiereaceae) and *Dracaena* Vand. ex L. (Asparagaceae).

Diagnosis: *Haemanthus pauculifolius*, together with *H. albiflos* and *H. deformis*, form a closely related group defined by an evergreen habit, upright white to green-veined, mostly ciliate spathe bracts and pure white flowers. *Haemanthus pauculifolius* most closely resembles *H. albiflos* in leaf shape and inflorescence habit, however, the two species differ in vegetative phenology and floral dimensions.

For most of the year *H. pauculifolius* is solitary-leaved, except for a short period in autumn when the senescing leaf of the previous season and the new leaf of the current season briefly overlap. *Haemanthus albiflos*, in contrast, has at least two or typically four or six leaves at any time. Furthermore, *H. pauculifolius* has few flowers (8–19) per inflorescence, and the flower head is slender (15–30 mm across), unlike the floriferous (25–50 flowers), fuller inflorescence of *H. albiflos* (25–70 mm across). The flowers of *H. pauculifolius* have a notably longer perigone and tube than those of *H. albiflos* (25–35 mm and 10–13 mm long versus 16–23 mm and 4–7 mm long, respectively).

Haemanthus pauculifolius is most like the pubescent plants of *H. albiflos* from semi-arid thicket within the Eastern Cape, as opposed to plants from the northern KwaZulu-Natal populations, which are glabrous-leaved, apart from a fringed margin.

Specimens examined

SOUTH AFRICA. MPUMALANGA. **2430** (Pilgrim's Rest): Blyderivierspoort Nature Reserve, Swadini area, just N of the confluence of the Ohrigstad and Blyde Rivers (–DB), *W.S. Matthews 624* (K, MO, NBG, PRE); *A.E. van Wyk 8703* (NBG, PRU); Blyderivierspoort Nature Reserve, Swadini area, along peninsula trail, *W.S. Matthews 625* (NBG). **2531** (Komatipoort): farm Brommers 370 JU, along hiking trail Mvoti (–CC), *Archer, Reid & De Sousa 1070* (NBG, PRE).

KWAZULU-NATAL. **2731** (Louwsburg): Vryheid: Coronation farm 2 of Schurwerant 9640, N of Coronation on the Bivane River (–CA), *Jacobsen 5515* (PRE); Coronation, Paris Dam site, *Crouch 831* (NH); *Symonds 3* (NH).

ESWATINI. **2631** (Mbabane): northern slopes of Komati River, E of bridge on main Pigg's Peak–Mbabane road (–AA), *Deall 4004* (NBG).

Inexact locality: mountains near Barberton, *Onderstall 1236* (PRE); Swaziland [Eswatini], *L.M. Mason sub hort. Bot. Reg. Edin. 673013* (E).

Subg. *Haemanthus*

Plants deciduous. *Bulb* obclavate or pyriform, often narrowed into a slender neck, round in cross section or compressed crosswise to distichous leaves; tunics in at least eight pairs at maturity, dying back horizontally then uniseriate and usually tiered or dying down obliquely in two opposite series, sometimes pinkish if exposed to light. *Leaves* hysteranthous, 1 or 2(3), concolorous or abaxial surface often flushed reddish near base or barred and speckled reddish brown or darker green. *Scape* pink, wine-red or bright red, often maculate, glabrous or rarely sparsely pubescent. *Spathe bracts* spreading or erect, shorter to longer than flowers, membranous, leathery or stiff and fleshy, pale to dark pink or red. *Inflorescence* spreading or compact. *Flowers* spreading or clustered and erect; pedicel (0.5–)3.0–20.0(–35.0) mm long, shorter than perigone, firm; perigone widely to narrowly funnelform or cylindric, $\pm$ (6–)14–25(–30) mm long, pale to dark pink or red, concolorous or often white-tipped; tube smooth, widening slightly to throat or cylindrical and shallowly grooved below tepal sinuses and gibbose at base of each tepal, 0.5–6.0(–9.0) mm long; tepals longer than tube, narrowly lanceolate or oblong, often gibbose at base and swollen at tip. *Stamens* longer than tepals. *Style* $\pm$ as long as stamens or rarely longer. *Berry* pink, red or whitish and translucent; walls soft, often copiously mucilaginous when ripe, rarely leathery. *Seeds* wine-red or brownish red, green within; embryo green.

Species 18: winter-rainfall and nonseasonal rainfall regions of southern Africa.



8

Haemanthus amarylloides*Jacq.*

Haemanthus amarylloides *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 4: 5, t. 408 (1804); *Herbert*: 233 (1837) [as *H. amaryllidioides*]. *Amaryllis haemanthoidea* *Tratt.*: 38 (1821), nom. illeg. superfl. Type: South Africa, Cape of Good Hope, illustration in *Jacqu*: t. 408 (1804), lecto., designated by Bjørnstad & Friis: 192 (1972).

Plants deciduous, green in winter, up to 250 mm high when flowering. *Bulb* solitary, pyriform to globose, $\pm$ round in cross section or slightly compressed, 30–75 mm diam., tunics unequal, imbricate, mostly with oblique or rarely horizontal margins, cream-coloured, withered parts sometimes persisting, brown. *Leaves* hysteranthous, 2(3), prostrate, spreading or erect, blade narrowly to broadly ligulate or oblong-lanceolate to elliptic 40–250(–340) $\times$ (8–)10–120 mm, plane, flexible or stiff or thick and firm, immaculate, abaxial surface blushed reddish proximally or not, glabrous, margin sometimes thickened, either green, yellowish green or red, smooth or rarely crenulate with minute rough papillae, apex obtuse or subacute. *Scape* slender to stout, 50–200 $\times$ 5–12 mm, pinkish cream-coloured to deep rose-pink or reddish pink, immaculate, glabrous or densely covered with minute, retrorse, $\pm$ rough hairs. *Spathe bracts* 4–9, spreading apart, shorter than or as long as flowers, triangular, (15–)20–38 $\times$ 3–11 mm broad at base, pale or deep pink, thin-textured, sometimes mottled with age, tips acute. *Inflorescence* widely obconical to hemispherical, 20–75 mm diam. *Flowers* 15–115, suberect to $\pm$ spreading; pedicel (8–)10–20(–23) mm long, pale pink or brownish pink; perigone (7–)12–19 mm long, pale or dark pink; tube 0.5–3.0 mm long, widening gradually distally; tepals widely spreading or somewhat erect, linear to narrowly lanceolate, (6–)11–16 $\times$ 0.7–3.0 mm, tips subacute. *Stamens* exerted by up to 7 mm; filaments white to pink; anthers 1–2 mm long, yellow. *Ovary* $\pm$ 2 mm diam., green to brownish pink. *Style* as long as stamens. *Berry* ovoidal, $\pm$ 7–12 mm diam., deep pink. *Seeds* ovoidal, $\pm$ 5 mm diam., dark wine-red. *Flowering time*: February to May. Figures 22, 24, 25.

Distribution and habitat: The distribution of *H. amarylloides* is characteristically disjunct across the southernmost Namaqualand Hardeveld and Knersvlakte. The northerly populations spread along the high-lying areas of Namaqualand from north of Springbok to the Grootvlei plateau and western foothills of the Kamiesberg mountains, whereas the southerly populations stretch along the western escarpment and Cape Fold mountains between Nieuwoudtville and Clanwilliam (Figure 23). Unlike the semi-arid, low-lying interval of the Knersvlakte, most habitats are located at $\pm$ 600 m above sea level, and they are seasonally moist. Rainfall varies from 200–360 mm per annum, although this is periodically augmented by late summer thundershowers in the north. In the southern part of the



Figure 22. *Haemanthus amarylloides* subsp. *amarylloides*. 1, inflorescence; 2, flower; 3, section of flower; 4, spathe bract; 5, bulb and hysteranthous leaves. *Snijman 590* (NBG), W of Nieuwoudtville. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 2, 5 = 12 mm; 3, 4 = 6 mm.

range, however, rain falls strictly in winter. Populations in Namaqualand inhabit low succulent shrubland, whereas those in northwestern Western Cape occupy semi-arid fynbos.

Diagnosis: *Haemanthus amarylloides* is distinguished by an obconic to hemispherical, spreading pink inflorescence, surrounded by 4–9 thin-textured spathe bracts. The flowers have tepals that are linear to lanceolate, 1.5–3.0 mm wide, and they vary in position from suberect to spreading from the vertical by up to $\pm 45^\circ$. The leaves, which vary from erect to flat on the ground, are narrowly ligulate to broadly elliptical and glabrous, and they are without markings apart from a pink blush towards the base of the abaxial surface. The bulb tunics die down only slightly obliquely and are either cream-coloured or entirely covered with layers of dark brown withered tunics.

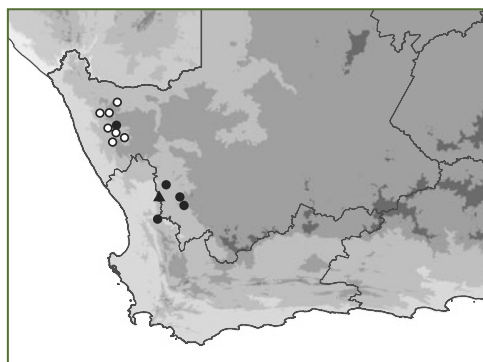


Figure 23. Distribution of *Haemanthus amarylloides* subsp. *amarylloides* (●); *H. amarylloides* subsp. *polyanthus* (○); *H. amarylloides* subsp. *toximontanus* (▲).

Haemanthus amarylloides encompasses marked vegetative variability among many small allopatric populations. The floral characters, however, show greater morphological cohesiveness within and between populations and these have provided the primary means of delimiting infraspecific taxa within this species. Three subspecies, based largely on differences in flower size and tepal orientation, are recognised here, as in Snijman (1984). To reassess the current classification, however, the geographic-based genetic variation within this complex warrants further study.

Nomenclatural note: The name *H. amarylloides* was repeatedly misapplied in the past to a superficially similar, yet distinct, species from the summer-rainfall region of southern Africa (Baker 1888, 1896; Sealy 1963; Friis & Nordal 1976). The evidence presented by Snijman (1982) showed that specimens from Namaqualand are the best match with Jacquin's description. Thus, the summer-rainfall species, previously mistakenly referred to as *H. amarylloides*, is now well known as *H. montanus*. The latter differs by having upright, synanthous to near-synanthous leaves that are slightly channelled and twisted, and by its remarkably large, green seeds.

Haemanthus amarylloides was first collected by Boos and Scholl in the late 18th century, followed by Miss A.J. Mostert, on the farm Cloudskraal near Nieuwoudtville in 1927. Most early collections were loosely referred to in South African herbaria as *H. pumilio*.

Key to subspecies:

- 1a. Scape $\pm$ rough to the touch; spathe bracts (5)6–9; perigone 7–10 mm long; tepals linear, widely spreading; leaves pliable, usually erect 8b. subsp. *polyanthus*

- 1b. Scape smooth to the touch; spathe bracts 4–6; perigone 12–19 mm long; tepals lanceolate, erect to slightly spreading; leaves firm, prostrate to erect:
 2a. Perigone (10–)12–14 mm long; leaves prostrate, spreading to erect, narrowly to broadly ligulate, 10–40 mm wide, firm but not fleshy, margin thick, smooth . . . 8a. subsp. *amarylloides*
 2b. Perigone 16–19 mm long; leaves appressed to the ground, oblong-lanceolate to elliptic, 55–120 mm wide, thick and fleshy, margin thick, minutely crenulate, at least distally . . .
8c. subsp. *toximontanus*

8a. subsp. *amarylloides*

Plants up to 250 mm high at flowering. *Leaves* prostrate, spreading or erect, blade narrowly to broadly ligulate, (5–)40–250 × 10–40 mm, firm-textured, bright green, margin ± raised, mostly red. *Scape* glabrous. *Spathe bracts* 4 or 5(6), 20–40 mm long. *Inflorescence* widely obconical. *Flowers* 15–40, slightly spreading, pale or dark pink; pedicel 5–15 mm long; perigone (10–)12–14 mm long; tepals slightly spreading, narrowly lanceolate. Figure 22.

Distribution and habitat. The typical subspecies is found in the vicinity of Grootvlei, west of Kamieskroon in Namaqualand, and on the Bokkeveld escarpment near Nieuwoudtville, with outlying populations to the southeast and reaching the southern limit close to Clanwilliam, Western Cape, where the only known population is surrounded by intensively farmed agricultural land (Figure 23). Soils associated with the Namaqualand populations are loamy sands derived from granite-gneisses, whereas in the northwestern Western Cape the populations occupy soils derived from sandstones and shales of the Cape supergroup. Populations are highly localised and appear to be confined to distinct habitats where additional groundwater keeps the soil moist during the growing season.

Diagnosis: *Haemanthus amarylloides* subsp. *amarylloides* is remarkably variable in the orientation and size of the leaves, ranging from prostrate to spreading or erect and narrowly to broadly strap-shaped. Nonetheless, the leaves are invariably firm in texture and most often have a slightly thickened margin. The widely obconical inflorescence is surrounded by 4 or 5(6), pink spathe bracts that are 20–40 mm long. The pale or dark pink flowers have a moderately long perigone (10–)12–14 mm long, and slightly spreading, narrowly lanceolate tepals. The inflorescence also varies in size, from more diminutive forms along the eastern rim of the distribution range, with an inflorescence ± 20 mm diam., to more robust individuals on the Bokkeveld escarpment.

Discussion: The isolated population recently discovered within intensively worked agricultural land close to Clanwilliam confirms that an earlier collection at Clanwilliam made by Compton and party (NBG 437/41) was incorrectly identified in Snijman (1984) as *H. amarylloides* subsp. *polyanthus* due to the floral measurements having been made on withered flowers.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **3017** (Hondeklipbaai): Grootvlei (–BB), Compton sub NBG 236/45 (NBG); Leighton 1395 (BOL); Müller-Doblies 79199 (NBG); Snijman 706 (NBG, PRE). **3119** (Calvinia): top

of Vanrhyns Pass (–AC), *Thomas s.n.* (K, NBG, PRE); *Barker 9785* (NBG); Cloudskraal, *Mostert sub Marloth 13486* (PRE); farm Arendskraal W of Nieuwoudtville, *Snijman 590* (NBG); *Snijman 599* (NBG); near farm Nuwefontein, 30 miles [48 km] S of Nieuwoudtville (–CA), *Burgers 499* (NBG); between farms Soutpan and Vryheid (–CD), *Snijman 763* (NBG).

WESTERN CAPE. **3218** (Clanwilliam): near Clanwilliam, *Compton & party sub NBG 437/41* (NBG); $\pm$ 2 km NE of Clanwilliam, on E side of Olifants River (–BB), *Gildenhuys s.n.* (NBG 154585); *Snijman 1442* (NBG).

8b. subsp. **polyanthus** *Snijman*

subsp. **polyanthus** *Snijman* in Journal of South African Botany 48: 99 (1982).

Type: South Africa, Cape Province [Northern Cape], 8 km W of national road towards Grootvlei, fl. 28 Mar. 1981, *Snijman 415* (NBG, holo.; K, MO, PRE, iso.).

Plants up to 200 mm high at flowering. *Leaves* erect, blade lorate to oblanceolate, 140–340 $\times$ 25–65 mm, soft and pliable. *Scape* $\pm$ rough with minute, retrorse, stiff hairs or somewhat glabrescent. *Spathe bracts* (5)6–9. *Inflorescence* becoming hemispherical. *Flowers* (40–)50–115, spreading, pale pink; pedicel 10–15 mm long; perigone 7–10 mm long; tepals widely spreading, linear. Figure 24.

Distribution and habitat. The subspecies is abundant in Namaqualand between the Bulletrap Pass north of Springbok and the Kamiesberg massif, within low succulent shrubland (Figure 23). Populations are usually large and after good autumn rain the bulbs flower prolifically, producing a beautiful display. *Haemanthus amarylloides* subsp. *polyanthus* and the typical subspecies are parapatric within the central parts of their distribution ranges, but unlike the latter, *H. amarylloides* subsp. *polyanthus* favours coarse, well-drained soils derived from granite-gneisses (Figure 7F, p. 27).

Diagnosis. *Haemanthus amarylloides* subsp. *polyanthus* has mostly upright, lorate to oblanceolate, shiny green, softly pliable leaves. The scape is most often rough with minute coarse hairs, and the inflorescence is widely spreading, comprising small, pale pink flowers in which the perigone is 7–10 mm long and the linear tepals spread to $\pm$ 45° from the vertical.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **2917** (Springbok): Bulletrap Pass (–BD), *Williamson s.n.* (NBG 167552); farm Biesjesfontein, S of Springbok (–DB), *Snijman 420* (K, NBG, PRE); 17 km from Spektakel turnoff towards Komaggas (–DC), *Snijman 185* (NBG, PRE). **3017** (Hondekliipbaai): ascending Killians Pass from the west (–BA), *Snijman 189* (NBG, PRE); 4.7 km E of Grootvlei (–BB), *Snijman 190* (K, MO, NBG, PRE); farm Skilpad, N of Grootvlei, *NBG Expedition 370167* (NBG); Bowesdorp, 8 km N of Kamieskroon, *Hall 4195* (NBG); 8 km W of national road towards Grootvlei, *Snijman 415* (K, MO, NBG, PRE); along Wallekraal road between farms Grootvlei and Nieuwe Plaats, *Van Berkel 306* (NBG); 1 km N of Darters Grave (–BD), *Snijman 192* (NBG, PRE); *Snijman 413* (MO, NBG); Karkams, *Snijman 411* (K, NBG, PRE). **3018** (Kamiesberg): eastern slopes of Welkom, Kamiesberg (–AC), *Snijman 312* (NBG, PRE); Kamiesberg, descending the Langkloof, *Snijman 1784* (NBG).

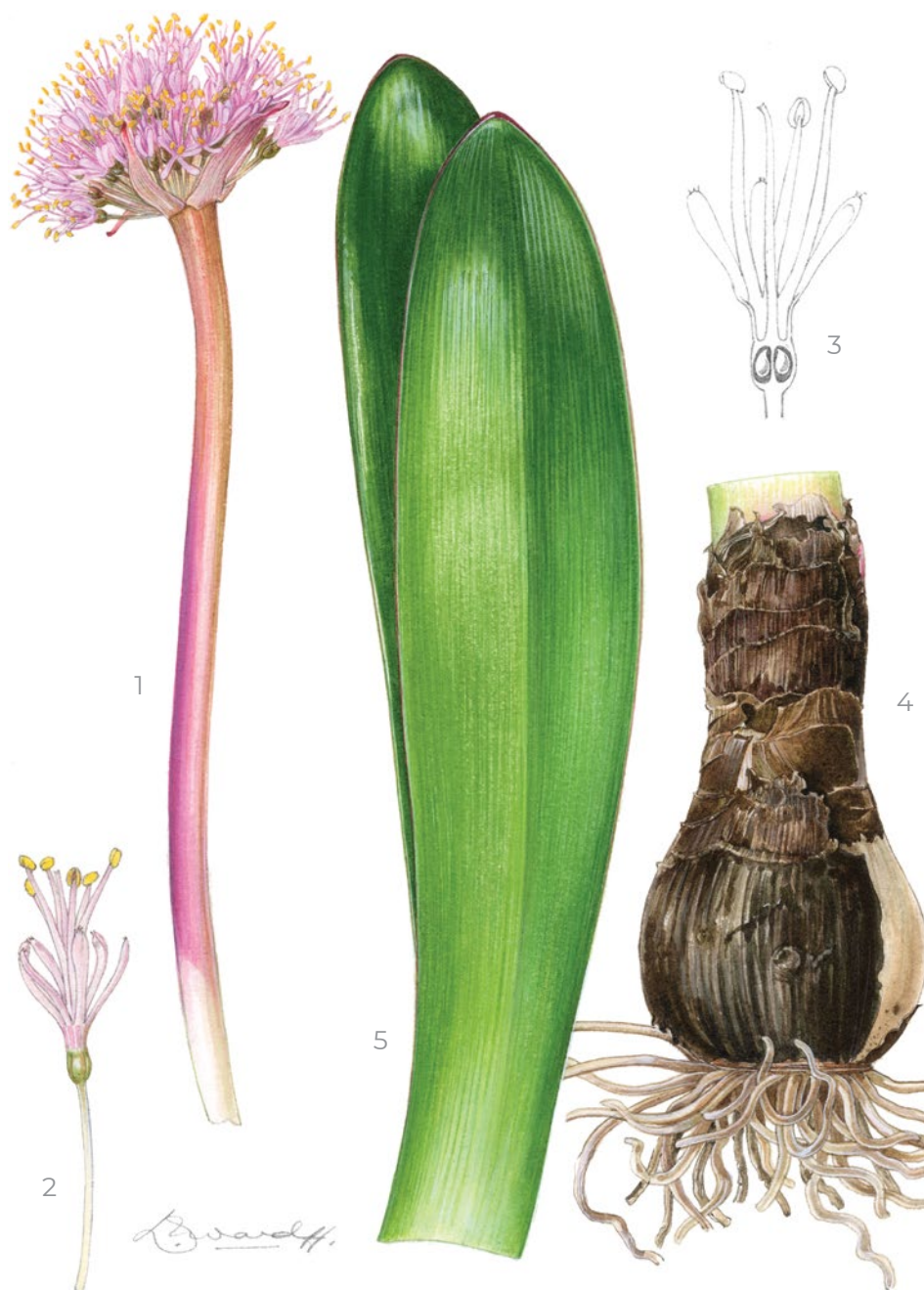


Figure 24. *Haemanthus amarylloides* subsp. *polyanthus*. 1, inflorescence; 2, flower; 3, section of flower; 4, bulb; 5, hysteranthous leaves. Snijman 190 (NBG), near Grootvlei. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 4, 5 = 12 mm; 2 = 6 mm; 3 = 3 mm.

8c. subsp. **toximontanus** *Snijman*

subsp. **toximontanus** *Snijman* in Journal of South African Botany, suppl. vol. 12: 90 (1984). Type: South Africa, Cape Province [Western Cape], top of Gifberg, S of Vanrhynsdorp, bulbs collected 6/4/1964, *E. Oliver s.n.* (NBG 77774, holo!; MO!, PRE 45481!, iso.).

Plants up to 250 mm high at flowering. *Leaves* appressed to the ground, blade oblong to broadly elliptical, 80–180 × 55–120 mm, thick, fleshy and bright green, margin thickened, minutely crenulate at least distally, usually red. *Scape* smooth. *Spathe bracts* 6, slightly spreading. *Inflorescence* tightly obconical. *Flowers* 30–50, suberect, rose-pink; pedicel 7–12 mm long; perigone 16–19 mm long; tepals suberect, narrowly lanceolate and overlapping. Figure 25.

Distribution and habitat: *Haemanthus amarylloides* subsp. *toximontanus* is endemic to the summit of the Gifberg and adjacent Matsikamma, southeast of Vanrhynsdorp, Western Cape (Figure 23). The massif stands somewhat apart from the main Bokkeveld escarpment since it is largely surrounded by the low-lying, semi-arid Knersvlakte in the north, and it is separated from the Nardouwsberg by the semi-arid Doring River valley in the south. The upper plateau supports Bokkeveld sandstone fynbos and a mosaic of small succulent and geophyte communities that occupy shallow pans on seasonally waterlogged pavement. *Haemanthus amarylloides* subsp. *toximontanus* is among several local endemics that inhabit these seasonally wet sites (Helme 2004).

Diagnosis: This subspecies has a characteristically compact habit. The leaves are firmly appressed to the ground, and they are thick and fleshy, with a raised red margin. The dark, rose-pink inflorescence is dense, with only slightly spreading flowers in which the perigone is 16–19 mm long, and the slightly overlapping tepals are held suberect.

Historical note: Bulbs were first collected in 1964 by E.G.H. Oliver, who distributed them to the Kirstenbosch National Botanical Garden and the Pretoria National Botanical Garden, where they later flowered.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3118** (Vanrhynsdorp): top of Gifberg (–DC), *E. Oliver s.n.* (NBG 77774, 82004, 85886, 94458, MO, PRE 45481, 45505); Gifberg plateau, *Van Jaarsveld* 4374 (NBG); *W. Olivier* 193 (K, NBG).



Figure 25. *Haemanthus amarylloides* subsp. *toximontanus*. 1, inflorescence; 2, bulb; 3, spathe bract; 4, flower; 5, prostrate, hysteroanthous leaves, cut to show thick texture; 6, section of flower. W. Olivier 193 (NBG), Gifberg. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–5 = 12 mm; 6 = 6 mm.

9

Haemanthus graniticus*Snijman*

Haemanthus graniticus *Snijman* in Journal of South African Botany, suppl. vol. 12: 91 (1984). Type: South Africa, Cape Province [Northern Cape], eastern slopes of farm Welkom, Kamiesberg, fl. 30 Mar. 1981, *Snijman 424* (NBG, holo.; K, PRE, iso.).

Plants deciduous, green in winter, up to 350 mm high when flowering. *Bulbs* forming clumps, obclavate, slightly compressed or almost round in cross section, 55–70 mm diam.; tunics thin, imbricate, ± distichous, with oblique margins, turning deep pink when exposed to light, mostly covered by withered brown papery remains. *Leaves* hysteranthous, 2(3), erect, blade narrowly to broadly lanceolate, 140–275 × 15–50 mm, plane or slightly channelled below, both surfaces shiny green, immaculate or slightly barred with red towards base of abaxial surface, entirely glabrous, margin smooth, green or red, apex acute or obtuse. *Scape* stout or slender, ± compressed, up to 240 × 5–16 mm, scarlet to deep red or pale carmine, immaculate, glabrous. *Spathe bracts* (4–)6 or 7, erect, set apart or slightly overlapping, shorter to longer than flowers, narrowly to broadly lanceolate, 30–47 × (6–)9–19 mm midway, red or pale carmine, firm but not fleshy, tips acute. *Inflorescence* compact, obovoid to obconical, 30–50 mm across. *Flowers* (15–)20–70, suberect; pedicel 7–14 mm long, red or pink; perigone 14–21 mm long, red to rose-pink; tube 2.5–5.0 mm long, slightly expanded upwards, ± gibbose at tepal base; tepals erect, narrowly oblong, 9–18 × 1–2 mm, tips obtuse. *Stamens* exerted by up to 7 mm; filaments mostly white; anthers 1.5–2.0 mm, yellow. *Ovary* 2–3 mm diam., greenish red or pink. *Style* slightly longer than stamens. *Berry* unknown. *Seeds* unknown. *Flowering time*: March to April, a month earlier in cultivation. Figure 26.

Distribution and habitat: The species is known from some of the wettest areas of Namaqualand, located southwest of Springbok and on the Kamiesberg mountains, Northern Cape, at elevations of 600–1 200 m above sea level (Figure 27). Populations of *H. graniticus* consist of large clumps of bulbs that are scattered in fine alluvium within rock crevices and along the edges of seasonal watercourses, fed by the run-off from adjacent granite-gneiss domes. Thus, at some sites the bulbs may become submerged for short periods during winter. Many of the geophytic taxa that inhabit these specialised, seasonally wet sites are endemic or near-endemic to the Kamiesberg massif (Helme 2009; Snijman 2013).

Diagnosis: *Haemanthus graniticus* is distinguished by a combination of floral and vegetative characters. The scape is unmarked, and the inflorescence is compact and surrounded by 6 or 7 erect,



Figure 26. *Haemanthus graniticus*. 1, inflorescence; 2, hysteranthous leaves; 3, bulb; 4, flower; 5, section of flower. *Snijman 425* (NBG), Kamiesberg. Artist: Fay Anderson. Scale bar: 1 = 12 mm; 2 = 14 mm; 3 = 13 mm; 4 = 8 mm; 5 = 6 mm.

thin-textured, lanceolate spathe bracts, which, like the flowers, vary from deep red to pale carmine. The leaves are erect, lanceolate, shiny green and entirely glabrous, only sometimes barred with red at the base of the abaxial surface. The bulb is well covered with withered brown tunics, whereas the fleshy tunics that die back obliquely turn dark pink if exposed to light.

In the vegetative phase *H. graniticus* is particularly difficult to distinguish from the sympatric *H. amarylloides* subsp. *polyanthus*, which has similarly shaped, erect, shiny green leaves. Despite growing close to each other, the two species, nevertheless, occupy different habitats. *Haemanthus graniticus* is typically found as dense clumps in fine textured soil, in seasonally wet sites, whereas *H. amarylloides* subsp. *polyanthus* grows singly in relatively drier, open patches in coarse soils derived from granite-gneisses.

Discussion: Bulbs of *H. graniticus* were first collected near Wildepaardehoek Pass and the Kamiesberg in the winter of 1980. At the time, the bulbs evoked no special interest as they were presumed to belong to *H. amarylloides* subsp. *polyanthus*. Only on returning to the Kamiesberg in March the following year, when the bulbs were seen to have brilliant red compact inflorescences, did it become apparent that they belonged to an undescribed species. Close inspection revealed *H. amarylloides* subsp. *polyanthus* growing close by, but while *H. graniticus* was in full bloom, the pink, spreading inflorescences of *H. amarylloides* subsp. *polyanthus* were just beginning to emerge above ground, apparently forming a partial reproductive barrier between the two taxa. The well-supported relationship between *H. graniticus* and *H. amarylloides* subsp. *polyanthus* (Figure 1), however, may suggest that occasional simultaneous flowering has led to introgression of the nuclear genome.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **2917** (Springbok): 23 km from Springbok to Wildepaardehoek Pass near farm Nooitgedacht (–DD), *Snijman 308* (MO, NBG). **3018** (Kamiesberg): eastern slopes of farm Welkom, Kamiesberg (–AC), *Snijman 311* (NBG, PRE); *Snijman 424* (K, NBG, PRE); *Snijman 425* (NBG); *Snijman 1782* (NBG).

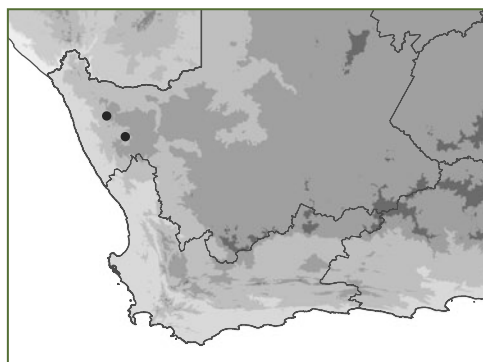


Figure 27. Distribution of *Haemanthus graniticus*.

10

Haemanthus nortieri*Isaac*

Haemanthus nortieri *Isaac* in Journal of South African Botany 3: 103 (1937); Snijman: 94 (1984). Type: South Africa, Cape Province [Western Cape], Nardouw mountains, Sept. 1933, *Salter 3622* (BOL, holo!).

Plants deciduous, green in winter, up to 300 mm high when flowering. *Bulb* solitary or rarely clumped, obovoid-globose, up to 100 mm diam., compressed; tunics horizontally tiered, cream-coloured, covered with dark papery remains. *Leaf* hysteranthous, 1(2), erect, blade obovate to broadly spatulate, 130–200 × 40–150 mm, narrowed to 15–50 mm at base, plane, thick and leathery, both surfaces dark green, flushed with red towards base, somewhat scabrous, sticky and sand-bearing, margin red or green, apex obtuse. *Scape* stout, erect, ± compressed, up to 300 × 8–15 mm, deep red, immaculate, ± scabrous, especially basally. *Spathe bracts* 5–8, erect, equalling or longer than flowers, ovate-lanceolate, 20–50 × 6–25 mm, red to deep dusky rose, somewhat leathery, tips acuminate. *In-florescence* compact, narrowly to broadly cyathiform, 30–70 mm across. *Flowers* 40–60, erect; pedicel 10–15 mm long, pinkish; perigone 14–18 mm long, pale scarlet, paler proximally; tube cylindrical, widening gradually upwards, 2–3 mm long; tepals erect, linear, 11–16 × 1.0–1.5 mm, tips obtuse. *Stamens* exerted by up to 11 mm; filaments reddish with white tips; anthers 1.5–2.0 mm long, yellow. *Ovary* ± 2 mm diam., green with a reddish blush. *Style* as long as stamens. *Berry* spheroidal, fleshy, ± 10 mm diam., reddish maroon. *Seeds* ovoid, 1 or 2 per berry, ± 5 mm diam., dark wine-red. *Flowering time*: March to April. Figure 28.

Distribution and habitat: Populations of *H. nortieri* are highly localised on mountain tableland southeast of Klawer, extending from just north of the Doring River valley on the lower Gifberg, southwards onto the Nardouws mountain range, Western Cape (Figure 29). The landscape, which is covered with semi-arid fynbos, is dominated by rocky outcrops with gullies and flats of deep sand. When undisturbed, *H. nortieri* grows in dense colonies of ten to thirty individuals, close to seasonal streams and on the seasonally moist edges of exposed sandstone rock sheets. Co-occurring species include scattered small trees of *Euclea tomentosa* E.Mey. ex A.DC. (Ebenaceae) and *Searsia undulata* (Jacq.) T.S.Yi, A.J.Mill. & J.Wen (Anacardiaceae), the asteraceous shrub *Athanasia trifurcata* (L.) L. and the restioid *Willdenowia incurvata* (Thunb.) H.P.Linder. Flowering often follows scattered thundershowers during March or April, whereafter a new leaf emerges in May and remains green until early October when conditions become increasingly hot and dry.

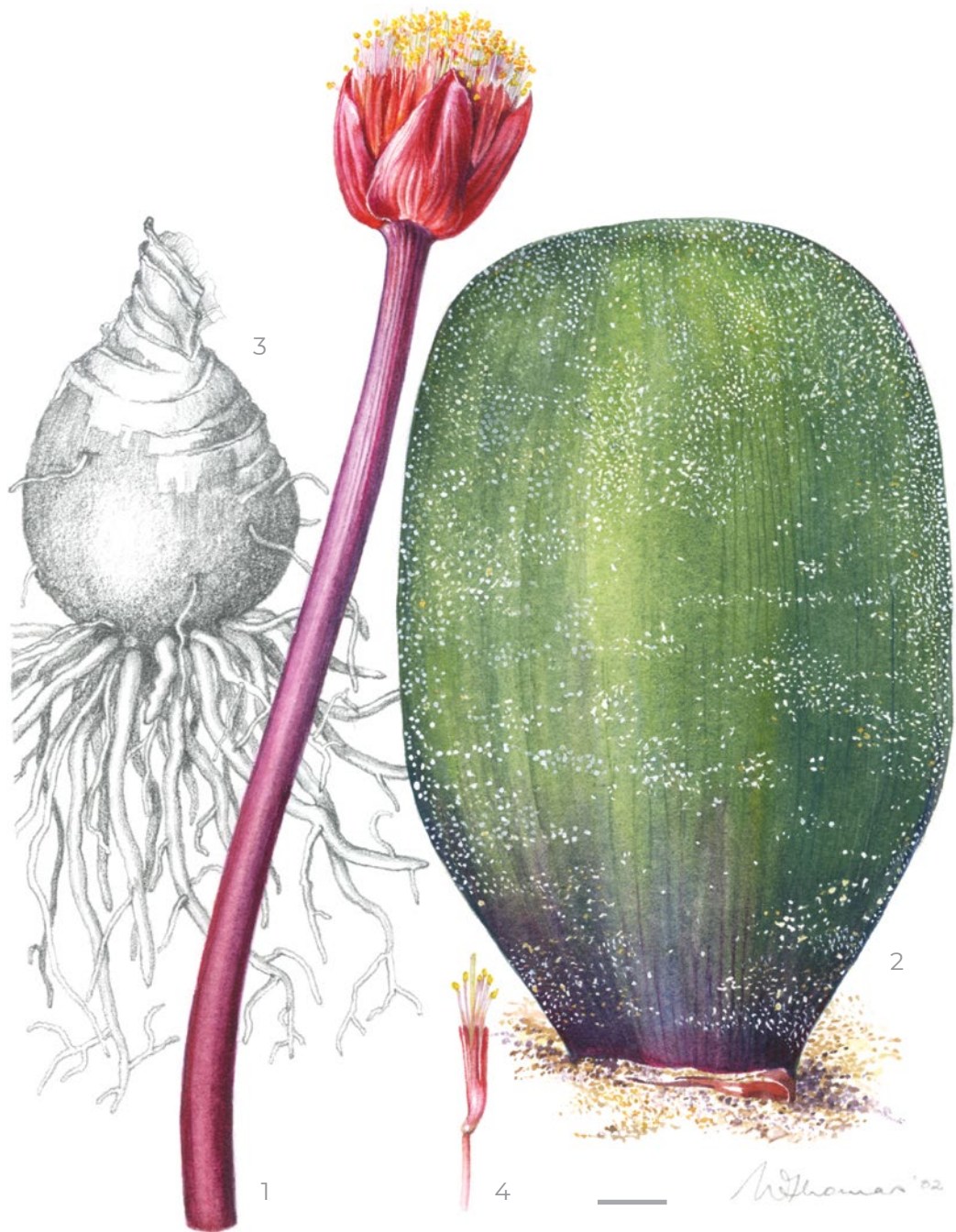


Figure 28. *Haemanthus nortieri*. 1, inflorescence; 2, erect, hysteranthous leaf bearing sand grains; 3, bulb; 4, flower. *Rourke 1071* (NBG), Nardouwsberg. Artist: Vicki Thomas. Scale bar: 1–4 = 10 mm.

Diagnosis: This slow-growing species is easily recognised by its habit of continuing to produce a solitary leaf into maturity. Rare individuals in the populations may be two-leaved, but the pattern is not consistent. Apart from the reduction in leaf number, the leaf morphology is also highly distinctive. The upright blade is thick, firm and leathery, varying in shape from broadly oblong to spatulate in outline. Most of the leaf surface is dark green, blending to dark maroon near the base, and it is sticky to the touch, hence the surface is frequently coated with grains of sand (Figure 3C).

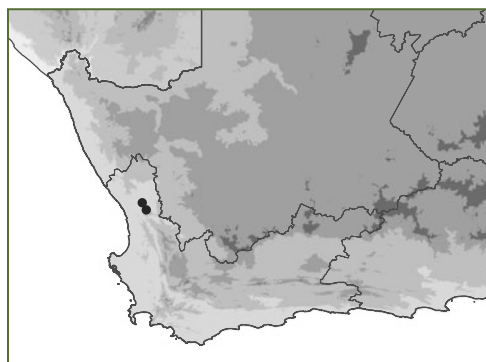


Figure 29. Distribution of *Haemanthus nortieri*.

Unlike its foliage, the inflorescence of *H. nortieri* has little that distinguishes it from many other red-flowered species. The deep red, unspotted scape, however, is characteristically rough to the touch due to minute rigid papillae covering the surface. Moreover, the five to eight leathery red spathe bracts are noticeably uniform in shape and size. Its affinity with other species is not readily obvious. However, the firmness of the leaf, and the leathery texture and shape of the spathe bracts suggest a possible alliance with *H. amarylloides* subsp. *toximontanus*.

Discussion: One of the most remarkable features of *H. nortieri* is the apparent infrequency of flowering. A bulb grown from a seed sown at Kirstenbosch National Botanical Garden in April 1979 took as many as 17 years to flower for the first time in April 1996 (Snijman et al. 2005). As yet, no study on the frequency of flowering in the wild has been done, but intermittent observations over a number of years indicate that populations flower only when conditions are suitable, although never abundantly so. Isaac's description of the bulb structure suggests that flower buds develop between successive pairs of leaves (Isaac 1937), so individuals are only capable of flowering every second year. The extra time needed for the bulbs to become fully mature most likely accounts for the species' natural rarity.

The specialised sticky leaf surfaces of *H. nortieri* are psammophorous, a trait in which sand grains are actively fixed to the plant by specialised epidermal features. Psammophory is regarded as an adaptation to reduce damage caused by abrasive, dry winds, although it may also enhance the plant's water- or thermal energy-budgets (Jürgens 1996). This trait is concentrated mainly within arid and semi-arid southern Africa, but it is also known within a few species elsewhere in the world. Within southern Africa marked leaf stickiness is shared with several other monocotyledonous plants, including species of *Strumaria* Jacq. and *Namaquanula* D.Müll.-Doblies & U.Müll.-Doblies within tribe Amaryllideae (Snijman 1994; Neinhuis et al. 1996).

Biographical note: *Haemanthus nortieri* was first discovered by P. le F. Nortier, a medical doctor of Clanwilliam, whose research on the biology of *Aspalathus linearis* (Burm.f.) R.Dahlgren led to the development of the rooibos tea industry (De Vos 1977).

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3118** (Vanrhynsdorp): Nardouw mountains (–DD), *Garside 4481* (K); *Nortier s.n.* sub NBG 850/35 (BOL, NBG, PRE); *Rourke 1071* (NBG); *Salter 3622* (BOL); *Snijman 1322* (NBG); *Snijman 1911* (NBG); *Snijman 1912* (NBG).

11

Haemanthus barkerae*Snijman*

Haemanthus barkerae *Snijman* in Journal of South African Botany 47: 832 (1981); Snijman & Weber: t. 2095 (1994). Type: South Africa, Cape Province [Northern Cape], 63.5 km from Calvinia towards Loeriesfontein, fl. NBG 14 April 1980, *Snijman 132* (NBG, holo.; PRE, iso.).

Plants deciduous, green in winter, up to 200 mm high when flowering. *Bulbs* forming clumps, globose, ovoid or obclavate, $\pm$ round or slightly compressed in cross section, up to 50 mm diam., tunics unequal, overlapping, with margins either horizontal or slightly oblique, cream-coloured, dead parts dark brown and papery, neck sometimes spotted with pink. *Leaves* hysteranthous, (1)2, recurved to suberect, blade narrowly to broadly ligulate or elliptic, 90–260(–340) $\times$ (7–)20–55(–80) mm, plane or canaliculate towards base, both surfaces dull to bright green or glaucous, glabrous or abaxial surface sparsely covered with hairs, 0.5–1.5 mm long, whitish towards base, extensively barred with dark green in proximal half and maroon near base, margin reddish or green, smooth or sparsely ciliate, apex acute to subobtusate. *Scape* erect, up to 170 $\times$ 4–10 mm, pale pink to brownish or deep pink, sometimes $\pm$ marbled, glabrous or occasionally sparsely covered with short hairs. *Spathe bracts* 4–6, spreading apart, shorter to longer than flowers, oblong-lanceolate, 20–50 $\times$ 4–16 mm, pale pink to magenta-rose, occasionally almost white, thin-textured but not membranous; tips acute. *Inflorescence* $\pm$ spreading, narrowly to broadly obconical, 25–60 mm across. *Flowers* 7–40; pedicel (4–)7–18 mm long, pale to dark pink or rarely reddish pink; perigone 11–15(–18) mm long, pale pink to deep pink; tube 1.5–3.0 mm long, narrowly campanulate, $\pm$ gibbose at tepal base; tepals spreading, narrowly oblong to lanceolate, 9–18 $\times$ 0.5–2.0 mm, tips obtuse to subacute. *Stamens* exerted by up to 10 mm; filaments pink to white; anthers 1.5–2.0 mm long, yellow. *Ovary* 2–3 mm diam., green to brownish pink. *Style* $\pm$ as long as stamens. *Berry* ovoidal, 10–15 mm diam., pale pink with a deep pink blush, becoming pulpy, translucent and aromatic when ripe. *Seeds* ovoidal, 5–6 mm diam., deep wine-red. *Flowering time*: March to April; up to a month earlier in cultivation. Figure 30.

Distribution and habitat: *Haemanthus barkerae* is distributed in a wide arc within Northern Cape, extending across the plateau between Loeriesfontein and Nieuwoudtville to the foothills of the Hantamsberg at Calvinia, then stretching southwards along the low-lying eastern rim of the Tanqua Karoo, as far as Elandsberg, Western Cape, in the extreme south (Figure 31). The relatively level plain of the Hantam Karoo, which reaches elevations of 400–1 200 m above sea level, receives an average 190 mm rain per year, with a high incidence of frost in winter. The eastern and southern



Figure 30. *Haemanthus barkerae*. 1, inflorescence; 2, flower; 3, section of flower; 4, bulb and hysteroanthous leaves; 5, section of leaf. *Snijman 132* (NBG), Calvinia/Loeriesfontein. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1 = 12 mm; 2 = 6 mm; 3 = 3.8 mm; 4 = 12.25 mm; 5 = 7 mm.

Tanqua Karoo is drier and warmer with an average of 110 mm rain annually, and a limited period of frost. The entire region has heavy clay soils derived from Ecca shales and Dwyka tillites of the Karoo sequence, and an extensive dolerite sill. Populations of *H. barkerae* are scattered throughout the area, varying in size from a few small clumps to groups of up to a hundred individuals, growing among rock outcrops or in the shelter of low bushes (Figures 5C and 6C). The surrounding vegetation is predominantly dwarf succulent shrubland, which includes low, small-leaved shrubs within the Hantam Karoo.

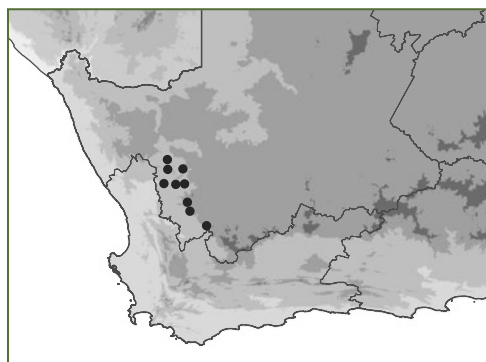


Figure 31. Distribution of *Haemanthus barkerae*.

Diagnosis: *Haemanthus barkerae* is the only pink-flowered species that possesses narrowly to broadly ligulate or elliptic leaves that are abaxially barred with dark green and maroon but are neither twisted nor sinuous. The bulb is round or somewhat compressed in cross section with the tunics dying down horizontally or slightly obliquely. The pale to deep pink inflorescence is obconical and surrounded by 4–6 spreading spathe bracts. The pale to dark pink or rarely reddish pink flowers are relatively small, with the perigone 11–15(–18) mm long.

It is often difficult to distinguish flowering plants of *H. barkerae* from those of the allopatric *H. amarylloides* subsp. *amarylloides*, since their pink inflorescences are remarkably alike. The two species, however, occupy differing soils that are derived from substrates belonging to separate but adjacent geological sequences. On the Bokkeveld escarpment near Nieuwoudtville, *H. barkerae* is confined to reddish clay soils derived from the Karoo supergroup, whereas *H. amarylloides* subsp. *amarylloides* is in nearby coarse nutrient-poor sands, derived from weathered sandstone of the Cape sequence. When in its vegetative phase, however, *H. amarylloides* subsp. *amarylloides* is easily distinguishable by its ligulate, firm-textured, plain green leaves.

Discussion: Plants of *H. barkerae* from the eastern Tanqua Karoo are somewhat larger than those from the Hantam Karoo, and their leaves are more variable, ranging in shape from narrowly ligulate to almost elliptic, with leaf pubescence somewhat longer and softer than the short, stiff hairs in the northern populations. Populations from the foothills of the Hantamsberg show the full range of leaf pubescence, ranging from short, somewhat rough hairs to long, soft hairs. Figure 30 depicts a compact plant with a rose-pink flower head from the high-lying Hantam Karoo. The inflorescences within populations from the more arid Tanqua Karoo are often paler pink.

Biographical note: The species commemorates W.F. Barker, curator of the Compton Herbarium from 1941 to 1972 (Rourke 1995), whose meticulous collections of *Haemanthus*, assembled from both the leafing and flowering phases, contributed greatly to our knowledge of the genus.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **3019** (Loeriesfontein): kloof 3 miles [4.8 km] S of Loeriesfontein (–CD), *E. Oliver s.n.* (NBG). **3119** (Calvinia): Kokerboomkop between Loeriesfontein and Nieuwoudtville (–AB), *Hiemstra & Hardick s.n.* sub NBG 899/71 (NBG); 63.5 km from Calvinia towards Loeriesfontein, *Snijman 132* (NBG, PRE); farm Brandkop, 46.2 km from Loeriesfontein towards Nieuwoudtville, *Snijman 136* (NBG, PRE); farm Charley-se-Hoek, Nieuwoudtville (–AC), *Hall 4134* (NBG); farm Glen Lyon, near Nieuwoudtville, *Mauve & I. Oliver s.n.* (PRE 57721); Nieuwoudtville Wildflower Reserve, *Perry & Snijman 2252* (NBG); 11 km E of Nieuwoudtville towards Calvinia, *Snijman 600* (NBG); 1.6 km from Calvinia/Loeriesfontein road towards Turon (–BC), *Snijman 130* (K, NBG); farm Grootvlakte near Toren, *Snijman 638* (NBG); Uitkyk between Nieuwoudtville and Calvinia, *Van Jaarsveld 8836* (NBG); Akkerdam, lower slopes of Hantamsberg (–BD), *Barker 9341* (NBG); Kareboomfontein, Calvinia, W of Rebunie (–DA), *Hanekom 2374* (PRE); Bloukrans Pass, *Hall* sub NBG 417/53 (NBG), *Snijman 128* (NBG); *Snijman 623* (NBG); farm Die Bos, between Ceres and Calvinia (–DC), *Snijman 96* (NBG, PRE); *Snijman 127* (NBG); *Stayner s.n.* (NBG); farm Dassieberg, S of Calvinia (–DD), *Snijman 620* (NBG). **3220** (Sutherland): between Uintjiesbos and Waaikop about 50 km SW of Middelpos (–AC), *Snijman 617* (NBG).

12

Haemanthus tristis*Snijman*

Haemanthus tristis *Snijman* in Journal of South African Botany, suppl. vol. 12: 54 (1984). Type: South Africa, Cape Province [Western Cape], 3.2 km towards Bakoven Kloof from the Karoo Poort/Sutherland road, fl. NBG 28 Mar. 1982, *Snijman 510* (NBG, holo.; PRE, iso.).

Plants deciduous, green in winter, up to 100 mm high when flowering. *Bulb* deep-seated, in clumps, pyriform, $\pm$ round in cross section, 45–60 mm diam., tunics thin, arranged in $\pm$ tiered horizontal layers, cream-coloured, outermost tunics leathery and pale brown. *Leaves* hysteranthous, 2, spreading, blade ligulate, 110–170 $\times$ 7–16 mm, shallowly channelled, thick, fleshy, dull green to glaucous, glabrous, abaxial surface flushed pink towards base, margin red, smooth, apex obtuse. *Scape* slender, up to 75 $\times$ 5–6 mm, pinkish to pale green, immaculate, glabrous. *Spathe bracts* 4 or 5, spreading apart, shorter than or as long as flowers, narrowly lanceolate, 20–30 $\times$ 3–7 mm wide at base, pale green to cream-coloured, ageing to pink, thin-textured, tips acute. *Inflorescence* lax, broadly obconical to hemispherical, 35–50 mm across. *Flowers* slightly spreading, 10–20; pedicel 6–12 mm long, pale green to cream-coloured; perigone 8–11 mm long, pale to deep cream-coloured, fading to pink; tube 1.5–3.0 mm long, gradually widening upwards; tepals widely spreading, linear, 7–10 $\times$ 1 mm, tips acute. *Stamens* exerted by up to 7 mm; filaments white to cream-coloured; anthers 1 mm long, yellow. *Ovary* $\pm$ 2 mm diam., pale green to cream-coloured. *Style* as long as stamens. *Berry* globose, $\pm$ 15 mm diam., walls thin, dry and leathery, becoming rugose, dull brownish red. *Seed* mostly solitary, $\pm$ 15 mm diam., dark wine-red when exposed to light. *Flowering time*: February to March. Figure 32.

Distribution and habitat: *Haemanthus tristis* is endemic to the southern Tanqua Karoo, Northern and Western Cape, an arid, low-lying basin situated in the rain shadow of the western Cape Fold mountains and drained by the Doring and Tanqua rivers (Figure 33). Populations are confined to seasonal washes, gravel beds and sheet-wash plains of the Tanqua River and its tributaries, at elevations of 400–600 m above sea level. The deep-seated bulbs grow as scattered clumps in deep coarse gravel or sandy loam derived from sediments of the Ecca and Dwyka groups of the Karoo supergroup (Figure 6D). The area, which may receive as little as 75 mm of rain per year, is very sparsely vegetated, mainly by dwarf succulent shrubs.

Diagnosis: The characteristically narrow leaves of *H. tristis* are 7–16 mm wide, shallowly channelled, fleshy, glabrous and dull green to glaucous. Apart from a flush of red towards the base and a thin



Figure 32. *Haemanthus tristis*. 1, inflorescence; 2, deep-seated bulb and inflorescence; 3, flower; 4, spathe bract; 5, section of flower; 6, filaments; 7, hysteranthous leaves; 8, seed germinating from within berry. *Snijman 510* (NBG), near Bakoven Kloof. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–3 = 14 mm; 4 = 5.8 mm; 5 = 3.2 mm; 6 = 4.8 mm; 7 = 6.7 mm; 8 = 15 mm.

border of red on the margin they lack other markings. As implied by the species epithet, the inflorescence is typically small and pale. The perigone is short, 8–11 mm long, and varies from whitish to deep cream-coloured, only turning pink as it fades. The berry, which encloses an especially large seed of ± 15 mm diam., has a thin, leathery, brownish red wall, a unique feature that differs from the typically succulent berries within other species of subg. *Haemanthus*.

Haemanthus tristis is inferred to be most closely related to *H. barkerae* due to their similar bulbs and inflorescences. The bulb tunics are arranged in tiered horizontal layers, and the flowers are loosely surrounded by 4 or 5 spreading, thin-textured, cream-coloured to pink spathe bracts. *Haemanthus barkerae* differs in having leaves that are frequently pubescent and consistently barred with red or dark green, a perigone that is invariably pink and comparatively long, 11–18 mm long, and in having fruits with pulpy walls.

Discussion: The unusually thin, dry, brownish red leathery berry wall and the especially large seed of *H. tristis* reflects a strategy that allocates more moisture to the seed than to the fruit wall itself, a possible adaptation to the particularly unreliable rainfall within the Tanqua Karoo. Due to their unique colour and texture the berries bear a surprising resemblance to the droppings of small antelope (Figure 6D).

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **3219** (Wuppertal): Ceres Tanqua Karoo, Potkleiberg S, SE corner on boundary with Platfontein (–BD), *Bayer 6246* (NBG). **3220** (Sutherland): Bo-Wadrif, 61 km from Sutherland to Gannaga Pass [Onder Karoo] (–AC), *Bayer 5271* (NBG).

WESTERN CAPE. **3219** (Wuppertal): E of Calvinia rd [road], S of Middeldam (Salt pans) Grootdam boundary (–DA), *Bayer 6225* (NBG); 3.2 km towards Bakoven Kloof from Karoo Poort/Sutherland road (–DD), *Perry 186* (NBG); *Snijman 209* (NBG); *Snijman 510* (NBG, PRE); farm De Vloeren, *Snijman 1262* (NBG, PRE).

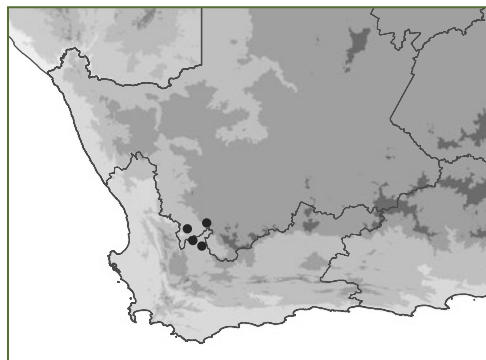


Figure 33. Distribution of *Haemanthus tristis*.

13

Haemanthus lanceifolius*Jacq.*

Haemanthus lanceifolius *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 1: 31, t. 60 (1797) [as *H. lanceaefolius*]; Herbert: 234 (1837); Baker: 67 (1888); Baker: 233 (1896). *Serena lanceifolia* (Jacq.) Raf.: 20 (1838) [as *S. lancifolia*]. Type: South Africa, Cape of Good Hope [Western Cape], illustration in Jacquin: t. 60 (1797), lecto., designated by Snijman: 80 (1984).

Plant deciduous, green in winter, up to 200 mm high when flowering. *Bulb* solitary or clumped, small, ovoid, $\pm$ round in cross section, up to 50 mm diam., tunics unequal, imbricate, with oblique margins, cream-coloured, mostly covered with dark brown withered remains. *Leaves* hysteranthous, 2, lightly appressed to the ground, blade oblong to elliptical, 70–150 mm $\times$ 50–95 mm, plane, leathery; adaxial surface dull green, roughish with a dense or sparse covering of minute tubercles, abaxial surface pale green, immaculate or rarely speckled with red, smooth, margin thickened, cartilaginous, maroon to hyaline, minutely crenulate or fimbriate with short, retrorse branched cilia, apex obtuse to subacute. *Scape* slender, up to 180 $\times$ 4–8 mm, pale to deep pink, sometimes marbled, slightly rough or smooth. *Spathe bracts* 6–7, spreading, soon becoming reflexed, shorter than to as long as flowers, narrowly triangular, 15–24 $\times$ 2.5–11.0 mm broad at base, pink, membranous. *Inflorescence* lax, becoming $\pm$ hemispherical, 25–60 mm diam. *Flowers* 20–65; pedicel 5–20 mm long, pink; perigone 6–9 mm long, pale pink or white and fading to pale pink; tube 1–2 mm long, gradually widening upwards; tepals widely spreading, linear, 5–7 $\times$ 0.5–1.5 mm, tips obtuse. *Stamens* exerted by up to 8 mm; filaments white to pink; anthers 1.0–1.5 mm long, yellow. *Ovary* 1–2 mm diam., green to brownish or deep pink. *Style* $\pm$ as long as stamens. *Berry* irregularly ovoidal, 10–11 mm diam., pink, pulpy and aromatic when ripe. *Seeds* 1 or 2 per berry, ovoidal, up to 6 mm diam., turning dark wine-red. *Flowering time*: March to April. Figure 34.

Distribution and habitat: Populations of *H. lanceifolius* are localised within a small area of the southern Knersvlakte, Western Cape, close to small seasonal rivers that flow from the Matsikamma catchment, as well as on the adjacent flats below the west-facing slopes of the Matsikamma massif (Figure 35). The area, which reaches elevations of $\pm$ 200 m above sea level and receives an average rainfall of 165 mm annually, is considerably wetter than other parts of the Knersvlakte due to the orographic effects of the adjacent mountains. The associated vegetation is low, succulent shrubland, which changes to spiny, asteraceous, dwarf shrubland in disturbed sandy areas. Fairly dense populations occupy loamy, slightly alkaline soils that are derived from exposed dolomite rock sheets, whereas



Figure 34. *Haemanthus lanceifolius*. 1, inflorescence; 2, spathe bracts; 3, flower; 4, section of flower; 5, adaxial surface of one of hysteroanthous, prostrate leaf pair; 6, transverse section of leaf; 7, bulb. *Snijman 147* (NBG), near Vanrhynsdorp. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 2, 5–7 = 12 mm; 3 = 6 mm; 4 = 2.5 mm.

smaller outlying populations of scattered plants occur on adjacent sandy flats.

Diagnosis: *Haemanthus lanceifolius* is distinguishable by a combination of vegetative and floral features. The leaves, which are lightly appressed to the ground, are leathery, ranging in shape from oblong to elliptical, much like the lowland western forms of *H. sanguineus*. The adaxial surface is characteristically rough due to a dense covering of small, raised tubercles, often confined to the leaf edges near the apex. Moreover, the leaf margin is cartilaginous and fringed with short, retrorse, branched cilia, which are reduced to minute crenulations in small plants. Like *H. tristis*, the perigone is remarkably small, 6–9 mm long, with a short tube 1–2 mm long, but the white to pale pink flowers have widely spreading, linear tepals, exposing well-exserted stamens that create a hemispherical, powderpuff-like inflorescence.

Discussion: Some plants of *H. lanceifolius* that grow in the loose sand adjacent to the nearby rock outcrops, are markedly smaller than those found in the loamy soils derived from dolomite rocks. Apart from the degree to which the tubercles cover the adaxial leaf surface and the extent to which the leaf margin is ciliate, these small plants have no other distinguishing features. This remarkable reduction in plant size is also known in populations of several other taxa; *H. humilis* subsp. *humilis* within marginal habitats of the Nama-Karoo; *H. pubescens* on exposed limestone on the west coast; as well as *H. coccineus* found within the shallow limestone soils of the Agulhas plain. In the absence of diagnostic features other than size, none of these diminutive plants are formally recognised as separate taxa.

Nomenclatural note: For almost two centuries *H. lanceifolius* was known only from Jacquin's plate (1797: t. 60). During this time Friis and Nordal (1976) included it in their *H. carneus* complex, with the stipulation that the glabrous leaf surface and scape, described for *H. lanceifolius*, was not otherwise known in the *H. carneus* complex. J.P.H. Acocks collected flowering material of *H. lanceifolius* from the wild in 1948, but in the absence of leaves the identity of the specimen remained uncertain. Collections of both leaves and flowers in 1979 and 1981, respectively, finally led to these plants being assigned the name *H. lanceifolius* (Snijman 1984). The leaves of the specimen illustrated in Figure 34 are more rounded, and the inflorescence is larger than those described by Jacquin (1797), but many bulbs in the population have narrow, oblong leaves, and few-flowered inflorescences that match Jacquin's description. The specimen, *Snijman 151* (NBG), which is a particularly good match of Jacquin's plate, provides further support that Jacquin's collectors, Boos and Scholl, travelled to Namaqualand during their visit at the Cape in the late 18th century (Garside 1942; Fraser & Fraser 2011).

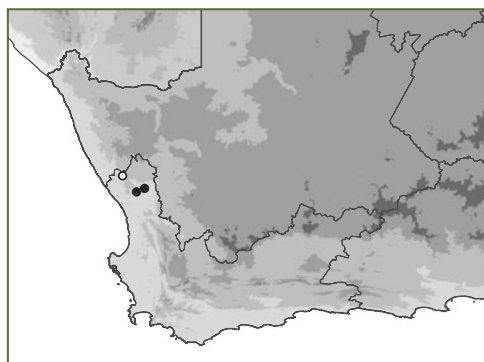


Figure 35. Distribution of *Haemanthus lanceifolius* (●); *H. humanii* (○).

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3118** (Vanrhynsdorp): farm Aties SW of Vanrhynsdorp (–DA), *Snijman 147* (K, NBG, PRE); N bank of Wiedourivier, between Klawer and Vanrhynsdorp, *Snijman 151* (NBG, PRE); *Snijman 434* (K, MO, NBG, PRE); *Snijman 1797a* (NBG); lower SW slopes of Matsikamma, farm Sandkraal (–DB), *Acocks 14177* (PRE); *Snijman 594* (NBG).

14

Haemanthus humanii*G.D.Duncan*

Haemanthus humanii *G.D.Duncan* in Curtis's Botanical Magazine 39 (2): 292, t. 1023 (2022). Type: South Africa, Western Cape, N of Bitterfontein, plentiful on flats and undulating quartz plains among dwarf succulents and geophytes, in Knersvlakte Quartz Vygieveld, Aug. 2018 [leaves], [*D. Human* sub] *G.D. Duncan s.n.* (NBG 1565121, holo!).

Plants deciduous, green in winter, up to 80 mm high when flowering. *Bulb* solitary, $\pm$ globose, 18–30 mm diam., shallow-seated, neck up to 5 mm long, tunics concentric, $\pm$ equal, with horizontally truncate margins, cream-coloured, covered with $\pm$ leathery, dry brown remnants. *Leaves* hysteranthous, 2(3), pressed flat on ground, blade elliptical, 18–45 $\times$ 16–35 mm, adaxial surface shiny green to glaucous-green, reddish when old, covered with longitudinal rows of close-set, translucent pustules, each bearing a suberect to slanting, 1.5–5.0(–10.0) mm long, reddish to pale brown, thick-walled, bristle-like trichome, abaxial surface smooth, pale green, immaculate, margin fringed with shorter pale brown trichomes. *Scape* $\pm$ erect, $\pm$ compressed, 55–70 $\times$ 5–6 mm, dull yellowish brown, sometimes reddish brown distally, immaculate, glabrous. *Spathe bracts* 5, suberect, narrowly lanceolate, 9–10 $\times$ 2–3 mm, membranous, deeply canaliculate, translucent white, white-veined. *Inflorescence* narrowly obconical, 35–40 mm across. *Flowers* 7–11, suberect to spreading; pedicel 8–10 mm long, dull green to greenish brown; perigone $\pm$ 10 mm long, white, fading to pink; tube 1 mm long; tepals held slightly apart, narrowly lanceolate, 9–10 $\times$ 1.0–1.5 mm, tips obtuse to subacute. *Stamens* $\pm$ as long as tepals, slightly spreading; inner filaments adaxially ridged for up to 2.5 mm above base then inwardly minutely hooked, white, drying pink; anthers $\pm$ 1 mm long, yellow. *Ovary* 1–2 mm diam., dull green. *Style* as long as to $\pm$ longer than stamens, white; stigma trifid. *Berry* ovoidal, 5 mm diam., greenish yellow. *Seeds* ovoidal, 7 $\times$ 4 mm, pale to deep reddish brown. *Flowering time*: late December to late January (in cultivation). Figure 36.

Distribution and habitat: The recently discovered *H. humanii* is currently known from two populations in southern Namaqualand, northeast of Bitterfontein, Western Cape (Figure 35), on low rolling hills at elevations of $\pm$ 300–350 m above sea level, within Knersvlakte Quartz Vygieveld (Mucina et al. 2006a). The populations, of $\pm$ 300 plants in total, grow in full sun, in shallow loamy gravel comprising white quartz pebbles, free of competition from plants with larger growth forms (Figure 5B). Growing with *H. humanii* is a suite of dwarf geophytes that have variously specialised leaf surfaces; *Bulbine mesembryanthoides* Haw. (Asphodelaceae), *Eriospermum paradoxum* Ker Gawl. (Ruscaceae),

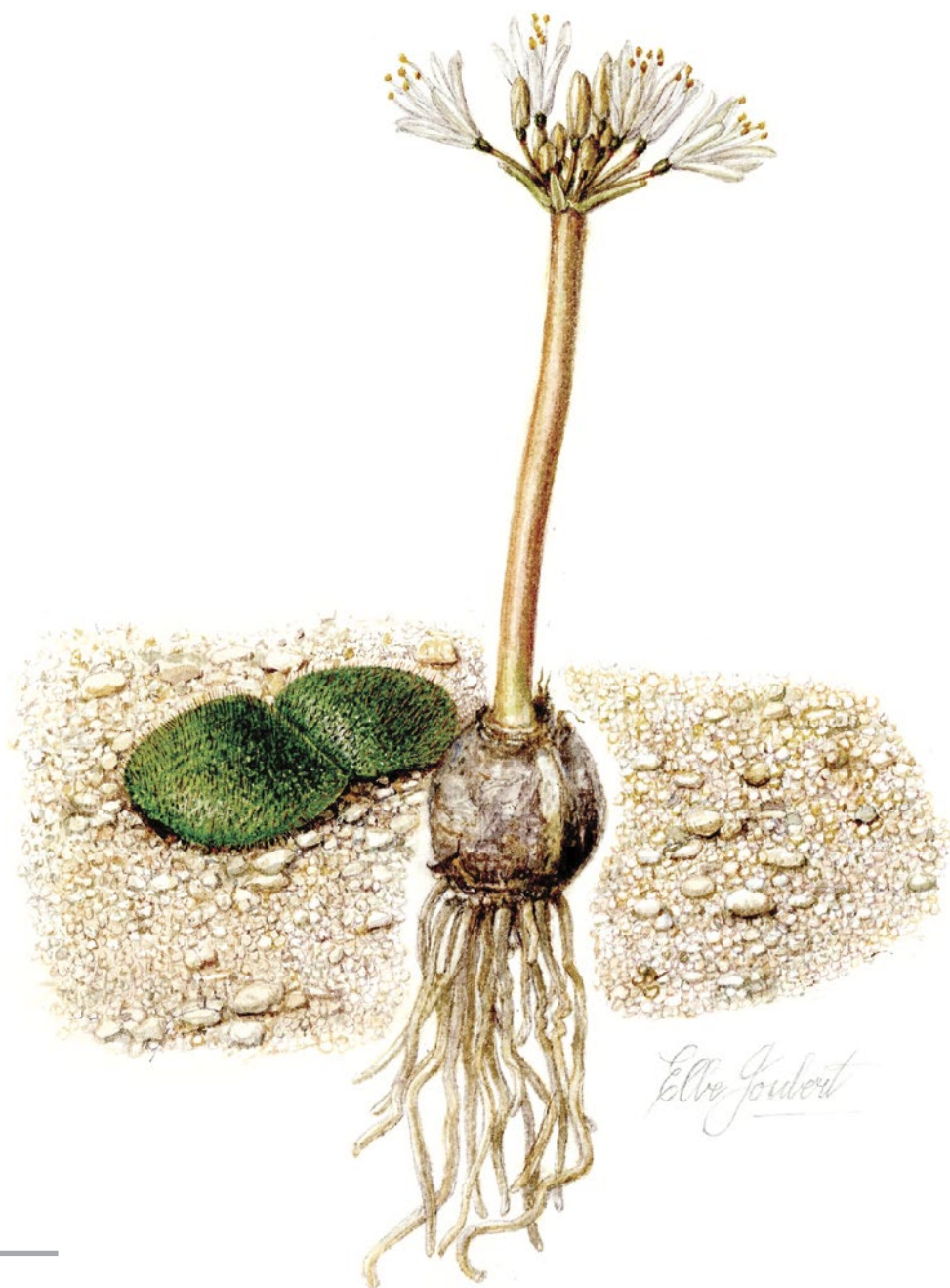


Figure 36. *Haemanthus humanii*. Habit of shallowly seated flowering bulb and prostrate, hysteroanthous leaf pair. Duncan s.n. (NBG), N of Bitterfontein. Artist: Elbe Joubert. With kind permission of the artist and *Curtis's Botanical Magazine*. Scale bar: bulb, inflorescence and leaves = 7 mm.

Lachenalia minima W.F.Barker, *L. trichophylla* Baker (Hyacinthaceae) and *Moraea pilifolia* Goldblatt (Iridaceae). These localised communities are confined to gentle, southwest-facing slopes close to sites where rainwater collects in shallow washes. Moisture in the form of dew and fog from the cool west coast adds to the precipitation in winter.

Diagnosis: Apart from its dwarf habit, *H. humanii* has several unique features that readily distinguish the plants. The presence of reddish to pale brown, bristle-like trichomes, arranged in remarkably regular, longitudinal rows on the adaxial leaf surface, is possibly the most distinctive feature of the species (Figure 3B). Varying from 1.5–5.0(–10.0) mm long within a single leaf, the trichomes have thick, minutely colliculate outer walls, and each trichome is attached to a translucent, multicellular pustule at the base. The trichomes contrast markedly with those of other *Haemanthus* species in their arrangement, shape and texture. Within *H. lanceifolius* and *H. sanguineus* the trichomes on the leaf margins are short, reddish and irregularly branched, whereas in other pubescent species they are mostly soft, white, uniseriate hairs.

Unlike other *Haemanthus* species from Namaqualand, *H. humanii* is relatively shallow-rooted and the subglobose bulb, with a short neck of ± 5 mm, grows close to the soil surface. As in *H. sanguineus* and *H. amarylloides* subsp. *toximontanus*, the two or rarely three leaves are firmly pressed to the ground, but they differ in being small, at most $\pm 45 \times 35$ mm in size.

When flowering, the species is recognised by a sparse inflorescence of ± 7 –11, white flowers that reach well above the short, thin-textured, white spathe bracts. The perigone tube is notably short (± 1 mm long), the tepals spread slightly apart by less than 30° from the vertical, and the inner filaments have a raised inner surface that terminates in a minute inwardly curved hook ± 2.5 mm above the base. This staminal feature is also known within the late-summer flowering *Namaquanula brucebayeri* D.Müll.-Doblies & U.Müll.-Doblies (tribe Amaryllideae) from the arid lower Orange River valley (Figure 34 in Snijman 1994). Within tribe Haemantheae, however, it is unique to *H. humanii*.

Haemanthus humanii has been recorded flowering under cultivation in late December and late January, unlike most other winter-rainfall *Haemanthus* species that are typically autumn flowering, from March to April. If confirmed in nature, this early flowering pattern may indicate that the species is adapted to flowering opportunistically in response to late summer thundershowers that periodically penetrate Namaqualand from the northeast.

Discussion: Owing to its remarkably distinct morphology, the affinities of *H. humanii* are not readily apparent. Nonetheless, the reddish-brown seed reliably places the species within subg. *Haemanthus*. The flower's shape, size and colour most closely resemble the flowers of *H. pumilio*, a species that is narrowly endemic to alluvium fynbos in southwestern Western Cape. Nevertheless, this cannot as yet be inferred to indicate their close alliance, since the foliage and bulb of *H. humanii* differ markedly from those of *H. pumilio*.

Superficially the dwarf habit, prostrate leaves, and variously shaped bristle-like trichomes bear a strong resemblance to the leaves of *Brunsvigia radula* W.T.Aiton and *B. namaquana* D.Müll.-Doblies &

U.Müll.-Doblies (tribe Amaryllideae), both habitat specialists that occupy dolomite outcrops and quartz patches, respectively, within Namaqualand and Bushmanland, Northern Cape (Snijman 2012). This striking convergence suggests that, in combination, these character states may have some adaptive value for coping within exposed, dry, stony habitats. Vogel and Müller-Doblies (2011) propose that many plants with such trichomes have the capacity to collect water droplets from dew and fog, thus supplementing soil moisture from rain. Studies have also shown that plants in Namaqualand that have a prostrate leaf habit attain higher temperatures compared with those that have an upright habit at midday (Rossa & Von Willert 1999). Thus, the role of specialised trichomes on the leaves of species like *H. humanii* might well include their ability to reduce the risk of photodamage through their impact on evapotranspiration, especially during hot berg winds that trigger maximum temperatures within Namaqualand in midwinter (Desmet & Cowling 1999).

Somewhat similar xeromorphic foliage has evolved in ecotypes of *H. humilis* subsp. *humilis* in relatively dry habitats in the vicinity of Makhanda, Qonce and Graaff-Reinet, in Eastern Cape, and Nelspoort, Western Cape. However, within these populations the trichomes on the adaxial leaf surface are short and they cover the surface irregularly and to varying degrees.

Biographical note: The species' epithet honours Free State horticulturist, Dawie Human, who first discovered the plants in 2018 and brought them to the attention of G.D. Duncan, specialist horticulturist at Kirstenbosch National Botanical Garden, who described the species together with botanical artist Elbe Joubert in 2022.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3018** (Kamiesberg): Namaqualand, between Bitterfontein and Kwanous (–CD), *Snijman & Manning 2401* (NBG); *Harrower s.n.* [images only] (NBG).

15

Haemanthus namaquensis*R.A.Dyer*

Haemanthus namaquensis *R.A.Dyer* in Flowering Plants of South Africa 20: t. 793 (1940); *Dyer*: 14, t. 315, fig. 3 (1948). Type: South Africa, Cape Province [Northern Cape], 10 miles [16 km], [cited as 16 miles, 25.7 km] NW of Steinkopf, July 1937, *Dyer* & *Verdoorn* 3674 (PRE 26355, holo.).

Plant deciduous, green in winter, up to 170 mm high when flowering. *Bulb* forming clumps, large, broadly ovate, compressed crosswise to leaves, up to 130 mm diam., tunics notably thick, imbricate and distichous, cream-coloured, with oblique margins, neck often flushed or speckled with pink if exposed. *Leaves* hysteranthous, 2, erect, blade oblong-lanceolate, 170–450 × 45–110 mm, markedly thick and tough, plane or ± channelled, green to glaucous, unmarked or abaxial surface whitish and sparsely speckled or barred with red proximally, glabrous, margin ± sinuate, particularly towards base, apex acute. *Scape* stout, ± compressed, up to 150 × 13–15 mm, plain red or slightly mottled, glabrous. *Spathe valves* 7 or 8, erect, slightly shorter than to as long as flowers, oblong-lanceolate, 32.5–40.0 × 6–15 mm, red, firm but not fleshy, tips somewhat acute. *Inflorescence* compact, ± compressed, ± 50 mm across. *Flowers* about 40; pedicel 10–20 mm long, pale scarlet to white; perigone slender, 18–25 mm long, scarlet with whitish tube and tips; tube 2.5–4.0 mm long, gibbose at base of each tepal; tepals erect, linear, 15.5–22.0 × 0.5–1.0 mm, tips obtuse. *Stamens* exerted by up to 9 mm; filaments pale scarlet with white tips; anthers yellow. *Ovary* 2–4 mm diam., pale green to pale scarlet. *Style* as long as stamens. *Berry* ovoidal, 10–12 mm diam., deep pink to plum-red. *Seeds* ovoidal. *Flowering time*: March to April, rarely February. Figure 37.

Distribution and habitat: Populations of *H. namaquensis* are concentrated along the central Richtersveld mountain ranges, southwards to the high-lying Anenous plateau and to the area just south of Spektakelberg, Northern Cape. Additional populations occur on inselbergs on the coastal forelands, close to Lüderitz in southern Namibia, and on Kourkammaberg, Northern Cape (Figure 38). This northwestern region ranges in elevation from 300–1 200 m above sea level and has an average annual precipitation of 100–200 mm in the form of rain and fog, with thundershowers in late summer. The geology and soils within the area are complex. *Haemanthus namaquensis*, however, occurs most often in soils derived from granite-gneisses and shale, usually between rocks or under low shrubs, on lower to upper slopes that are sparsely covered by low succulent shrubland. Populations of as many as 20 plants have been seen at some sites, often growing in small clumps, but generally the number of widely scattered bulbs is less (Figure 3E).



Figure 37. *Haemanthus namaquensis*. 1, habit of inflorescence and bulb with two emerging hysteranthous leaves, one cut off shortly above the base, the other folded back to show adaxial and abaxial surfaces; 2, detail of abaxial leaf surface. *Dyer & Verdoorn 3674* (PRE), NW of Steinkopf. Artist: Cythna Letty. Scale bar: 1 = 15 mm; 2 = 10 mm.

Diagnosis: The species is most easily recognised in the vegetative state by the erect, oblong-lanceolate, sinuous-edged leaves that are notably broad (45–110 mm wide), thick and tough (Figure 3E). These characteristics determine the form of the bulb, which is large and has especially thick, imbricate, distichous tunics. The leaves of *H. namaquensis* approach those of some northern Namaqualand forms of *H. coccineus* in size and shape, but they are never arched and succulent with in-rolled margins as in the latter. In contrast, their tough texture causes the dry leaf blades to break down slowly, often leaving untidy remnants around the bulb's neck. It is possible that the tough leaves enable the bulbs to withstand the severe winter winds that sweep through corridors within the Richtersveld mountain complex (Jürgens 1996).

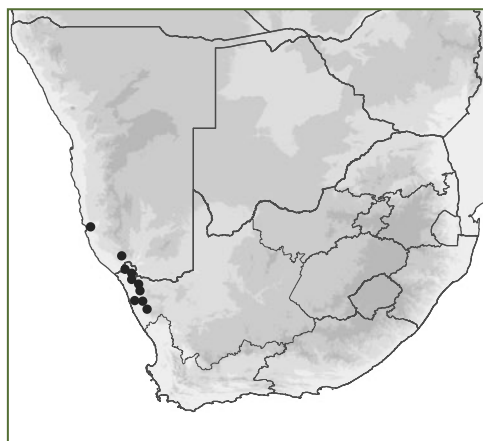


Figure 38. Distribution of *Haemanthus namaquensis*.

The inflorescence in *H. namaquensis*, held on a plain red or slightly mottled, glabrous scape, is surrounded by 7 or 8, erect, bright scarlet, oblong-lanceolate, firm spathe bracts, which are often considerably shorter than the flowers. As is characteristic of other species in the northwest, the perigone tube is gibbose at the base of each tepal.

Haemanthus namaquensis and *H. crispus* are the only two species that possess sinuate leaves, although this feature is sometimes considerably reduced in some individuals of *H. namaquensis*. In addition, they share a derived karyotype (Vosa & Snijman 1984) that suggests a close alliance, despite their marked differences in size.

Discussion: When Dyer and Verdoorn discovered the species in 1937, it was known only from the type locality near Steinkopf, Northern Cape. The species has since been recorded in southern Namibia, the Richtersveld and more widely in northern Namaqualand. It is nevertheless apparent that the species is rare, and that the populations are small and widely scattered.

Bulbs of *H. namaquensis* flower poorly at Kirstenbosch National Botanical Garden (Duncan et al. 2016), which mirrors the flowering pattern in nature (Craib 1998). This trait of flowering sparingly may be a physiological response to the species' exceptionally harsh, drought-prone habitat that is conserved under cultivation, thus contributing to the species' natural rarity (see Rees 1984).

Specimens examined

NAMIBIA. **2615** (Lüderitz): southern diamond area, Tsaukhaib [Tsau Khaeb] (–CB), *Hardy* 4489 (PRE). **2716** (Witpütz): near Spitskop (–DC), *Van Berkel* 489 (NBG).

SOUTH AFRICA. NORTHERN CAPE. **2816** (Oranjemund): Remhoogte, Richtersveld (–BD), *Herre s.n.* sub SUG 3678 (BOL). **2817** (Violsdrif): eastern slopes of Cornellsberg (–CA), *Bruyns 3231* (NBG); 12 km NW of Eksteenfontein towards Khubus (–CC), *Snijman 170* (NBG). **2917** (Springbok): 16 miles [25.7 km] NW of Steinkopf (–BA), *Dyer & Verdoorn 3674* (PRE 26355); Klipfontein, Steinkopf, *Herre s.n.* sub SUG 3638 (BOL); top of Anenous Pass, *Du Plessis 403* (NBG); Kosies road, *Roux 247* (NBG); 1 to 4 km W of Steinkopf, *Snijman 157* (MO, NBG); ± 5 km N of the Steinkopf/Port Nolloth road towards Kosies, *Snijman 159* (NBG); 1.5 km N of Kosies homestead, *Van Berkel 402* (K); ± 5 km before Kosiesberg, S of Kosies, *Williamson 3670* (NBG); Horees area, SW of Steinkopf (–BC), *Oliver 7758* (NBG); along road to Eyams, near turnoff to Witwater, *Snijman 1597* (NBG); Kourkammaberg (–CD), *Snijman 1604* (NBG); *Van Jaarsveld & Drijfhout 3380* (NBG); Komaggas, Kirkenberge (–DC), *Herre s.n.* sub SUG 3681 (BOL); NE of Komaggas, 17 km from Spektakel mine turnoff towards Komaggas, *Snijman 183* (NBG). **3017** (Hondeklipbaai): about 3 km SW of the village of Karkams (–BD), *Van Berkel 294* (NBG).

16

Haemanthus crispus*Snijman*

Haemanthus crispus *Snijman* in Journal of South African Botany 47: 829 (1981). Type: South Africa, Cape Province [Western Cape], Namaqualand, 61 km N of Vanrhynsdorp towards Nuwerus, fl. 28 Mar. 1981, *Snijman 410* (NBG, holo.; K, MO, PRE, S, iso.).

Haemanthus undulatus Herb.: 233 (1837), nom. illeg., non *H. undulatus* (L.) Thunb.: 58 (1794) = *Nerine undulata* (L.) Herb. Type: South Africa, 'Africa Australis', without precise locality, *Masson s.n.* (BM911852, holo.!).

Plants deciduous, green in winter, up to 175 mm high when flowering. *Bulb* mostly forming clumps or occasionally solitary, obclavate to globose, round in cross section or slightly compressed, up to 60 mm diam., tunics unequal, in tiered horizontal layers, cream-coloured, outer parts brown and papery. *Leaves* hysteranthous, (1)2(3), suberect or spreading, blade lorate, 110–200(–350) × 7–20(–33) mm, canaliculate, green or glaucous, sparsely to densely covered with short, stiff hairs or entirely glabrous, abaxial surface with dark green and maroon blotches, somewhat ribbed towards base, margins sinuate to undulate throughout or towards base only, rarely entirely flattened, usually outlined with red, apex acute. *Scape* up to 150 × 3.5–12.0 mm, red, immaculate or with darker red mottling, rarely pale to deep pink, glabrous. *Spathe bracts* 4 or 5(6), erect, equalling flowers or sometimes slightly longer, broadly to narrowly angular-obovate or spatulate, 22–40 × (6–)13–35 mm broad above middle, ± equal in shape and size, coral to scarlet or rarely pink, waxy; tips mostly obtuse and mucronate, occasionally ± acute. *Inflorescence* compact, obovoid to obconical, 15–40 mm wide. *Flowers* erect, 6–25; pedicel 0.5–4.0(–7.0) mm long, pale scarlet or rarely pink; perigone 15–26 mm long, coral to scarlet or rarely pink, whitish at base and tips; tube 1.5–5.0(–9.0) mm long, gibbose at base of each tepal; tepals erect, linear to narrowly spatulate, 12–20 × 0.7–2.0 mm, tips swollen and obtuse. *Stamens* exerted by up to 10 mm; filaments whitish to pale scarlet or pink; anthers 1–2 mm long, yellow. *Ovary* 2–4 mm diam., green to pinkish. *Style* reaching up to anthers. *Berry* spherical, 13–20 mm diam., pale pink and pulpy when ripe, tightly clustered. *Seeds* 1–4 per berry, globose, up to 10 mm diam., dark wine-red. *Flowering time*: March to April (May). Figure 39.

Distribution and habitat: *Haemanthus crispus* straddles the Northern and Western Cape provinces from southwestern Richtersveld in the north, through Namaqualand, to slightly south of Clanwilliam, and it extends from the west coast onto the escarpment between Loeriesfontein in the north to just east of Uitspankraal, bordering on the mid-Tanqua Karoo in the south (Figure 40). Mean annual



Figure 39. *Haemanthus crispus*. 1, ageing and fresh inflorescences; 2, spathe bract; 3, flower; 4, bulb and hysteranthous leaves; 5, section of flower. *Van Jaarsveld 5327* (NBG), Sannagas. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–4 = 12.6 mm; 5 = 6.3 mm.

rainfall over the area varies from 120–360 mm, and the soils change from sand near the coast to heavy clay soil on the Bokkeveld plateau. The underlying substrates vary from granite-gneisses in the Richtersveld and Namaqualand, to shales on the inland plateau and sandstone in the south. The associated vegetation cover is predominantly low succulent shrubland in the north and semi-arid fynbos in the south. Populations usually comprise numerous, large clumps of bulbs (Figure 7E), but in the extreme west and east the bulbs tend to be more solitary and widely scattered.

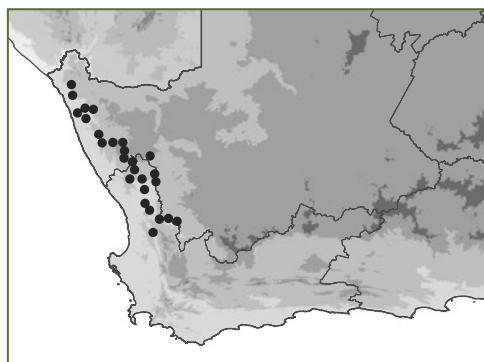


Figure 40. Distribution of *Haemanthus crispus*.

Diagnosis: As the name suggests, *H. crispus* is primarily distinguished by the conspicuously sinuous leaf edge (Figure 3D). The undulations usually extend the full length of the leaf, but occasionally they are limited to near the base. Another unusual character is the deeply channelled leaf blade, which gives the abaxial surface a ribbed appearance. The scape supports 4 or 5(6), broad (13–35 mm wide), equally blunt, angular-obovate spathe bracts, which are remarkably similar in size and shape, and a neat flower head of tightly clustered flowers, held on short (0.5–4.0 mm long), firm pedicels.

Discussion: The species varies considerably in the size, colour and pubescence of the leaves, but with no apparent geographic pattern. The blade may be markedly narrow or broad (7–33 mm wide), green or glaucous, and either covered with short stiff hairs or not. Only rarely are the leaves somewhat smooth edged and then they may be confused with the equally narrow leaves of *H. arenicola*, which grows sympatrically with *H. crispus* on the sandy coastal plain of northern Namaqualand. The bulb morphology of the two taxa, however, is sufficiently different to distinguish the species in the vegetative state.

The floral characters of *H. crispus* are not as variable as those of the leaves. The inflorescence is typically red, although populations near Kosies (Williamson 3668), Northern Cape, and the escarpment at Koebe Pass (Van Berkel 209, Snijman 428), Western Cape, differ in having narrow (6–13 mm wide), more sharply angular-obovate, pink spathe bracts. The occurrence of occasional, pink-flowered forms in a predominantly a red-flowered species is not unusual, and is also known in *H. canaliculatus*, *H. pubescens* and *H. sanguineus*.

The bulb of *H. crispus* has tunics that die down horizontally to form tiered layers, rather than obliquely as in most other species within subg. *Haemanthus*. This bulb form is shared with the Hantam Karoo and Tanqua Karoo species *H. barkerae* and *H. tristis*, which differ in having plane-edged, narrow leaves and spreading pale-coloured inflorescences.

Nomenclatural note: For many years *H. crispus* was referred to in South African herbaria as *H. undulatus* Herb. The use of Herbert's name, however, is invalidated by the prior existence of *H. undulatus* (L.) Thunb., a synonym of *Nerine undulata* (L.) Herb.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **2917** (Springbok): near Kosies (–BA), *Williamson* 3668 (NBG); Steinkopf (–BC), *Stayner* sub KG 347169 (MO, NBG); about 10 km S of turnoff to Komaggas along road to Soebatsfontein (–CD), *Snijman* 187a (NBG); Niegramoep (–DA), *Wikner s.n.* (SAM 63136); farm Driekoppe, S of Springbok (–DB), *Snijman* 421 (K, NBG, PRE); O’Okiep, *Giffen* sub *Marloth* 11955 (PRE); Concordia, *Krapohl* sub *Marloth* 5788 (PRE); Sannagas (–DC), *Van Jaarsveld* 5327 (NBG). **3017** (Hondeklipbaai): 8 km W of national road N7 towards Grootvlei (–BB), *Snijman* 414 (MO, NBG, PRE); 4 km W of farm Outuin, ascending Kamiesberg Pass, *Snijman* 423 (K, MO, NBG, PRE); farm Windheuvel between Wallekraal and Garies (–BC), *Snijman* 708 (NBG); Brakdam, 12 km N of Garies (–BD), *Bayer* 349 (NBG); Darters Grave, 22 miles [35 km] N of Garies, *Booyesen* 12 (NBG); *Middlemost* 2157 (NBG); *Snijman* 412 (NBG, PRE). **3018** (Kamiesberg): SW slopes of Kamiesberg, along Studers Pass (–AC), *Snijman* 426 (NBG, PRE); about 4.5 km S of Welkom (–AC/CA), *Van Berkel* 117 (NBG, PRE); 14.5 km N of Bitterfontein towards Garies (–CC), *Snijman* 427 (K, NBG, PRE); Kliprand rd [road] near Brandewynskraal (–DC), *Desmet* 1908 (NBG); farm Steenkampskraal, Nuwerus District, *Hall* 4113 (NBG). **3019** (Loeriesfontein): farm Haasriver, NW of Loeriesfontein (–CA), *Snijman* 664 (NBG); farm Taaiboshoek, NW of Loeriesfontein, *Snijman* 643 (NBG, PRE). **3119** (Calvinia): about 11 km NE of Grasberg towards Theunisdorp (–AA), *Snijman* 140 (NBG).

WESTERN CAPE. **3118** (Vanrhynsdorp): 61 km N of Vanrhynsdorp towards Nuwerus (–AB), *Snijman* 410 (K, MO, NBG, PRE, S); 2 km N of Bitterfontein towards Garies, *Van Berkel* 119 (K, NBG, PRE); just beyond turnoff to Middelkraal on road towards Komkams (–AC), *Snijman* 704 (NBG); 66 km N of Klawer beyond Koekenaap (–AD), *Snijman* 701 (NBG); 2 km S of gate to Sandkraal farmhouse (–DB), *Snijman* 429 (NBG); top of Koebee Pass, *Van Berkel* 209 (NBG); *Snijman* 428 (K, MO, NBG, PRE); Nuwerus, Graaitjiesgat (–BA), *Bruyns* 12566 (NBG); Knersvlakte, Vanrhynsdorp, Rooiberg (–BC), *Desmet* 1953 (NBG); Klawer (–DC), *Compton* sub NBG 308/22 (BOL); 2.6 miles [4.2 km] W of N7 road from Trawal towards Skurfkop, *Hardick* sub NBG 889/71 (NBG, PRE); top of Nardouws Pass ascending from near Trawal, *Snijman* 289 (NBG); N of Bulshoek Barrage (–DD), *Barker* 7304 (NBG). **3119** (Calvinia): foot of Vanrhyns Pass (–AC), *Snijman* 142 (NBG); *Snijman* 1771 (NBG). **3218** (Clanwilliam): Nardouskloof, near foot of Pass (–BB), *Manning* 2332 (NBG); farm Alpha at Algeria turnoff (–BD), *Fisher* 13 (NBG). **3219** (Wuppertal): Pakhuis (–AA), *Salter* 7523 (NBG); Zwart Vley, near upper waterfall E of Uitspankraal on Doringrivier (–AB), *Snijman* 1222 (NBG); Tanqua Karoo, farm Twee Damme, ± 15 km NNW of Elandsvlei (–BA), *Vlok s.n.* (NBG 184553).

17

Haemanthus coccineus*L.*

Haemanthus coccineus *L.*, Species plantarum 1: 325 (1753); Baker: 71 (1888); Baker: 240 (1896). *Haemanthus latifolius* Salisb.: 216 (1796), nom. illeg. superfl. Type: South Africa, Cape of Good Hope [Western Cape], illustration in Commelin, Horti medici Amstelodamensis rariorum, vol. 2: t. 64 (1701), lecto., designated by Bjørnstad & Friis: 190 (1972).

Haemanthus carinatus *L.*: 413 (1762). *Haemanthus coccineus* var. *carinatus* Herb.: 236 (1837). Type: ad Cap. Bon. Spei. [Cape of Good Hope], precise locality and collector unknown, possibly not preserved.

Haemanthus coarctatus Jacq.: 30, t. 57 (1797). *Haemanthus coccineus* var. *coarctatus* (Jacq.) Herb.: 236 (1837). *Perihemia coarctata* (Jacq.) Raf. [as *Perihema coarctata*]: 20 (1838). Type: South Africa, Cape of Good Hope, illustration in Jacquin, Plantarum rariorum horti caesarei Schoenbrunnensis, vol. 1: t. 57 (1797), lecto., designated by Friis & Nordal: 65 (1976).

Haemanthus tigrinus Jacq.: 29, t. 56 (1797). Type: South Africa, Cape of Good Hope, illustration in Jacquin, Plantarum rariorum horti caesarei Schoenbrunnensis, vol. 1: t. 56 (1797), lecto., designated by Snijman: 96 (1984).

Haemanthus crassipes Jacq.: 7, t. 412 (1804). Type: South Africa, Cape of Good Hope, illustration in Jacquin, Plantarum rariorum horti caesarei Schoenbrunnensis, vol. 4: t. 412 (1804), lecto., designated by Snijman: 96 (1984).

Haemanthus hyalocarpus Jacq.: 5, t. 409 (1804). Type: South Africa, Cape of Good Hope, illustration in Jacquin, Plantarum rariorum horti caesarei Schoenbrunnensis, vol. 4: t. 409 (1804), lecto., designated by Friis & Nordal: 65 (1976).

Haemanthus moschatus Jacq.: 6, t. 410 (1804). Type: South Africa, Cape of Good Hope, illustration in Jacquin, Plantarum rariorum horti caesarei Schoenbrunnensis, vol. 4: t. 410 (1804), lecto., designated by Friis & Nordal: 65 (1976).

Haemanthus coccineus var. *grandivalvis* Herb.: 236 (1837). Type: South Africa, Cape of Good Hope, illustration in Ker Gawler in Curtis's Botanical Magazine 27: t. 1075 (1808), lecto., designated by Friis & Nordal: 65 (1976).

Haemanthus concolor Herb.: 238, t. 31, fig. 2 (1837). Type: South Africa, Cape Province, XX·26 [10 Oct. 1826], Burchell bulb no. 276, [K, lecto.], designated by Friis & Nordal: 65 (1976)].

Haemanthus callosus Burch. ex Baker: 71 (1888). Type: South Africa, Cape Province, Burchell bulb no. 129, [K, lecto.], designated by Friis & Nordal: 65 (1976)].

Haemanthus splendens Dinter: 181 (1923). Type: South West Africa [Namibia], Klinghardtberge, Sept. 1922, *Dinter 4450* [M, lecto.!; B, K, isolecto.!, designated by Friis & Nordal: 67 (1976)]. [*Haemanthus coccineus* var. *albus* Stanford: 70 (1943), *nom. nud.*, invalid name, without description.]

Plants deciduous, green in winter, up to 400 mm high when flowering. *Bulb* solitary or clumped, elongate-ovoid to broadly ovoid or depressed ovoid, compressed crosswise to distichous leaves, 30–150 mm diam., tunics imbricate, distichous, thick, cream-coloured, sometimes speckled with red in upper parts, margins oblique, withered and brown. *Leaves* hysteranthous, 2(3), suberect to spreading or prostrate, blade narrowly to broadly, elliptical or oblong (60–)150–450(–700) × (25–)85–150(–210) mm, plane or shallowly channelled in lower half, fleshy, adaxial surface bright to dull green or glaucous, immaculate or occasionally with dark green or maroon markings, glabrous, abaxial surface pale green or glaucous, immaculate or barred with maroon over whole surface or towards base, sometimes heavily barred with dark green on a whitish background, glabrous or pubescent towards edges and apex or over whole surface, margin sometimes red, smooth or softly ciliate, occasionally revolute, apex obtuse to acute. *Scape* usually stout, 60–370 × (5–)10–20 mm, cream to pale green to pale red with deep red spotting or deeper red streaks, occasionally plain red, glabrous or rarely pubescent. *Spathe bracts* 6–9(–13), erect and overlapping, rarely somewhat spreading, shorter to longer than flowers, irregular, broadly to narrowly oblong or lanceolate to elliptic, obovate or spatulate, 20–60 × (7–)15–48 mm, coral, vermilion or scarlet, stiff and fleshy, rarely somewhat thin, occasionally softly ciliate, tips acute to obtuse. *Inflorescence* compact, cyathiform to campanulate and ± compressed, or occasionally spreading and obconical, 30–100 mm across. *Flowers* (20–)25–100, mostly erect; pedicel (2–)5–15(–18) mm long, cream to pale green or reddish; perigone 14–30 mm long, coral to scarlet with white tube and tips or concolorous; tube 2–5 mm long, widening upwards, gibbose at base of each tepal; tepals usually erect or rarely slightly spreading, narrowly oblong to spatulate, 12–26 × 1.0–3.5 mm, tips swollen, obtuse to acute. *Stamens* exerted by up to 10 mm; filaments pale scarlet, usually white-tipped; anthers 1–2 mm long, yellow. *Ovary* 2–4 mm diam., pale green. *Style* as long as stamens. *Berry* ± ovoid, soft and pulpy, ± 15 mm diam., white to pale or deep pink, becoming translucent. *Seeds* 1–3 per berry, ovoid, 8–10 mm diam., dark wine-red. *Flowering time*: February (in the east) to April (in the west). Figures 41 and 42.

Distribution and habitat. *Haemanthus coccineus* is widely distributed throughout the winter-rainfall region of southern Africa, from southern Namibia to the Cape Peninsula, Western Cape, and thence eastwards to near Makhanda, Eastern Cape, where rainfall becomes increasingly nonseasonal (Figure 43). Likewise, the populations occupy a large range of habitats. Soils are derived from granites, shale, quartzite, sandstone or limestone, and rainfall varies over the area from 100–1 100 mm per annum. Elevations range from sea level to mountain slopes of 1 200 m above sea level, and the associated vegetation varies from Succulent Karoo to renosterveld and fynbos. Population size varies from dense stands of hundreds of individuals to small groups of only a few bulbs. Sites most favoured are shaded kloofs and rock crevices, as well as on flats in the shelter of low bushes and shrubs (Figures 6A, 6B and 7C).

Diagnosis: Plants of *H. coccineus* are among the most succulent and boldly variegated within *Haemanthus*. The spreading or rarely prostrate leaves, which are characteristically fleshy, vary greatly in



Figure 41. *Haemanthus coccineus*. 1, inflorescence; 2, bulb; 3, hysteranthous leaves; 4, infructescence; 5, seeds and mucilaginous funicles; 6, flower; 7, section of flower. *Snijman 87a* (NBG), Albertyn/Caledon. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 3–6 = 12.6 mm; 2 = 20 mm; 7 = 6.3 mm.



Figure 42. *Haemanthus coccineus*. 1, inflorescence; 2, bulb; 3, hysteroanthous leaves; 4, flower; 5, spathe bracts; 6, section of flower. Roux 502 (NBG), Walmer. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–5 = 12.5 mm; 6 = 6.25 mm.

size and shape, from narrowly to broadly oblong or elliptical and (25–)80–150(–210) mm wide. Abaxially they are most often barred or spotted in contrasting colours of dark green or red. Similarly, the scape is variously blotched or streaked with red, only rarely remaining immaculate. The usually dense flower head is distinguished by 6–9(–13) stiff, fleshy, overlapping red spathe bracts of variable shape, most often closely surrounding the flowers or rarely spreading slightly apart. Furthermore, the base of each tepal is gibbose, above which the tepal is curved slightly inwards then held erect, terminating in a slightly swollen tip. The possession of basally gibbose tepals is shared with several other closely allied, red-flowered species within subg. *Haemanthus*, namely, *H. arenicola*, *H. crispus*, *H. dasyphyllus*, *H. leipoldtii*, *H. namaquensis*, *H. pubescens* and *H. unifolius*.

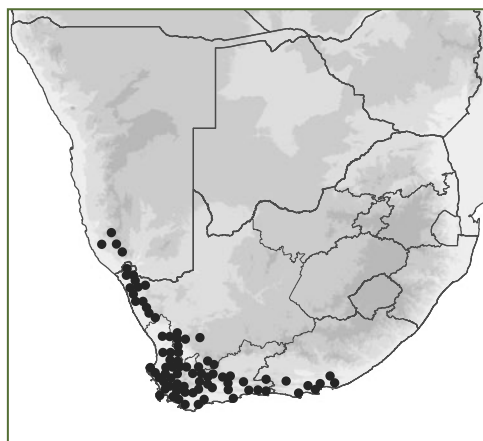


Figure 43. Distribution of *Haemanthus coccineus*.

Discussion: *Haemanthus coccineus* is the most widely ranging and variable species in the winter-rainfall region of southern Africa. Since many geographical races can be distinguished, the possibility of recognising infraspecific taxa has been carefully considered, but the complexity of the variation pattern makes formal subdivision impracticable.

The broadest trend discernible across the distribution range indicates that specimens of *H. coccineus* from the west are more succulent in both vegetative and floral parts than those in the east, where populations usually have thinner leaves and thinner, spreading spathe bracts that give the inflorescence a somewhat lax appearance. In addition, populations in the west flower mostly near the end of March and the leaves are strictly hysteroanthous, whereas populations east of Oudtshoorn flower earlier, in February, and sometimes have leaves emergent with the inflorescence. These differences have been maintained in most of the bulbs grown under uniform conditions at Kirstenbosch National Botanical Garden, suggesting that the bulb's phenology may be conserved. This broad east to west trend is common to several other geophytic species within the Core Cape Floristic Region and is correlated with the decline in the proportion of winter rain east of 21° E (Procheş et al. 2005). From here to the easternmost boundary of the species' distribution range, rain may fall at any time of the year, but with peaks in spring and autumn.

In addition to the above broad trends, several regional races are worthy of mention. In plants from the extreme north, matching Dinter's southern Namibian *H. splendens*, the scape is plain red, the barring on the leaves is diminished, and pubescence is often limited to a ciliate margin. Further south in Namaqualand, plants have very succulent bright green leaves, mostly with in-rolled margins, and in plants from southern Namaqualand, matching Jacquin's *H. moschatus*, the abaxial leaf surface is mostly heavily barred with dark green, usually on a whitish background, with pubescence towards the edges.

In the mountainous areas of southwestern Western Cape, from Piketberg to Worcester, bulbs have plane-edged, ciliate leaves with bold red barring on the abaxial surface. Of all the races this has the most strikingly spotted scape. In the past, these specimens were frequently identified in South African herbaria as Jacquin's *H. tigrinus*.

Coastal populations in the southwestern and southern Western Cape vary considerably in leaf shape and markings. The leaves may be immaculate or slightly barred, and glabrous or ciliate. Most specimens, however, are characterised by a spotted scape and extremely broad, blunt, fleshy spathe bracts that dominate the inflorescence (Figure 41). These floral characters are very similar to those of the type illustration of *H. coccineus*.

Inland populations from Montagu to Makhanda in the east have consistently glabrous, glaucous leaves with fine red spotting and barring on the abaxial surface, whereas the inflorescence is usually brilliant red and concolorous. From Oudtshoorn eastwards the spathe bracts are particularly narrow and acuminate, and the inflorescence is lax so that the differences in floral characters between *H. coccineus* and *H. sanguineus* in this region are somewhat obscured. It is often only possible to distinguish the two species in the vegetative phase. Specimens from near Gqeberha match Burchell's type of *H. concolor* (Figure 42).

Included among the above widely distributed variants are certain restricted races that have special interest. Specimens from the mountains near Clanwilliam (*Roux 184*, K, MO, NBG) are extremely large, with leaves up to 700 × 210 mm. In contrast, bulbs from the De Hoop Nature Reserve, near Bredasdorp, which grow in shallow soils overlying limestone pavement, show extreme dwarfism. Some leaves reach only 50 × 40 mm (*Snijman 113*, K, NBG, PRE). Lastly, bulbs collected from the steep rocky slopes of river gorges near Calitzdorp have leaves heavily spotted with red and green on both surfaces (*Snijman 395*, K, MO, NBG, PRE, S).

On rare occasions a white form of *H. coccineus* has been reported. The white form matches typical *H. coccineus* in all respects, but it has a pale green immaculate scape and lacks barring on the leaves.

Specimens examined

NAMIBIA. **2616** (Aus): farm Kubub, Lüderitz (–CB), *Giess 11005* (WIND); Aus townlands, *De Winter & Hardy 7922* (PRE, WIND). **2715** (Bogenfels): Klinghardt's mountains (–BC), *Dinter 4450* (K, M); *Williamson 3254* (BOL).

SOUTH AFRICA. NORTHERN CAPE. **2816** (Oranjemund): SW slopes of Cornells Kop (–BD), *Snijman 174* (NBG); Helskloof, *Snijman 172* (NBG); Doring Poort, W side of Ploegberg (–DB), *Van Zijl 106* (K, MO, NBG). **2817** (Vioolsdrif): 33 km from Eksteenfontein towards Khubus (–CA), *Snijman 171* (NBG); 10.5 km from Eksteenfontein towards Khubus (–CC), *Snijman 169* (NBG). **2916** (Port Nolloth): Port Nolloth (–BD), *Herre* sub SUG 3652 (BOL). **2917** (Springbok): Karrachab Poort, S of Lekkersing (–AA), *Snijman 176* (NBG); latitude 29° 10', longitude 17° 41' (–BA), *Van Berkel 307* (NBG); 4 miles [6.4 km] E of Grootmis (–CA), *Hiemstra 482* (NBG, PRE); Rooivlei (–CC), *Van Jaarsveld 5413* (NBG); Komaggas (–DC), *Herre* sub SUG 3660, SUG 3672 (BOL). **3017** (Hondekliapaai): 1 km E of junction of Soebatsfontein/Kamieskroon road towards Killians

Pass (–BA), *Snijman 188* (NBG); 24 miles [38.6 km] NW of Garies (–BD), *Salter & Creasey* sub NBG 893/37 (NBG). **3018** (Kamiesberg): 18 miles [29 km] S of Garies (–CA), *Stayner s.n.* sub NBG 1026/71 (MO, NBG, PRE); 68 km N of Nuwerus, *Van Berkel 318* (NBG). **3119** (Calvinia): Charley-se-Hoek, Nieuwoudtville (–AC), *Snijman 99* (B, K, MO, NBG, PRE, S); second gate between Grasberg and Theunisdrift, *Snijman 139* (NBG, PRE); Calvinia, 23.6 km W of town on road to Nieuwoudtville (–BC), *Manning 3490* (NBG); farm Rietfontein between Calvinia and Loeriesfontein, *Snijman 1776* (NBG); Vanrhyns Pass, *Snijman 141* (NBG); 8½ miles [13.7 km] NE of Lokenburg (–CA), *Acocks 19193* (K, PRE). **3220** (Sutherland): Ouberg Pass, W of Sutherland (–AD), *Bruyns 2553* (NBG); 5 km SW of Windheuwel along the Sutherland/Ceres road (–CC), *Snijman 208* (K, NBG); northern slopes of Verlatekloof (–DA), *Snijman 207* (B, K, MO, NBG, PRE); 82 km N of Laingsburg on road to Komsberg via Moordenaars Karoo (–DB), *Snijman 206* (K, MO, NBG, PRE).

WESTERN CAPE. **3118** (Vanrhynsdorp): hillside above Bitterfontein (–AB), *Hiemstra 410* (NBG); Vanrhynsdorp (–DA), *Strey 3901* (PRE); Vleikraal, E of Klawer, *Walters 126* (STE); Sandkraal (–DB), *Smith 6408* (NBG). **3119** (Calvinia): mountains above farm Dagbreek (–CB), *Snijman 358* (NBG); Doornbosch (–CC), *Martin 1154* (NBG). **3217** (Vredenburg): Paternoster Bay (–DD), *Axelson 399* (NBG). **3218** (Clanwilliam): Lamberts Bay (–AB), *Wagener s.n.* (NBG); Bulshoek Dam; *Snijman 1792* (NBG); farm Dagbreek, 22 km N of Clanwilliam (–BB), *Roux 184* (K, MO, NBG, PRE); 30 km S of Clanwilliam (–BD), *Goldblatt 1847* (MO, NBG); Brakfontein, *Van Jaarsveld 4329* (NBG, PRE); 1.5 km SW of Goedverwacht (–DC), *Hardick & Hiemstra 150* (B, K, MO, NBG, PRE); 20 miles [32.2 km] N of Porterville (–DD), *Compton & party* sub NBG 2002/36 (NBG); Piketberg, *Liebenberg 5590* (PRE); 7 miles [11.3 km] N of Piketberg, *Salter 4425* (BOL). **3219** (Wuppertal): Gatdeurkop, Algeria Forest Station (–AC), *Viviers 136* (NBG); Zuurfontein farm, Matjieskloof (–AD), *Low 7751* (NBG); new Elands Kloof Pass (–CA), *Thorns* sub NBG 142/47 (NBG); Skoongesig, Koue-Bokkeveld (–CC), *Hanekom 2093* (PRE); Winkelhaaks River (–DC), *Thorns* sub NBG 397/44 (NBG). **3317** (Saldanha): Saldanha Bay (–BB), *Lawrence* sub NBG 150/47 (NBG). **3318** (Cape Town): Ysterfontein (–AC), *Rourke 1190* (NBG); farm Geelkuil, near Malmesbury (–BA), *Thompson 13* (NBG, PRE); 2 miles [3.2 km] S of Porterville (–BB), *Loubser 2082* (NBG); *Loubser 2100* (NBG); Oudepost (–BC), *Mathews* sub NBG 662/30 (BOL, K); Bokbaai (–CB), *NBG Expedition* sub NBG 910/72 (K, NBG, PRE); in fruticibus clivis Montis Tabularis (–CD), *Dummer 1346* (E); Table Mountain, *Harvey s.n.* (BM); Devils Peak, *Marloth 595* (PRE); Fernwood Buttress, *Wasserfall 134* (NBG); Vissers Hok (–DC), *Compton 15625* (BOL, NBG); *Leighton 439* (BOL); Klein Langverwacht above Kuils River, *Oliver 3737* (K); Jonkershoek (–DD), *Esterhuysen 18481* (BOL); Paradise Gorge, Stellenbosch Mountain, *Garside 455* (K); *Garside s.n.* (K); southern slopes of Simonsberg, *Snijman 196* (B, K, MO, NBG, PRE). **3319** (Worcester): De Tronk near Groot Winterhoek (–AA), *Low 917* (NBG); Groothoek (–BC), *Ashton 1* (NBG, PRE); Hex River valley, *H. Bolus s.n.* (BOL); *Snijman 1* (MO, NBG); farm Leliefontein, W of Du Toits Kloof (–CA), *Snijman 149* (NBG, PRE); Worcester (–CB), *Esterhuysen 10171* (BOL); *Van Breda 10395* (PRE); Worcester Veld Reserve, *Olivier 68* (STE); Karoo Garden Veld Reserve, *Snijman 84* (B, K, MO, NBG, PRE); Klein Drakenstein, foot of Wemmershoek mountains (–CC), *Esterhuysen 18594* (BOL); farm Salem, *Galpin 11059* (K, PRE); Bellvue at foot of Jonaskop (–CD), *Snijman 3* (MO, NBG, PRE); Robertson (–DD), *Melle* sub NBG 2207/15 (BOL). **3320** (Montagu): farm Jagerskraal near Pieter Meintjies station (–AD), *Snijman 200* (NBG); Matjiesfontein (–BA), *Bolus* sub NBG 2046/14 (BOL); Whitehill Ridge, *Compton 15614* (NBG); *Olivier s.n.* (NBG); 36 km NE of Laingsburg along Moordenaars Karoo road (–BB), *Snijman 204* (NBG, PRE); Waboomsberg, farm Highlands (–CA), *Rourke 1666* (NBG, PRE); 25 km W along Witteberg road from junction off Laingsburg/Ladismith road (–CB), *Snijman 202* (B, K, MO, NBG, PRE); Montagu Baths (–CC), *Page s.n.* (BOL); Bellair Dam (–DA), *Rourke 1699* (NBG, PRE). **3321** (Ladismith): Ladismith (–AD), *Herre* sub SUB 3665 (BOL); SE of Calitzdorp dam (–BC), *Snijman 406* (MO, NBG, PRE); Huisriver Pass (–DA), *Bruyns 2222* (NBG, PRE); *Snijman 407* (K, MO, NBG); Calitzdorp Spa, *Snijman 369* (NBG, PRE); *Snijman 396* (NBG); farm Rietvlei, *Snijman 395* (K, MO, NBG, PRE, S); Melkhoutessenbosch, Mossel Bay division (–DC), *Muir 2066* (BOL, PRE). **3322** (Oudtshoorn): 5 km from Oudtshoorn towards George (–CA), *Snijman 397* (K, MO, NBG, PRE). **3418** (Simonstown): Cape Point (–AB), *Middlemost 1668* (MO, NBG); hills above Kalk Bay, *Wolley-Dod 952* (BOL); between Buffels Bay and

Paulsberg (–AD), *Leighton s.n.* (BOL); Macassar (–BB), *Nichols 16* (K, NBG, PRE); Elephant Rock Mountain, Betty's Bay (–BD), *Boucher 1471* (K, PRE); Betty's Bay, *Fisher 16* (NGB, PRE); *Snijman 94* (K, MO, NBG). **3419** (Caledon): Kraal Rock cliffs Hermanus (–AC), *Horrocks 166* (NGB); beach at Onrust River *Leighton 414* (BOL); 1 km SW of farm Avontuur along Albertyn/Caledon road, *Snijman 87a* (K, MO, NBG, PRE); Danger Point (–CB), *Hiemstra 120* (B, NBG); *Hiemstra 125* (NGB, PRE). **3420** (Bredasdorp): Potberg (–AD), *Burgers 2196* (B, NBG); *Burgers 2287* (NGB); De Hoop, *Lewis* sub NBG *153/57* (MO, NBG); *Snijman 113* (K, NBG, PRE); *Williams s.n.* (NGB); Cape L'Agulhas (–CC), *Leighton* in herb. Bol. 657 and 679/33 (K). **3421** (Riversdale): between Ystervarkfontein and Gouritz River Mouth (–BD), *Forrester s.n.* (NGB); Gouritz River Mouth, *Snijman 317* (K, MO, NBG, PRE).

EASTERN CAPE. **3323** (Willowmore): Willowmore (–AD), *Herre* sub SUG *3682* (BOL). **3324** (Steytlerville): track N of Enkeldoorn, Baviaanskloof (–CA), *Snijman 349* (NGB); farm Dam-se-Drif, Baviaanskloof, *Snijman 399* (MO, NBG, PRE); 3 km E of Sandvlakte, Baviaanskloof, *Snijman 401* (K, MO, NBG, PRE). **3325** (Gqeberha): Vaaldam, Uitenhage [Kariega] District (–CA), *Marais s.n.* (NGB); Sundays River bridge between Addo and Port Elizabeth [Gqeberha] (–DA), *Snijman 494* (NGB); Port Elizabeth [Gqeberha] area (–DC), *Batten s.n.* (NGB); Walmer, *Roux 502* (NGB, PRE); *Snijman 321* (K, NBG, PRE); *Tarr* sub NBG *994/70* (NGB); *Urton s.n.* (K, MO, NBG). **3326** (Makhanda): 1 km S of Doringkom along Kommadagga/Alicedale road (–AC), *Snijman 472* (K, NBG, PRE).

18

Haemanthus dasyphyllus*Snijman*

Haemanthus dasyphyllus *Snijman* in Journal of South African Botany, suppl. vol. 12: 105 (1984). Type: South Africa, Cape Province [Northern Cape], farm Langberg, NW of Loeriesfontein, fl. NBG 4 Mar. 1983, *Snijman* 647 (NBG, holo.; K, PRE, iso.).

Plants deciduous, green in winter, up to 275 mm high when flowering. *Bulbs* clumped, elongate-ovoid, $\pm$ round or compressed crosswise to distichous leaves, 45–60 mm diam., tunics imbricate, distichous, with oblique margins, cream-coloured, mostly covered with light brown papery remnants. *Leaves* hysteranthous, (1)2, erect, blade narrowly to broadly lanceolate, 190–330 $\times$ 26–70 mm, mostly twisted, often channelled, both surfaces pale green with a few red bars at base of abaxial surface, mostly covered with long soft white hairs, sometimes on abaxial surface or margins only, apex subacute. *Scape* 30–230 $\times$ 4–10 mm, pale red or cream with darker red speckling, softly pilose or glabrous. *Spathe bracts* 5 or 6, erect, shorter or as long as flowers, oblong-lanceolate, 30–45 $\times$ 5–20 mm, firm, coral to scarlet, tips obtuse or subacute. *Inflorescence* compact, narrowly obconical to oblong, 25–50 mm across. *Flowers* 20–50, $\pm$ erect; pedicel 4–15 mm long, whitish; perigone 14–25 mm long, coral to scarlet, white below and on tips; tube 3–7 mm long, gibbose below each tepal; tepals erect, linear to narrowly spatulate, 11–20 $\times$ 1 mm, tips obtuse and swollen. *Stamens* exerted by up to 10 mm; filaments, reddish, white-tipped; anthers 2 mm long, yellow. *Ovary* $\pm$ 2 mm diam., pale green. *Style* $\pm$ as long as filaments. *Berry* $\pm$ ovoidal, $\pm$ 8–12 mm diam., flushed with deep to pale pink. *Seeds* $\pm$ ovoidal, 6–8 mm diam., turning dark wine-red. *Flowering time*: February to March. Figure 44.

Distribution and habitat: Scattered populations of *H. dasyphyllus* are distributed along the elevated northeastern rim of the Succulent Karoo that borders on Bushmanland. The distribution covers eastern Namaqualand, northeastern Knersvlakte, Kubiskouberg and Langberg, northwest of Loeriesfontein, Northern Cape (Figure 45). Elevations reach $\pm$ 600–1 000 m above sea level, with annual rainfall of $\pm$ 150 mm per annum. Localised populations are typically found on granite-gneisses or shale, in sparse succulent shrubland. This easterly region lies close to the winter- and summer-rainfall interface, hence *H. dasyphyllus* often flowers from as early as February to late March, in response to scattered thundershowers in late summer.

Diagnosis: *Haemanthus dasyphyllus* is distinguished by its pale green, lanceolate leaves with a covering of white hairs, on both surfaces, only the abaxial surface, or just on the leaf edges. The leaf blades



Figure 44. *Haemanthus dasyphyllus*. 1, inflorescence; 2, flower; 3, infructescence; 4, bulb and bulblet; 5, hysteranthous leaves. Snijman 647 (NBG), Langberg. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 3–5 = 13.3 mm; 2 = 6.6 mm.

are erect, usually twisted and speckled with red at the base. The colour and markings of the leaves most closely approach those of *H. unifolius*, which differs in being typically unifoliate with a covering of short patent hairs. In contrast, the hairs of the bifoliate *H. dasyphyllus* are long, soft and somewhat shaggy. The scarlet inflorescence, surrounded by 5 or 6 erect, oblong-lanceolate spathe bracts, is compact and held on a scape that is often softly hairy.

Discussion: *Haemanthus dasyphyllus* was first collected by H.W.R. Marloth in the Kubiskouberg in 1926 and thirty years later by J.P.H. Acocks on the Langberg. Due to the hairiness and barring of the leaves, the specimens were misidentified as *H. pubescens* and *H. tigrinus*. Further collections from the same area in 1982 finally allowed these plants to be formally described (Snijman 1984).

Note: The species is known locally by the vernacular name *donkie-ore*.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **3018** (Kamiesberg): SW of Grootklip, Langberg (–DB), *Acocks 19049* (PRE); farm Langberg, *Bayer 2770* (NBG); *Bayer 2771* (NBG); *Snijman 647* (K, NBG, PRE); *Snijman 665* (MO, NBG, S); Namaqualand, farm Aasvoëlkop, between Loeriesfontein and Kliprand, *Snijman 1779* (NBG). **3019** (Loeriesfontein): farm Haasrivier, 52 km from Loeriesfontein to Taaiboshoeck (–CA), *Snijman 1299* (NBG); Kubiskouw Mountain (–CD), *Marloth 12857* (PRE).

WESTERN CAPE. **3018** (Kamiesberg): farm Kamaboes, 27 km SW of Kliprand towards Bitterfontein (–DA), *Snijman 1312* (NBG); Knersvlakte, farm Uilklip (–DC), *Manning 2956* (NBG); *Snijman 1423* (NBG).

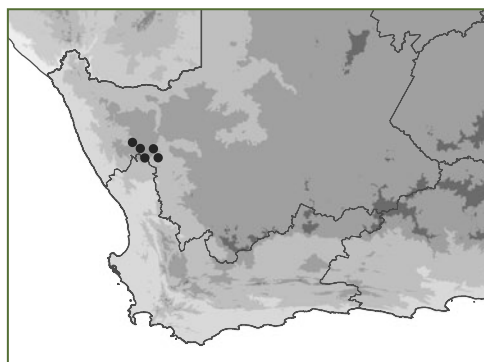


Figure 45. Distribution of *Haemanthus dasyphyllus*.

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Haemanthus unifolius*Snijman*

Haemanthus unifolius *Snijman* in Journal of South African Botany, suppl. vol. 12: 109 (1984). Type: South Africa, Cape Province [Northern Cape], 24 km E of Narapberg, fl. 29 Mar. 1981, *Snijman* 416 (NBG, holo.; K, MO, NBG, PRE, iso.).

Plants deciduous, green in winter, up to $\pm$ 200 mm high when flowering. *Bulb* solitary, globose to obclavate, circular in cross section or slightly compressed towards leaf blade, up to 55 mm diam., tunics unequal, in tiered horizontal layers, whitish, usually covered with withered brown remnants. *Leaf* hysteranthous, 1(2), erect or laterally curved, blade narrowly to broadly obovate or elliptic, 100–200(–490) $\times$ 25–90(–135) mm wide midway, narrowing to 5–15(–30) mm at base, plane, both surfaces pale green, minutely speckled with red towards base, densely or thinly tomentose, margin often red, entire, apex acute or obtuse. *Scape* slender, erect, up to 180 $\times$ 4–10 mm, pale scarlet, immaculate or very faintly spotted, glabrous or sparsely covered with soft retrorse hairs. *Spathe bracts* 4–6, erect, shorter or longer than flowers, oblong-lanceolate or obovate, 20–45 $\times$ 6–25 mm, scarlet, stiff but not fleshy, tips obtuse to acute. *Inflorescence* compact, narrowly obovoid, 18–50 mm across. *Flowers* 6–30, erect; pedicel (3–)5–12 mm long, white to reddish; perigone 13–25 mm long, scarlet with white on tube and tepal tips; tube 2–5 mm long, gibbose at base of each tepal; tepals erect, linear to narrowly lanceolate or spatulate, 11–21 $\times$ 1–3 mm, tips obtuse to acute. *Stamens* exerted by up to 8 mm; filaments white; anthers $\pm$ 1.5 mm long, yellow. *Ovary* 2–3 mm diam., green. *Style* as long as stamens. *Berry* ovoidal, $\pm$ 13 mm diam., pale pink to white, becoming soft, pulpy and translucent. *Seeds* ovoidal to spheroidal, 8–10 mm diam., dark wine-red. *Flowering time*: March to April or a month earlier in cultivation. Figure 46.

Distribution and habitat: Populations of *H. unifolius* are scattered from southwestern Richtersveld to the high-lying Anenous plateau, southwards along the Namaqualand escarpment to Spektakelberg, ultimately reaching the vicinity of Soebatsfontein, Northern Cape (Figure 47). Most of the area is situated at elevations of 500–1 200 m above sea level and the average annual rainfall varies from 120 mm on the lowlands to 200 mm at higher elevations. The area between Steinkopf and Spektakelberg, west of Springbok has clay-rich, heavy soils derived from Nama shales and quartzites that are able to hold water more efficiently than in the coarse sand derived from granite-gneisses on the foothills below the escarpment (Mucina et al. 2006a). The species occurs mostly in stony habitats, as well as sandy open places on gentle south-facing slopes surrounded by dwarf succulent shrubs.

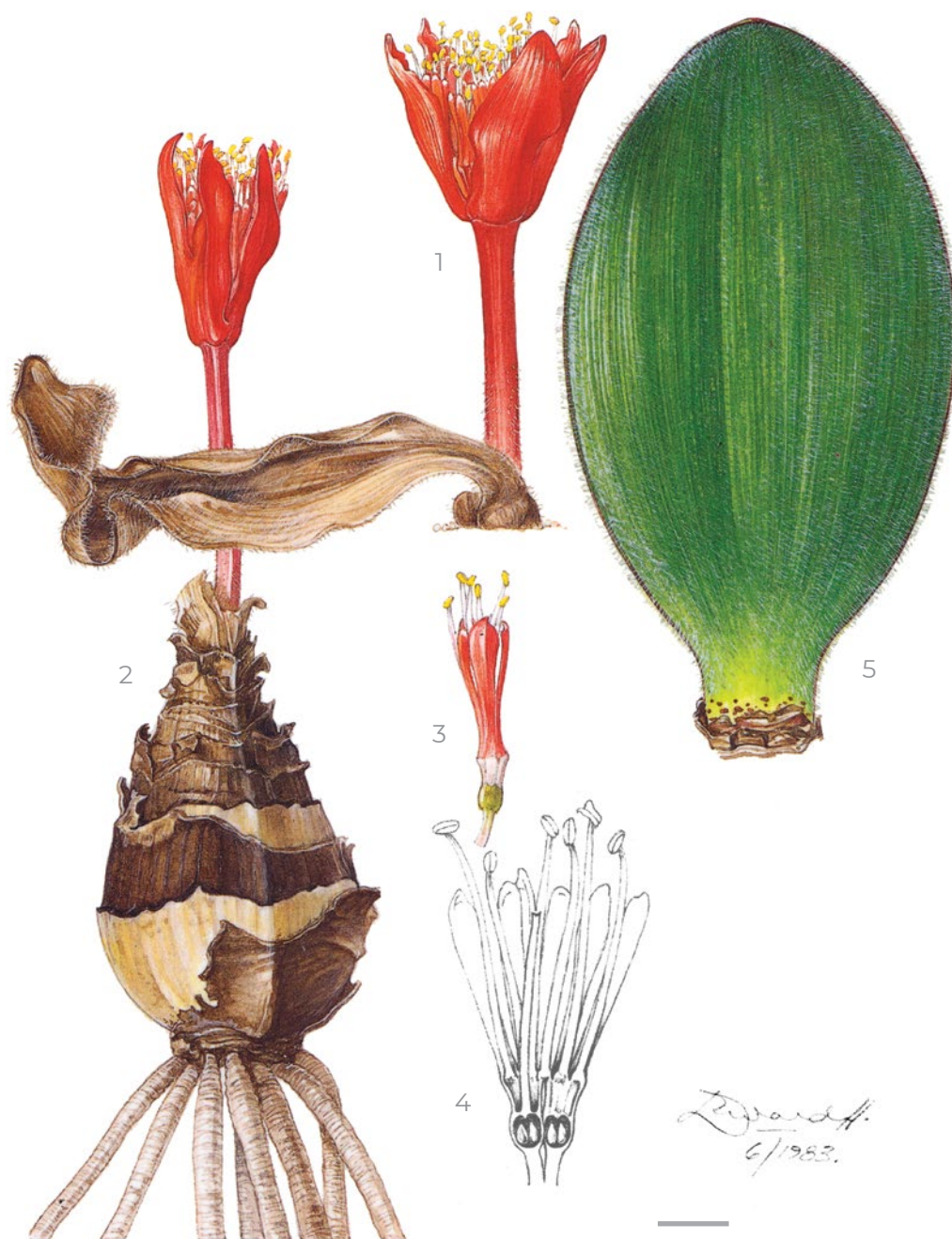


Figure 46. *Haemanthus unifolius*. 1, inflorescence and previous season's dry leaf; 2, bulb and inflorescence; 3, flower; 4, section of flower; 5, erect, hysteroanthous leaf. *Snijman 181* (NBG), near Spektakel Pass. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 2, 5 = 11.8 mm; 3 = 8.6 mm; 4 = 6.25 mm.

Diagnosis: *Haemanthus unifolius* is easily distinguished by its solitary, erect, densely or thinly tomentose, pale green leaf. Only rarely are the plants bifoliate, but then the obclavate bulb is diagnostic. It is either round in cross section or compressed in the same plane as the leaf blade, and the bulb tunics are arranged in tiered horizontal layers. The compact inflorescence, surrounded by 4–6, erect, oblong-lanceolate spathe bracts, is scarlet and somewhat slender, comprising 6–30 erect flowers (Figure 7D).

Discussion: All species of *Haemanthus* are unifoliate in the juvenile stage. As they mature, however, the majority become bifoliate, except within three species which remain predominantly unifoliate, namely *H. unifolius* and *H. nortieri* within subg. *Haemanthus*, and *H. pauculifolius* within subg. *Serena*.

Observations on *H. unifolius* and *H. nortieri* cultivated at Kirstenbosch National Botanical Garden, nevertheless, suggest that the unifoliate state may sometimes be intermittent, since a few individuals were single-leaved one year, two-leaved the next and then single-leaved again. A study of the life history of *H. nortieri* showed that none of the ten mature bulbs dissected by Isaac (1937) had ever been bifoliate, suggesting that the occurrence of leaf-pairs in the wild is infrequent. This reduction in leaf number is possibly offset by the leaf's upright habit that may serve to enhance the interception of the sun's rays during the cool winter months.

Bulbs and leaves of the species were first collected by Rev. G. Meyer near Steinkopf in 1927, but the flowers remained unknown for a further half century until the species was discovered in flower and subsequently described (Snijman 1984).

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **2917** (Springbok): Anenous Pass (–BA), *Müller-Doblies* 79115a (NBG, PRE); *Snijman* 177 (MO, NBG); *Snijman* 419 (K, NBG); Pypklip Poort, *Van Berkel* 309 (NBG); 5 km N of the Steinkopf/Port Nolloth road towards Kosies, *Snijman* 158 (NBG); at turnoff to Kosies from the Steinkopf/Port Nolloth road, *Snijman* 160 (NBG, PRE); Steinkopf (–BC), *Marloth* 12657 (PRE); *Meyer* sub *Marloth* 13396 (PRE); Besondermeid, *Du Plessis* 417 (NBG); Komaggas Reserve (–CB), *Van Berkel* 301 (NBG); Nigramoep (–DA), *Herre* 3539 (BOL); *Herre* 3669 (BOL, STE); 20.2 km W of Springbok towards Spektakel Pass, *Snijman* 181 (NBG, PRE); Spektakel Pass, *Van Berkel* 120 (MO, NBG); along the Komaggas/Spektakel road, *Van Berkel* 303 (NBG); 51.4 km from Springbok towards Komaggas, over Spektakel Pass, *Snijman* 182 (K, NBG, PRE); 4 miles [6.4 km] N of Komaggas (–DC), *Wisura* 1693 (NBG). **3017** (Hondeklipbaai): near Canariesfontein along road towards Soebatsfontein from Springbok (–BA), *Van Berkel* 404 (NBG).

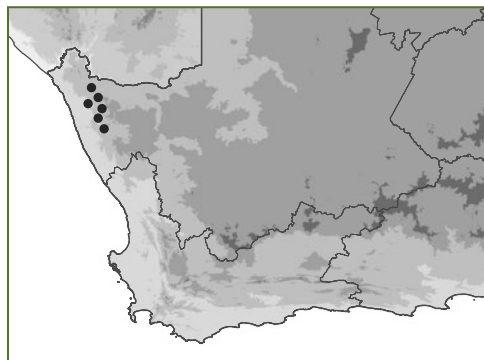


Figure 47. Distribution of *Haemanthus unifolius*.

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Haemanthus arenicola*(Snijman) Snijman*

Haemanthus arenicola (*Snijman*) *Snijman*, stat. nov. *Haemanthus pubescens* subsp. *arenicola* Snijman [as subsp. *arenicolus*] in Journal of South African Botany, suppl. vol. 12: 118 (1984). Type: South Africa, Cape Province [Northern Cape], farm Kannikwa 156, ± 20 km NE of Port Nolloth, fl. 29 Mar. 1981, *Van Berkel 313* (NBG, holo.!, PRE!, iso.).

Plants deciduous, green in winter, up to ± 300(–500) mm high when flowering. *Bulbs* deep-seated, forming clumps, ± 80 mm diam., ± elliptical in cross section, basal disc sometimes well-developed, tunics moderately slanting downwards, with pale brown papery margins. *Leaves* hysteranthous, 2(3), spreading, blade narrowly ligulate (100–)150–350 × 15–40 mm, channelled, adaxial surface glabrous, abaxial surface speckled with red towards base, rarely immaculate, covered with long, soft, white hairs over entire surface or near edges, rarely glabrous, margin red, fringed with long soft hairs, rarely smooth. *Scape* stout, erect, ± compressed, 80–410 × 6–9 mm, scarlet, with minute darker speckles proximally, glabrous. *Spathe bracts* 4(5), erect, longer than flowers by (20–)30–80 mm, oblong-lanceolate, 50–70(–135) × 16–35 mm, acute, scarlet, stiff and fleshy. *Inflorescence* compact, narrowly obconical, ± 40 mm across. *Flowers* ± 20–30, suberect; pedicel 6–9 mm long, pale red; perigone 20–30 mm long, scarlet with whitish tube and tips; tube 4–5 mm long, gibbose below each tepal base; tepals nipped-in above tube then erect, linear, 14–25 × 1.0–1.5 mm, swollen at tip. *Stamens* exerted by ± 10 mm; filaments pale red; anthers 2–3 mm long, yellow. *Ovary* 2–3 mm diam., pale green. *Style* equalling stamens, reddish. *Berry* ovoidal, ± 20 mm diam. *Seeds* ovoidal, ± 15 mm diam., dark wine-red. *Flowering time*: March to April. Figure 48.

Distribution and habitat: *Haemanthus arenicola* is confined to semi-arid sandveld, along the flat to slightly undulating coastal forelands of northern Namaqualand, Northern Cape, from southeast of Alexander Bay, southwards to the vicinity of Wallekraal, north of the Groenrivier (Figure 49). Due to its proximity to the cold Atlantic Ocean the area receives 60–150 mm precipitation annually, often in the form of fog or dew. Small, isolated populations of about 20 or less, scattered individuals are confined to stabilised, deep, gritty, poorly leached, red, aeolian sands amongst a sparse covering of dry grasses and dwarf shrubs (Figure 5A). In recent years the area has become severely degraded by surface mining operations for heavy minerals, the impacts of which reach far beyond the immediate area being mined, well into the adjacent lowland ecosystem (Carrick & Krüger 2007).



Figure 48. *Haemanthus arenicola*. 1, inflorescence; 2, flower; 3, section of flower; 4, bulb; 5, hysteranthous leaves; 6, leaf habit. *Van Berkel 313* (NBG), farm Kannikwa. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1, 2, 5 = 12.5 mm; 3 = 6.25 mm; 4 = 18 mm; 6 = 100 mm.

Diagnosis: The species differs from the other sand-loving species of *Haemanthus*, namely *H. leipoldtii* and *H. pubescens*, by its narrow, strap-shaped leaves 15–40 mm wide that are spreading and slightly canaliculate, with the abaxial surface sparsely covered with long soft hairs. Only rarely are the leaves glabrous. As in *H. leipoldtii*, the brilliant red inflorescence is surrounded by 4 or rarely 5, remarkably long, suberect spathe bracts, a highly specialised state compared with those within other taxa. The bracts are scarlet, stiff and waxy, and unlike the somewhat blunter spathe bracts of *H. pubescens* they are characteristically oblong-triangular in outline with acute tips.

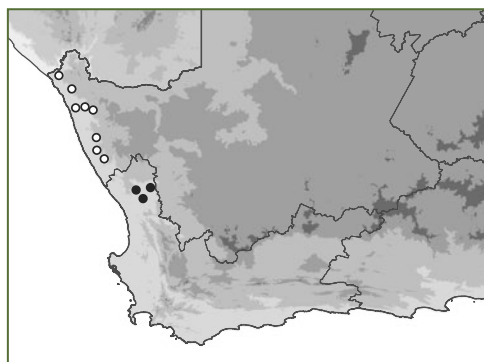


Figure 49. Distribution of *Haemanthus arenicola* (○); *H. leipoldtii* (●).

The bulbs of *H. arenicola* are less compressed than those of its allies and the basal disc tends to persist for several years without withering away. Thus, the deeply buried bulbs are usually markedly elongated and they often have an extended rooting zone that gives rise to numerous, long, contractile roots capable of reaching moisture reserves deep below the surface. The basal disc in other taxa invariably remains somewhat flat, thus giving rise to a narrow ring of roots around its periphery.

The features distinguishing *H. arenicola* from the closely related *H. leipoldtii* are more fully discussed under the latter.

Discussion: Bulbs of this species were first collected in leaf in 1979. Inflorescences, however, were only seen two years later when N. van Berkel gathered the type material in the red sands of the Oograbies plain, east of Port Nolloth. Although the distribution is extensive along the semi-arid coastal forelands of northern Namaqualand, the bulbs are relatively scarce and widely scattered.

The decision to elevate the taxon from subspecific rank within *H. pubescens* to species level, is supported by its geographical isolation and its morphological distinctness from other members of this sandveld group, as fully discussed under *H. pubescens*.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE. **2816** (Oranjemund): Alexander Bay, E of Buchenberg (–DD), *Williamson & Leach 2980a* (BOL). **2917** (Springbok): farm Kleinduyn 154 (–AA), *Van Berkel 152* (NBG); *Van Berkel 272* (NBG); farm Oograbies West 153 (–AA), *Van Berkel 310* (NBG); extreme NE corner of farm Kannikwa 156, *Van Berkel 313* (NBG, PRE); Rooivlei near Kleinsee (–CC), *Van Jaarsveld 5413* (NBG); ± 1 km S of turnoff towards Komaggas from Soebatsfontein (–CD), *Snijman 186* (NBG); 10.6 km S of turnoff to Komaggas on road to Soebatsfontein, *Snijman 187b* (NBG); between Soebatsfontein and Kourkammaberg, Oubees-se-Sand (–DC), *Snijman 1803* (NBG); farm Oubees se Sand, *Van Berkel 175* (NBG). **3017** (Hondeklipbaai): Namaqualand, SE of Kookfontein (–BA), *Manning s.n.* (NBG 157811); ± 5 km from Wallekraal towards Soebatsfontein (–BC), *Van Jaarsveld 5286* (NBG); farm Kwoap 494 (–DA), *Van Berkel 314* (NBG).

21

Haemanthus leipoldtii*(Snijman) Snijman*

Haemanthus leipoldtii (*Snijman*) *Snijman*, stat. nov. *Haemanthus pubescens* subsp. *leipoldtii* Snijman in Journal of South African Botany, suppl. vol. 12: 117 (1984). Type: South Africa, Cape Province [Western Cape], farm Sandkraal, S of Vanrhynsdorp, fl. 31 Mar. 1981, *Snijman 430* (NMG, holo.; K, MO, PRE, S, iso.).

Plants deciduous, green in winter, up to 250 mm high when flowering. *Bulb* solitary, broadly ovoid, ± 60 mm diam., compressed crosswise to distichous leaves, tunics with oblique, pale brown papery margins. *Leaves* hysteranthous, 2, prostrate, blade broadly oblong, $120\text{--}200 \times 45\text{--}85$ mm, plane and glabrous, adaxial surface shiny green to glaucous, abaxial surface sometimes speckled with red, margin red, fringed with soft white hairs, sometimes only distally, apex obtuse to subacute. *Scape* stout, erect, $\pm$ compressed, $75\text{--}205 \times 6\text{--}9$ mm, plain red, glabrous or rarely sparsely hairy. *Spathe bracts* 4 or 5, erect, longer than flowers by up to 40 mm, oblong-lanceolate, $50\text{--}80 \times 15\text{--}28$ mm, subacute, apiculate, scarlet, stiff and fleshy. *Inflorescence* compact, narrowly obconical, 25–50 mm across. *Flowers* 15–40, erect; pedicel 6–10 mm long, pale red; perigone 19–30 mm long, scarlet, with whitish tube and tips; tube 4–5 mm long, distinctly gibbose at base of each tepal; tepals nipped-in above tube then erect, linear, $18\text{--}25 \times \pm 1$ mm, swollen at tip. *Stamens* exserted by ± 12 mm; filaments scarlet with white tips; anthers 1–2 mm long, yellow. *Ovary* 2–3 mm diam., pale green. *Style* $\pm$ as long as stamens. *Berry* large, globose, ± 20 mm diam., pale pink to white, pulpy when ripe. *Seeds* ovoidal, $\pm 7\text{--}10$ mm diam., dark wine-red. *Flowering time*: February to early April. Figure 50.

Distribution and habitat. *Haemanthus leipoldtii* is known from a small area of Namaqualand, in the sandveld just north and east of the lower Olifants River valley, in the vicinity of Klawer and Trawal, Western Cape, at elevations of 100–200 m above sea level (Figure 49). Populations of scattered individuals are found in deep, yellowish, acid sands, together with restioid species within open shrubland, comprising *Dodonaea viscosa* Jacq. (Sapindaceae), *Euphorbia mauritanica* L. (Euphorbiaceae) or *Didelta spinosa* (L.f.) Aiton (Asteraceae). Precipitation in the area reaches almost 200 mm per annum in the form of winter rain and fog that condenses on the adjacent north–south trending western Cape Fold mountains. Flowering, however, is often induced by late summer thundershowers.

Diagnosis: The species is characterised by prostrate, uniformly glabrous, flat, broad leaves, apart from the margins which are fringed with soft white hairs. Together with the closely allied *H. arenicola*, the two species possess remarkably large, stiff, fleshy, red spathe bracts, which are the longest in



Figure 50. *Haemanthus leipoldtii*. 1, inflorescence (head bent forward to illustrate flowers); 2, prostrate, hysteranthous leaves; 3, bulb; 4, section of flower; 5, flower. *Snijman 430* (NBG), W of Matsikamma. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–3, 5 = 12.5 mm; 4 = 6.25 mm.

the genus. In some individuals of *H. leipoldtii* the bracts reach up to 80 mm in length (*Snijman 430*, NBG), whereas in *H. arenicola* spathe bracts of up to 135 mm long have been recorded (*Snijman 1805*, NBG). *Haemanthus leipoldtii* is distinguished from the latter by its broader (45–85 mm wide), oblong leaves that spread flat on the ground, in contrast to the slightly arched, strap-shaped, 15–40 mm wide, channelled leaves of *H. arenicola* that are typically covered with long, soft, white hairs on the abaxial surface, at least towards the edges.

The bulb tunics in both *H. leipoldtii* and *H. arenicola* have well developed sheaths, unlike those of *H. pubescens* that are one-sidedly reduced and resemble specialised bulb scales. Moreover, the flowers of *H. leipoldtii* and *H. arenicola* are distinctly pedicellate (6–10 mm and 6–16 mm, respectively), differing from the shorter pedicels in *H. pubescens* (1–6 mm long).

Discussion: To accommodate the taxonomic changes made to this group of sandveld taxa, as discussed under *H. pubescens*, this taxon is elevated here to species rank. Superficially, the flat leaves of *H. leipoldtii* may be mistaken for the prostrate leaves of *H. lanceifolius*, a distantly related species that is also endemic to the vicinity of Klawer. However, the latter occurs mostly in soils overlying dolomite substrates. Moreover, the leaves of the latter have a rough adaxial surface, and the somewhat thickened, cartilaginous margin is fringed with recurved, multicellular, often branched cilia that are reduced to a minutely crenulate margin in outlying plants.

Biographical note: The species epithet honours C.L. Leipoldt, poet, journalist, medical practitioner and plant collector, who first gathered bulbs of this species in the Olifants River valley in 1929.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3118** (Vanrhynsdorp): 1 mile [1.6 km] S of Wiedouw River (–DA), *Hall 1082* (NBG); 6.5 km N of Klawer, *Snijman 431* (MO, NBG); Vleikraal, E of Klawer, *Walters 122* (STE); Klawer (–DC), *Snijman 432* (K, NBG, PRE).

Inexact localities: between Klawer and Clanwilliam, *Leipoldt s.n.* (BOL); the weir, Olifants River valley, *Leipoldt s.n.* (BOL).

22

Haemanthus pubescens*L.f.*

Haemanthus pubescens *L.f.*, Supplementum plantarum: 193 (1782) [1781]; Baker: 73 (1888); Baker: 241 (1896); Friis & Nordal: 68 (1976). *Haemanthus angustifolius* Salisb.: 217 (1796), nom. illeg. superfl. *Leucodesmis pubescens* (L.f.) Raf.: 19 (1838). Type: South Africa, without locality, *Thunberg s.n.*, sheet 7927 in herb. Thunb. [UPS, lecto., designated by Friis & Nordal: 68 (1976)].

Haemanthus quadrivalvis Jacq.: 30, t. 58 (1797); Ker Gawler: t. 1523 (1813). Type: South Africa, Cape of Good Hope [Western Cape], illustration in Jacquin: t. 58 (1797), lecto., designated by Friis & Nordal: 68 (1976).

[*Haemanthus trispathinus* M.Roem.: 37 (1847), nom. nud., invalid name, without description.]

Plants deciduous, green in winter, up to 250 mm high when flowering. *Bulb* broadly ovoid, strongly compressed crosswise to distichous leaves, 45–80 mm diam., readily forming bulblets, tunics fleshly, loosely imbricate, distichous, with oblique margins, cream-coloured. *Leaves* hysteranthous, 2, spreading to prostrate, blade ligulate to oblong-elliptic, 100–200 × (10–)15–35(–60) mm, plane, adaxial surface dark green, densely covered with white patent hairs, abaxial surface pale green, unmarked or with red spotting towards base, glabrous or sparsely pubescent, margin sometimes red, apex subacute. *Scape* slender to stout, 40–250 × 5–13 mm, red or rarely pink, unmarked or occasionally with darker markings, glabrous or sparsely pubescent. *Spathe bracts* 4 or 5(–7), erect, equalling or up to ± 20 mm longer than flowers, broadly to narrowly obovate or spatulate, abruptly reduced to a short point at apex, equally sized, (20–)30–60(–90) × (8–)20–30 mm broad in upper half, red or rarely pink, stiff, fleshy, waxy, rarely ciliate on margins. *Inflorescence* compact, narrowly obconical, 15–35 mm across. *Flowers* 4–25, erect; pedicel 1–3(–6) mm long, white to reddish; perigone 20–27 mm long, scarlet or rarely pink, with whitish tube and tips; tube 2–5 mm long, distinctly gibbose at base of each tepal; tepals nipped-in above base then erect, linear to narrowly oblong, 10–22 × 0.7–1.5 mm, swollen at tip. *Stamens* exerted by up to 12 mm; filaments scarlet with white tips; anthers 1–2 mm long, yellow. *Ovary* 2–3 mm diam., pale green. *Style* ± as long as stamens. *Berries* tightly clustered, large, globose, 16–22 mm diam., pale pink to white, soft and pulpy. *Seeds* subglobose, ± 5 mm diam., wine-red. *Flowering time*: March to April, occasionally late February. Figure 51.

Distribution and habitat: *Haemanthus pubescens*, treated here in the narrow sense and not as in Snijman (1984), occupies sand fynbos on the west coast from the vicinity of Graafwater in the north to



Figure 51. *Haemanthus pubescens*. 1, inflorescence; 2, flower; 3, bulb; 4, adaxial surface of one of hysteranthous, prostrate leaf pair. NBG 28/80 (NBS), near Malmesbury. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1 = 8.6 mm; 2–4 = 12 mm.

the northern outskirts of Cape Town in the south, and eastwards to the vicinity of Somerset West, Western Cape, at low elevations of < 250 m above sea level (Figure 52). Rain in the area, averaging 235–575 mm per year, falls almost exclusively in winter. Scattered populations occupy deep, white Tertiary sands, and less frequently loamy pockets of soil overlying weathered limestone or exposed Cape granite rocks, predominantly within asteraceous and restioid fynbos. These geophyte-rich sandy habitats include several burrowing herbivores, notably species of mole-rats (Rodentia: Bathyergidae), which through their foraging habits can act as dispersal agents. Like other geophytes here, the bulbs of *H. pubescens* readily produce vegetative offsets that not only have the potential to lessen underground depredation but also to benefit from short-distance dispersal (Procheş et al. 2006). When undisturbed by predators *H. pubescens* forms large colonies.

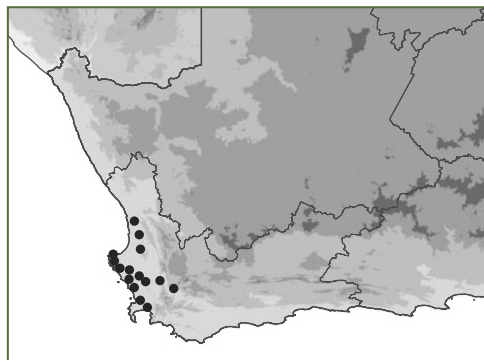


Figure 52. Distribution of *Haemanthus pubescens*.

Diagnosis: As implied by its name, *H. pubescens* is most easily recognised by the white patent hairs densely covering the adaxial leaf surface (Figure 3F). The outspread, flat leaves have a narrow base that widens to 10–60 mm midway and then narrows to a subacute tip. Significant features of the deep-seated bulbs are the strongly compressed form, crosswise to the distichous leaves, and the markedly one-sided reduction of the tunic sheath, which leads to a scale-like appearance. The attractive bright red or rarely carmine to pink inflorescences are closely surrounded by 4 or 5(–7), stiff, fleshy spathe bracts, which vary in length from equalling to overtopping the flowers by up to 20 mm. The regular shape of the bracts within each flower head is reliably diagnostic, either obovate or spatulate, invariably ending abruptly in a distinct point, whereas the tightly clustered flowers have notably short pedicels 1–3(–6) mm long. Depending on local conditions the plants show great variability in size, with the most diminutive forms growing on limestone outcrops.

Discussion: In the last revision of *Haemanthus* (Snijman 1984), *H. pubescens* was amplified to include two subspecies that are geographically widely separated from each other: one set of populations within the low-lying sand plains of northern Namaqualand and the other within the lower Olifants River valley. Both taxa possess inflorescences somewhat like those of typical *H. pubescens* from south of the lower Olifants River valley, although their spathe bracts and pedicels are markedly longer. The vegetative features distinguishing each taxon, nevertheless, are clearly discrete.

On review, the morpho-geographic patterns underlying the above infraspecific treatment within *H. pubescens* are at variance with those supporting the subspecific treatments within *H. humilis* and *H. amarylloides*. The widespread *H. humilis* encompasses two series of populations distinguished by small differences in perianth size and stamen length (Snijman 1984). Where populations of the two series are sympatric, however, intermediate plants occur. A similar morpho-geographic pattern exists

within *H. amarylloides*, despite the distribution pattern being more fragmented. Nevertheless, in some areas where populations of the differing series abut each other, plants with intermediate floral dimensions are present.

Following Stuessy (1990), when genetic and reproductive data are absent, characteristics useful for distinguishing subspecies include morphological distinctness, whether geographical patterns are cohesive, and whether there is a likelihood of natural hybridisation along any contact zones. The morpho-geographic patterns within *H. humilis* and *H. amarylloides* comply with these subspecific criteria but the patterns within *H. pubescens sensu lato* differ in this respect.

In addition to their morphological and geographical discreteness, the impacts of extensive open caste mining for heavy minerals along the Namaqualand coast (Carrick & Krüger 2007), and the expansion of agricultural lands along the lower Olifants River valley near Vredendal and Klawer (Raimondo & Von Staden 2009) continue to diminish the probability of contact zones developing between populations of the infraspecific taxa. *Haemanthus pubescens sensu* Snijman (1984) is therefore re-circumscribed here to include only those populations with densely hairy adaxial leaf surfaces and scale-like bulb tunics that are ecologically and geographically isolated from the populations previously recognised as subspecies from north of the Olifants River. In so doing the rank of the remaining taxa is raised to that of species. Their diagnostic features and distribution ranges are fully described under the respective species treatments.

Nomenclatural note: The name *H. pubescens* has been cause of considerable confusion in the past. Ker Gawler mistakenly applied the name to specimens of *H. albiflos* in a note following the illustration of *Curtis's Botanical Magazine* (1813: t. 1523) and again in *Edwards's Botanical Register* (1819: t. 382), an error that was repeated by Loddiges in the *Botanical Cabinet* (1823: t. 702). The mistaken identity apparently arose through comparison of a hairy-leafed form of *H. albiflos* with a sterile specimen of *H. pubescens* collected by Masson, and subsequently lodged in the British Museum.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3217** (Vredenburg): Steenberg Cove (–DB), *Barker* 9719 (NBG, PRE); Cape Columbine Lighthouse, Hopefield (–DD), *Hall* (NBG 80951); *Horrocks* (NBG 88671). **3218** (Clanwilliam): near Graafwater (–BA), *Thomas s.n.* (NBG); between Redelinghuys and Aurora (–CB/DA), *Barker* 9739 (NBG, STE); ½ mile [0.8 km] W of Piketberg (–DD), *Hiemstra* sub NBG 888/70 (MO, NBG). **3317** (Saldanha): Saldanha Bay (–BB), *Hall* 694 (NBG); *Marloth* 10194 (PRE); Hoedjies Bay, *Hall* 710 (NBG, PRE). **3318** (Cape Town): Donkergat (–AA), *Bayliss* 7293 (NBG); Langebaan, *Marloth* 13179 (PRE); Hopefield (–AB), *Letty* 108 (PRE); just N of Berg River near Hopefield, *Mauve & I. Oliver s.n.* (PRE 58349); farm Swartwater, 8 miles [12.9 km] NW of Darling (–AD), *Rourke* 1206 (NBG); farm Adventure near Malmesbury (–BC), *Downton s.n.* sub NBG 28/80 (K, NBG); *Snijman* 106 (B, NBG); farm La Fontaine, W of Riebeeck Kasteel (–BD), *Snijman* 89 (K, NBG); between Saxonwold and Mamre (–CB), *Rourke* 1197 (NBG); Milnerton (–CD), *L. Bolus s.n.* (BOL 19154); near Kalbaskraal (–DA), *Snijman* 1787 (NBG); Doornhoogte, Cape Flats (–DC), *Ecklon & Zeyher* 78.5 (E, PRE); ridge near Durbanville, *Galpin* 12690 (K, PRE); Klein Langverwacht, *Oliver* 3737 (STE, MO); farm Boompies, Bellville, *Olivier s.n.* (NBG 93829); Joostenbergvlakte, *Roux* 289 (MO, NBG). **3319** (Worcester): Wellington, Elandsberg [Private] Nature Reserve (–AC), *Snijman* 1677 (NBG); Breede River (–CA), *Mauve & I.*

Oliver s.n. (PRE 51861). **3418** (Simonstown): Macassar, E of Sjeik Josaf se Kramat [Sheikh Jusuf Kramat] (–BB),
Nichols 15 (AD, B, K, MO, NBG, PRE).

Inexact localities: near Cape Town, Mar. 1811, *Burchell 892* (K); Cape Flats, Mar. 1885, herb. *MacOwan 2544* (E);
Prom. b. Spei, *Masson* (BM); hort. Stellenbosch, Apr. 1920, *Garside 1380* (K).

23

Haemanthus sanguineus*Jacq.*

Haemanthus sanguineus *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 4: t. 407 (1804); *Herbert*: 255, t. 31, fig. 5 (1837); *Baker*: 71 (1888); *Baker*: 238 (1896). Type: South Africa, Cape of Good Hope [Western Cape], illustration in *Jacquin*: t. 407 (1804), lecto., designated by Friis & Nordal: 65 (1976).

Haemanthus rotundifolius Ker Gawl.: t. 1618 (1814). Type: South Africa, Cape of Good Hope [Western Cape], illustration in Ker Gawler in *Curtis's Botanical Magazine* 39: t. 1618 (1814), lecto., designated by Friis & Nordal: 68 (1976).

Haemanthus lambertianus Schult. & Schult.f.: 891 (1830). Type: South Africa, Prom. Bon. Spei. [Western Cape], *Niven s.n. comm. Lambert 1826*, in herb. Martius [BR 864430, lecto. [image!], designated by Friis & Nordal: 68 (1976)]. *Haemanthus rotundifolius* var. *multivalvis* Herb.: 235 (1837). Type: South Africa, Prom. Bon. Spei. [Western Cape], *Niven s.n. comm. Lambert 1826*, in herb. Martius [BR 864430, lecto. [image!], designated here as for *Haemanthus lambertianus* Schult. & Schult.f.]. Syntype: South Africa, Cape Province, *Burchell* bulb no. 129, [K, lecto.!, effectively designated for *H. callosus* Burch. ex Baker by Friis & Nordal: 65 (1976) = *H. coccineus* L.].

Haemanthus incarnatus Burch. ex Herb.: 237, t. 31, fig. 1 (1837). Type: South Africa, Cape Province [Eastern Cape], Krakakamma, *Burchell 4556* in herb. Hookerianum 1867 (inflorescence on top left corner of sheet) [K, lecto.!, designated by Friis & Nordal: 65 (1976)].

Haemanthus cooperi E.G.Hend.: 430 (1874). Type: South Africa, Cape of Good Hope [Western Cape], sketch of a plant from Cooper which flowered at Kew in 1863 [K, lecto.!, effectively designated by Baker: 70 (1888)].

Plants deciduous, green in winter, up to $\pm$ 300 mm high when flowering. *Bulb* solitary, small to large, narrowly to broadly ovoid, compressed crosswise to leaves, 40–100 mm diam., tunics thick, imbricate, distichous, cream-coloured, margins oblique, pale to dark brown. *Leaves* hysteranthous, 2, prostrate, usually firmly appressed to the ground, rarely spreading, blade broadly to narrowly elliptical to oblong or rotund, broader than long, as broad as long, or occasionally much longer than broad, 90–400 $\times$ 35–280 mm, plane, thick and leathery, adaxial surface dark dull green, rough with minute asperities, rarely smooth, abaxial surface pale green, shiny and smooth, immaculate or rarely slightly spotted with red towards base, margin cartilaginous, red or hyaline, smooth or fimbriate with short, retrorse, branched cilia, occasionally only towards apex. *Scape* stout or slender, up to

270 × 7–27 mm, usually considerably compressed, markedly furrowed towards apex, bright red to deep wine-red or pink, immaculate, glabrous. *Spathe bracts* 5–11, suberect but standing apart, sometimes slightly spreading, shorter than or as long as flowers, narrowly to broadly oblong-lanceolate or ovate, 20–70 × 7–50 mm, lateral spathe bracts mostly keeled and falcate, red to wine-red or pink, thinly leathery, becoming striate with age, tips obtuse to acute. *Inflorescence* ± compressed, narrowly to widely cyathiform or occasionally lax and somewhat spreading, 30–80 mm across. *Flowers* suberect, (15–)25–150; pedicel 8–35 mm long, whitish to pink or red; perigone 15–32 mm long, bright red to salmon or pale pink, sometimes white on tube and tepal tips; tube 2–9 mm long, widening gradually upwards; tepals standing slightly apart, narrowly oblong to lanceolate, 10–24 × 1–4 mm, tips acute. *Stamens* exerted by up to 10 mm; filaments pink to red with white tips; anthers 1–4 mm long, yellow. *Ovary* ± 2–3 mm diam., pink to red. *Style* ± as long as stamens. *Berry* subglobose to irregularly ovoid, ± 15–20 mm diam., cream with a pink blush or deep red to wine-red, becoming soft and translucent. *Seeds* ovoid, 5–8 mm diam., dark wine-red. *Flowering time*: January to April. Figure 53.

Distribution and habitat. *Haemanthus sanguineus* is widespread along the Cape Fold mountains and coastal forelands of Western Cape, from the vicinity of Nardouwsberg and Pakhuisberge in the north to the Cape Peninsula in the south and extending eastwards to the vicinity of Gqeberha and Addo, Eastern Cape (Figure 54). The species is found in renosterveld or fynbos, on clay or sandy soils, at elevations varying from sea level to mountain peaks of 1 200 m above sea level, with an annual rainfall of 450 mm in the drier northwest to 1 400 mm on the higher mountain ranges in the southwest. The populations are localised and usually small, comprising up to twenty individuals. Flat open terrain is the most favoured habitat, but in the vicinities of Worcester and Ceres many populations occupy mountain kloofs on steep, shaded slopes. Although not dependent on fire for flowering, populations in fire-prone fynbos habitats flower especially well after wildfires.

Diagnosis: *Haemanthus sanguineus* is recognised by a combination of vegetative and floral features. The leaves, which are prostrate and most often firmly appressed to the ground (Figure 3A), are characteristically leathery, mostly rough and dark green on the adaxial surface, whereas the abaxial surface is paler green and smooth. In addition, the leaf margin is characteristically cartilaginous, red to opaque and either smooth or fimbriate with short, retrorse, multiseriate, branched cilia. The unmarked scape is more compressed than in other taxa and is often furrowed, especially immediately below the flower head. Held erect to slightly spreading, the spathe bracts are lightly leathery, often becoming striate with age. Due to the compression of the flower head, the surface of most bracts is plane, but the lateral bracts are carinate and shaped somewhat like a boat. Individual flowers in the flower head are held at varying heights within small clusters, revealing the multiple helicoid cymose arrangement within the inflorescence more clearly than in most other species of the genus. The species forms a small group with its close allies, *H. canaliculatus* and *H. pumilio*, that are endemic to the Core Cape Floristic Region.

Discussion: As presently circumscribed, *H. sanguineus* is an extremely polymorphic species, incorporating several ecological races centred mostly in the mountains and valleys within the vicinity of



Figure 53. *Haemanthus sanguineus*. 1, inflorescence; 2, flower; 3, spathe bracts; 4, bulb; 5, portion of one of hysteranthous, prostrate leaf pair. *Snijman 656* (NBG), Kirstenbosch estate. Artist: Ellaphie Ward-Hilhorst. Scale bar: 1–3 = 12 mm; 4, 5 = 18 mm.

Worcester, Western Cape. The great diversity in size of vegetative and floral parts, as well as the many subtle differences in flower colour among populations, makes it impractical to recognise infraspecific taxa. Despite the variation appearing to be continuous within the species, some notable forms are nevertheless distinguishable, without being formally recognised.

In the vicinity of Ceres, *H. sanguineus* has robust inflorescences and many spathe bracts (Bayer s.n., NBG 119598) that match Herbert's *H. rotundifolius* var. *multivalvis*. In the Du Toits Kloof and Bains Kloof mountains near Worcester, populations occur on high, sunny plateaus, as well as on steep, moist, shaded slopes. Specimens from the plateaus are very like those found in the coastal forelands, although they are mostly smaller in size and have inflorescences that are looser, and they are brilliant red in colour. Populations extending down the slopes, however, show extreme plasticity. This is particularly evident in specimens collected from the precipitous banks of the Krom River: Esterhuysen 25436 (BOL, PRE), Snijman 95 (NBG) and Viviers 58 (NBG). These collections have leaves much longer than they are wide, almost ligulate in shape and loosely spreading. The inflorescence is extremely lax, with loosely spreading flowers and spathe bracts, and the tepals are particularly broad (3–4 mm wide).

Coastal populations in the southwest have leaves that are firmly appressed to the ground and are mostly wider than long. The inflorescences are compressed and compact, and the flowers mostly exceed the spathe bracts, giving them a typical paintbrush-like appearance. Floral colours are predominantly red to wine-red.

Populations in the sandveld near Malmesbury and Darling, often found in association with exposed Cape granite, and in the sandy Breede River flats between Worcester and Swellendam, however differ in having unusually pale inflorescences, although a few red forms may also be present. The leaves of these plants are broad and prostrate, showing no difference from other lowland specimens of *H. sanguineus*, but the scape and spathe bracts are deep to pale pink, with even paler pink flowers. In addition, the pedicels are often long (20–25 mm) and the perigone is generally small with a short tube (2–4 mm long) and narrow tepals (1–2 mm wide). The shorter, paler flowers in these drier areas possibly attract various small insects, unlike the large brown satyrid butterfly, *Aeroptes tulbaghia*, and the sunbirds that visit the red flowers produced elsewhere in the distribution range (Figure 8C and D).

In the east, from Oudtshoorn to Gqeberha, *H. sanguineus* is easily confused in the flowering stage with *H. coccineus*, the only other red-flowered species in this area. Here the differences between the two species are not as pronounced as elsewhere since the inflorescences of both species in this region

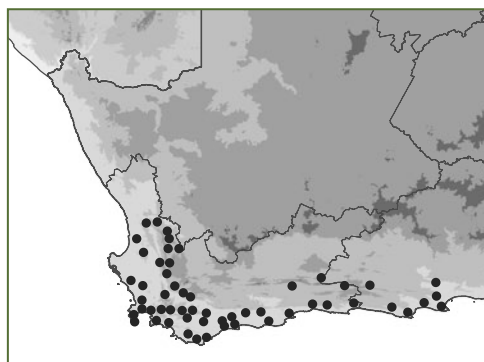


Figure 54. Distribution of *Haemanthus sanguineus*.

are somewhat lax. The vegetative parts, nevertheless, distinguish the two species; the leaves of *H. sanguineus* are rough and leathery, whereas those of *H. coccineus* are smooth and fleshy.

Haemanthus sanguineus and *H. coccineus* are thought to occasionally hybridise when sympatric populations are induced to flower simultaneously in response to fire. Evidence of this was noted at a newly burnt site on the Simonsberg near Stellenbosch in February 1980, when several plants intermediate between the two species were apparent. Without fire, however, *H. sanguineus* flowers slightly in advance of *H. coccineus*.

Nomenclatural note: Prior to 1984, the earliest name, *H. sanguineus*, had been confused with *H. coccineus* (Friis & Nordal, 1976). Thus, plants of the species were known by the later names, *H. rotundifolius* in Western Cape, and *H. incarnatus* in Eastern Cape. The lectotype of *H. sanguineus* matches the less common forms of the species from cool, shady habitats, probably due to similar low-light conditions under which the original bulb was cultivated in the Schönbrunn garden, Vienna (Snijman, 1984). The diagnostic dark red, furrowed scape and the keeled lateral spathe bracts are nevertheless clearly depicted in the original illustration.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3118** (Vanhynsdorp): 3.5 km N of Skurfkop (–DC), *Snijman* 653 (NBG); Nardouw mountains (–DD), *Müller-Doblies* 79128A (NBG). **3218** (Clanwilliam): Pakhuis Pass (–BB), *Barker* 4706 (NBG); Clanwilliam, without collector NBG 2904/14 (BOL); De Hoek, Piquetberg division (–DD), *Lewis* 2378 (SAM). **3219** (Wuppertal): top of Pakhuis Pass (–AA), *Lewis* 2385 (SAM); *Snijman* 433 (B, NBG); Cedarhout Kloof, southern Cedarberg (–AC), *Esterhuysen* 20041 (BOL); Hexberg, Cold Bokkeveld mountains (–CA), *Esterhuysen* 18439 (BOL); Skoongesig, Bokfontein, Ceres (–CB), *Hanekom* 1781 (PRE); top of Dasklip Pass (–CC), *Loubser* 2102 (NBG); new Elands Kloof Pass (–DC), *Bayer s.n.* (NBG 119598); *Thorns* sub NBG 141/47 (NBG). **3318** (Cape Town): farm Swartwater, near Darling (–AD), *Rourke* 1209 (NBG); *Snijman* 109 (K, MO, NBG, PRE); Tinie Versfeld Nature Reserve, Darling, *Snijman* 108 (NBG); 4 miles [6.4 km] N of Malmesbury (–BC), *Barker* 4495 (NBG); Mamre Hills (–CB), *Hall* sub NBG 246/48 (NBG); Cecilia Gorge (–CD), *Esterhuysen* 12641 (BOL); Signal Hill, *Guthrie* 16946 (BOL); Table Mountain, *Moyle Rogers s.n.* (BM); *Schonnberg* in herb. Galpin 4966 (PRE); ex Leg. *Alexander Prior* (K); Wynberg Hill, *Pillans* 10600 (MO); Kirstenbosch estate, *Snijman* 91 (NBG); *Snijman* 656 (NBG); Camps Bay, herb. *Maude s.n.* (BM); Kanonkop, Tygerberg (–DC), *Rourke* 1665 (NBG); Stellenbosch (–DD), *Duthie* 1448 (BOL); *Garside* 454 (K); *Van Rensburg* 1963 (K); Simonsberg foothills, *Richfield s.n.* (NBG); southern foothills of Simonsberg, *Snijman* 195 (B, K, NBG, PRE); Schoongezicht farm, *Snijman* 197 (NBG, PRE); *Snijman* 198 (NBG). **3319** (Worcester): Great Winterhoek (–AA), *Compton* 4614 (BOL); *Galpin* 12589 (PRE); Ceres (–AD), *Herre* sub SUG 12921 (BOL); Hawequas mountains (–CA), *D'Ewes s.n.* (NBG, PRE); *Oliver* 3734 (STE); Du Toits Kloof, *Drège* 1840 (K); *Esterhuysen* 20177 (BOL); NBG Expedition sub NBG 511/70 (NBG); *Snijman* 95 (NBG); Krom River Kloof off Du Toits Kloof, *Esterhuysen* 25436 (BOL, PRE); *Viviers* 58 (NBG); Breede River flats, near Rawsonville (–CB), *Perry* 1284 (NBG); Felix Berg (–CC), *Esterhuysen* 7737 (BOL); April Peak, Wemmershoek mountains, *Esterhuysen* 16822 (BOL); Klein Drakenstein mountains, *Galpin s.n.* (BOL); French Hoek, *Ridley* sub NBG 3903/15 (BOL); *Schlechter* in herb. Austro-Africanæ 10264 (BM, BOL, E, GRA, K, MO, PRE); Moddergat (–CD), *Perry* 715 (NBG); Villiersdorp, *Van Breda s.n.* (PRE 36958); Upper White River on Keerom Mountain (–DA), *Gillett* 819 (STE); Jonas Kop (–DC), *Snijman* 81 (NBG); at turnoff to Eilandia, from Worcester/Robertson road, *Snijman* 210 (NBG, PRE); *Snijman* 392 (K, NBG); just SE of Silver Oaks farm along Robertson/MacGregor road, *Snijman* 211 (NBG);

Snijman 393 (K, NBG, PRE); 1.6 km along Eilandia road from Worcester/Villiersdorp road, *Snijman 408* (MO, NBG, PRE). **3320** (Montagu): southern slopes at foot of Langeberge, near Heidelberg (–DD), *Esterhuysen 14462* (BOL). **3321** (Ladismith): farm Droogkraal S of Potgieterspoort (–BD), *Snijman 404* (NGB, PRE); Attakwas-kloof (–DD), *Nichols 399* (NGB). **3322** (Oudtshoorn): George, edge of Witfontein Forest Reserve (–CD), *Moriarty 321* (NGB); Herold, N of Outeniqua mountains, *Vlok 385* (NGB). **3418** (Simonstown): Duiker Point, W side of Karbonkelberg (–AB), *Leighton s.n.* (BOL); Bergvliet farm, *Purcell 205* (SAM); *Purcell 210* (SAM); hills W of Simonstown, ex herb. *Wolley-Dod 1162* (K); Slangkop, Kommetjie, *Moriarty s.n.* (NGB); Noordhoek, *Cullett 3557* (K); Vasco da Gama Peak, Cape Point (–AD), *Compton 15533* (NGB); Faure siding (–BB), *Garside 453* (K); near Somerset Strand, *Nel 1438* (STE); Palmiet River mouth (–BD), *Boucher 1130* (PRE, STE); Betty's Bay, *Snijman 93* (NGB). **3419** (Caledon): Kleinmond (–AC), *Rourke 1189* (NGB); ± 1 km before farm Avontuur on the Albertyn/Caledon road, *Snijman 87a* (NGB); Drayton siding (–BA), *Strauss 94* (NGB); near Dirkuyskraal between Viljoenshof and Buffelsjachtbaai (–DA), *Snijman 385* (NGB). **3420** (Bredasdorp): Bontebok Park (–AB), *Liebenberg 7975* (K, PRE); southern bank of Breede River, *Stayner* sub KG 71/73 (NGB); Swellendam, *Thode A2399* (K, PRE); near entrance to Bontebok Park (–AB/BA), *Rourke 1697* (B, K, NBG); De Hoop Nature Reserve, Windhoek (–AD), *Thompson 3466* (STE); Wydgelee (–BC), *Rourke 1694* (K, NBG, PRE). **3423** (Knysna): Plettenberg Bay (–AB), *Goldblatt 5473* (NGB). **3424** (Humansdorp): Tsitsikamma National Park, near Eerste River (–AA), *Liversidge s.n.* (NGB).

EASTERN CAPE. **3323** (Willowmore): pass between Avontuur and Uniondale (–CA), *Fourcade 2927* (K); Nuwe-kloof, NW entrance to Baviaanskloof (–DA), *Müller-Doblies 79067A* (NGB); *Snijman 354* (NGB, PRE); *Snijman 398* (NGB). **3325** (Gqeberha): Krakakamma (–CD), *Burchell 4556* (K); Parsons' Vlei, *Long 534* (K); *Long 542* (K, PRE), *Long 604* (K); Redhouse (–DC), *Paterson 489* (BOL, K); *Paterson* sub NBG 603/14 (BOL); *Snijman 495* (NGB).

24

Haemanthus canaliculatus*Levyns*

Haemanthus canaliculatus *Levyns* in Journal of South African Botany 32: 75 (1966); Friis & Nordal: 67 (1976); Obermeyer: t. 1803 (1980); Snijman: 67 (1984). Type: South Africa, Cape Province [Western Cape], marshy places above Rooi Els, 27 Feb. 1961 [fl.], *Levyns 11105* (BOL, holo!).

Plants deciduous, green in winter, up to ± 250 mm high when flowering. *Bulb* forming clumps, narrowly ovoid, up to 90 mm diam., strongly compressed crosswise to distichous leaves, tunics distichous, thick, fleshy, cream-coloured, margins oblique, without withered brown remains. *Leaves* mostly hysteranthous, (1)2, rarely 3 or 4 if persisting beyond one year, suberect to spreading, blade narrowly ligulate, $170\text{--}400 \times 5\text{--}27$ mm, canaliculate, succulent, both surfaces shiny green, barred with darker green and reddish towards base, especially abaxially, apex obtuse. *Scape* erect or curved, up to $200 \times 4\text{--}10$ mm, $\pm$ compressed, deep red to reddish pink, occasionally finely spotted with deeper red towards base, glabrous. *Spathe bracts* 5–7, somewhat spreading, slightly shorter or longer than flowers, narrowly to broadly lanceolate, $25\text{--}70 \times 6\text{--}20$ mm, brilliant red or rarely reddish pink, somewhat leathery, tips acute to subacute. *Inflorescence* loosely spreading, 30–90 mm across. *Flowers* 15–45; pedicel 6–15 mm long, reddish; perigone narrowly funnelform, 20–30 mm long, bright red or rarely reddish pink; tube 3–6 mm long, widening gradually upwards; tepals standing slightly apart, lanceolate, $17\text{--}24 \times 3.0\text{--}4.5$ mm, tips acute. *Stamens* exerted by up to 8 mm; filaments red or pink; anthers 1.5 mm long, yellow. *Ovary* ± 2.5 mm diam., reddish. *Style* mostly exceeding stamens by up to 8 mm. *Berry* irregularly globose, ± 20 mm diam., reddish. *Seeds* 1–3, mostly ellipsoidal, up to 10 mm diam., shiny, deep wine-red. *Flowering time*: February to March or later in cultivation. Figure 55.

Distribution and habitat: *Haemanthus canaliculatus* is limited to a small area of the southwestern coast between Rooi Els and Onrus, Western Cape (Figure 56). This narrow coastal strip, elevated to ± 30 m above sea level, receives an average of 650 mm rain per year. Seepages from the adjacent Cape Fold mountains contribute to the coastal shelf having several vleis and shallow depressions in which peaty soils become waterlogged in winter. Small, isolated populations of *H. canaliculatus* are confined to these unique habitats, which for most of the time support a dense, closed community of fynbos. Thus, in fire-free periods *H. canaliculatus* is rarely seen. When the fuel-load is sufficiently high, however, these areas are prone to summer fires and after two weeks the red inflorescences emerge, creating a striking display within the blackened landscape (Figure 5D).



Figure 55. *Haemanthus canaliculatus*. 1, inflorescence (a pale form grown at Kirstenbosch National Botanical Garden) ; 2, flower; 3, spathe bract; 4, bulb and bulblet; 5, hysteroanthous leaves; 6, section of leaf. *Van Es-sen s.n.* (NBG), Pringle Bay. Artist: Ellaphie Ward-Hillhorst. Scale bar: 1–3, 5, 6 = 12.5 mm; 4 = 13 mm.

Diagnosis: *Haemanthus canaliculatus* is easily recognised by having succulent, deeply channelled, narrow leaves, 5–27 mm across when pressed, that are characteristically barred with red near the base. The leaves are typically deciduous and absent during summer, but if plants occupy sites that remain wet all year round, then the old leaves may persist for up to two years. The pronounced leaf succulence determines the characteristics of the bulb tunics, which are loosely arranged and thick with oblique truncate margins. *Haemanthus canaliculatus* is inferred to be most closely allied to *H. sanguineus* due to the similarity in their spreading red inflorescences and thin leathery spathe bracts, a likeness most easily seen in the easternmost forms of *H. sanguineus*.

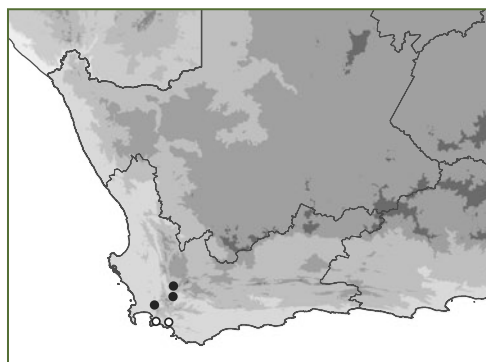


Figure 56. Distribution of *Haemanthus canaliculatus* (○); *H. pumilio* (●).

Discussion: *Haemanthus canaliculatus* has never been known to flower in nature except after summer fires, hence the initial belief that it was an obligate pyrophyte and that fire was vital to initiate flowering (Levyns 1971). Bulbs grown in lightly shaded pots at Kirstenbosch National Botanical Garden, however, flower without special treatment. Therefore, the effect of clearing the natural habitat, rather than fire itself, is the likely trigger for the inflorescence to emerge. For much of the time the sites occupied by *H. canaliculatus* are densely covered with ericoid shrubs, thus the habit of restricting flowering to times when the habitat is open and competition is minimal, may help to conserve the bulb's stored resources. The species does, however, readily reproduce vegetatively through the formation of bulblets, which may be an adaptation to compensate for its infrequent flowering.

The brilliant red inflorescence, which appears in late-summer, is specially adapted to attract the strong-flying, large brown, satyrid butterfly, *Aeropetes tulbaghia*, as well as Southern Double-collared Sunbirds. In years when the soil is sufficiently moist, the frequently sympatric *Kniphofia uvaria* (L.) Oken (Asphodelaceae) flowers intermixed with *H. canaliculatus*, producing remarkable floral displays (Levyns 1966).

The species was first collected by Mrs M. Brunt after a fire at Betty's Bay in 1943. However, Margaret Levyns was only able to gather material to describe the species after another fire swept through the area in 1960. Unlike this habitat specialist, populations of *H. coccineus* and *H. sanguineus* within fynbos generally favour more open sites where they are able to flower more freely.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3418** (Simonstown): Hangklip estate, near Rooi Els (–BD), Levyns 11105 (BOL); Levyns 11140 (BOL); Levyns 11223 (BOL); Hangklip, Lavranos 11980 (PRE); Pringle Bay, Jackson s.n.

(NBG); *Van Essen s.n.* (NBG 126815); Betty's Bay, *Brunt s.n.* (BOL 23215, BOL 23216); *Brunt* sub NBG 110/45 (NBG); *Oliver 3090* (PRE); *Oliver 3092* (PRE); *Porter s.n.* (NBG); *Rourke 688* (NBG); *Rourke 1229* (K, MO, NBG, PRE); *Topper s.n.* (K, NBG, PRE). **3419** (Caledon): Onrus, opposite Sea View Caravan Park (–AC), *Perry 1906* (NBG).

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Haemanthus pumilio*Jacq.*

Haemanthus pumilio *Jacq.*, *Plantarum rariorum horti caesarei Schoenbrunnensis*, vol. 1: 32, t. 61 (1797); *Herb.*: 234 (1837); Baker: 67 (1888); Baker: 233 (1896); Snijman: 77 (1984). Type: South Africa, Cape of Good Hope, [Western Cape], illustration in Jacquin: t. 61 (1797), lecto., designated by Friis & Nordal: 70 (1976).

Plants deciduous, green in winter, up to ± 180 mm high when flowering. *Bulb* forming clumps, small, narrowly ovoid, up to 55 mm diam., strongly compressed crosswise to distichous leaves, tunics fleshy, distichous, cream-coloured, margins oblique, transparent and membranous when old. *Leaves* hysteranthous, 2, suberect, blade narrowly ligulate, $55\text{--}130 \times 3\text{--}15$ mm, $\pm$ plane, twisted, fleshy, glabrous, both surfaces shiny green with red bars near base of abaxial surface, apex obtuse. *Scape* slender, $\pm$ compressed, $45\text{--}180 \times 3\text{--}6$ mm, reddish pink, rarely slightly marbled, glabrous. *Spathe bracts* 4–6, spreading apart, shorter or as long as flowers, narrowly triangular, $10\text{--}30 \times 3\text{--}10$ mm, pale to deep pink, membranous. *Inflorescence* lax and spreading, broadly obconical, 10–50 mm across. *Flowers* 4–25, $\pm$ spreading; pedicel 3–15 mm long, pale green to pink or reddish pink; perigone 8–12 mm long, white to pale pink to rose-pink; tube 1.0–1.5 mm long, gradually widening upwards; tepals spreading, linear to narrowly lanceolate, $6.5\text{--}11.0 \times 1\text{--}2$ mm, tips obtuse to acute. *Stamens* erect, exerted by up to 5 mm; filaments pale to deep pink; anthers 1.0–1.5 mm long, yellow. *Ovary* 1.5–2.0 mm diam., green to reddish pink. *Style* slightly exceeding stamens. *Berry* ovoidal, ± 10 mm diam., becoming reddish pink, firm and fleshy. *Seeds* 1–4 per berry, ovoidal, ± 5 mm diam., turning dark wine-red. *Flowering time*: March to April. Figure 57.

Distribution and habitat. *Haemanthus pumilio* is confined to patches of the critically endangered alluvium fynbos (Rebelo et al. 2006) between Hermon and Stellenbosch (Figure 56). These low-lying plains reach elevations of $\pm 60\text{--}150$ m above sea level and receive ± 450 mm rain annually during winter. The species inhabits periodically waterlogged silty soils in somewhat grassy areas within a matrix of low, fire-prone fynbos shrubland, where the bulbs form small clumps (Figure 5E). An ever-diminishing number of populations remain. One is within the Duthie Nature Reserve, University of Stellenbosch, where Markötter (1936) studied the species' reproductive biology prior to any significant ecological disturbance of the area. Recent studies of *H. pumilio* reveal a dramatic decline in plant numbers at this site, probably due to changes in the water table and the absence of wildfires that reduce the competing plant cover, particularly of grasses (Summerville & Van der Walt 1992; Madzivire 2021).



Figure 57. *Haemanthus pumilio*. 1, bulb and hysteranthous leaves; 2, inflorescences; 3, flower; 4, section of flower; 5, berries. *Snijman 668* (NBG), Stellenbosch. Artist: Fay Anderson. Scale bar: 1, 5 = 13 mm; 2 = 10.4 mm; 3, 4 = 8.3 mm.

Diagnosis: The phylogenetic analysis by Conrad (2008) indicates that *H. pumilio* is one of three closely related species endemic to the Core Cape Floristic Region that are sister to the remaining taxa within subg. *Haemanthus*. The other members are *H. canaliculatus* and *H. sanguineus*. Vegetatively, *H. pumilio* is most like *H. canaliculatus* since the bulbs in both species are strongly compressed crosswise to the distichous leaves, and the succulent, strap-shaped leaves are characteristically narrow, glabrous and slightly barred with red on the abaxial surface. The leaves of *H. pumilio*, however, are twisted and have an almost plane surface, unlike the straight, deeply channelled succulent leaves of *H. canaliculatus*. Within this group *H. pumilio* is unique in having distinctly small, white to pink flowers (perigone 8–12 mm long), as opposed to the larger, typically red flowers of *H. canaliculatus* (perigone 20–30 mm long) and the red or pink flowers of the generally more robust *H. sanguineus* (perigone 15–32 mm long).

Because of their similar spreading pink inflorescences, dried material of *H. pumilio* has often been misidentified as the unrelated *H. amarylloides* from Northern Cape and Western Cape (Friis & Nordal 1976). Living plants, however, reveal ample differences between the species in vegetative morphology, most notably that the leaves in *H. amarylloides* are straight and devoid of barring.

Specimens examined

SOUTH AFRICA. WESTERN CAPE. **3318** (Cape Town): between Klapmuts and Paarl (–DD), *Burgers 2345* (NBG); Stellenbosch, *Duthie 1351* (BOL); *Duthie s.n.* (PRE 36886, 36887); *Garside s.n.* (BOL); Stellenbosch flats, *Garside 1377* (K); *Oliver 152* (NBG); *Olivier s.n.* (NBG); Groot Drakenstein, Paarl, *Hulse s.n.* (NBG); Klein Welmoed, *Pillans 9968* (BOL); flats at Duthie Nature Reserve, *Snijman 248* (K, MO, NBG); *Snijman 668* (NBG). **3319** (Worcester): Wellington, Elandsberg [Private] Nature Reserve (–AC), *E. Parker* sub *Snijman 1682* (NBG); Salem farm at base of Klein Drakenstein (–CC), *Galpin 10741* (PRE); *Galpin s.n.* (BOL).



Incompletely known taxon

Haemanthus sp.

South Africa, Northern Cape, Pellaberg, near top N of Swartmodder, *Van Jaarsveld & Kritzinger 8062* (NBG).

Plants deciduous, up to ± 150 mm high when flowering. *Bulb* narrow, ± 30 mm diam., tunics concentric, equally long, covered with numerous dry, brown layers. *Leaves* near-synanthous, 2, recurved or prostrate, narrowly elliptical, plane or channelled distally, $80\text{--}150 \times 35\text{--}60$ mm, $\pm$ thin-textured, glabrous, pale green, immaculate. *Scape* erect, $20\text{--}130 \times \pm 7$ mm, grooved, glabrous, pink, immaculate. *Spathe bracts* suberect, 5 or 6, narrowly elliptic, $22\text{--}30 \times 7\text{--}10$ mm, pale to deep pink, thin-textured. *Inflorescence* obconical, $25\text{--}40$ mm across. *Flowers* 8–10, suberect; pedicel 5–9 mm long, pink; perigone narrowly funnellform, $16\text{--}18$ mm long; tube 2–4 mm long, smooth, widening distally; tepals suberect, linear, $\pm 15 \times 0.7$ mm, tips obtuse. *Stamens* exserted by up to 5(–10) mm; filaments white; anthers ± 1.5 mm long, yellow. *Ovary* ± 2.5 mm diam. *Style* $\pm$ equalling stamens. *Fruit* unknown. *Flowering time*: mid-February.

Discussion: Four herbarium specimens currently represent this taxon: *Desmet 2499, 3066*; *Van Jaarsveld 6654* and *Van Jaarsveld & Kritzinger 8062*, all in NBG. Collectively they show inflorescences in the initial stages of flowering, leaves at various stages of growth, and bulbs in longitudinal section.

The taxon is known from only two localities on Groot Pellaberg and Ghaamsberg, which belong to a group of inselbergs that rise above the surrounding flat plains of northern Bushmanland, within the east Gariep Centre of Endemism, Northern Cape (Jürgens 1991, 1997; Van Wyk & Smith 2001). The floristic links within this centre are complex. Apart from species of the Nama-Karoo on the drier northern slopes, it includes elements from the temperate Succulent Karoo on the more mesic southern slopes, as well as taxa of tropical affinity. Consequently, the distributions of numerous taxa within this centre are disjunct with links to the Richtersveld, central Namib and the southeastern Cape (Jürgens 1997).

The east Gariep *Haemanthus* grows among hard, quartzite rocks, on well-shaded, steep southern slopes and cliffs, at elevations of 500–1 000 m above sea level. The Ghaamsberg population inhabits seepages, protected by rock overhangs, and grows together with mosses and liverworts. Precipitation

in the area is usually less than 100 mm annually, mainly from thunderstorms between February and April. The high mountains, however, obtain extra moisture in winter from clouds driven inland from the west (Desmet 2000).

The dried herbarium material lacks sufficient detail to allow identification with any certainty. However, it appears not to have the features known within the Succulent Karoo taxa of *Haemanthus*. This raises the possibility that this east Gariep taxon may share older floristic links within southern Africa and that it may be a relict of the nonseasonal-rainfall scrub vegetation that once dominated landscapes across southern Africa (Cowling et al. 2005). Fresh material is still needed to determine the identity and affinities of this interesting plant.



Evolution

Biogeographic history

To date, only two phylogenetic studies on tribe Haemantheae, based on combined plastid and nuclear ribosomal DNA data, have embarked on a biogeographic analysis of the group. Meerow and Clayton (2004) proposed a preliminary hypothesis based on low sampling, followed by Conrad (2008) who undertook a more extensively sampled analysis that included estimations of divergence times within the lineage.

Based on the correlation, noted by Patterson and Givnish (2002), of a rhizomatous growth habit, net-veined leaves and baccate fruits with the colonisation of low-light habitats within various lineages of Liliales, Meerow and Clayton (2004) inferred a similar correlation within Haemantheae, given that all these traits are present within the tribe. Among the shade-loving taxa within the tribe, *Clivia* Lindl. and *Cryptostephanus* Welw. ex Baker possess rhizomes, whereas both rhizomes and bulbs, as well as net-veined foliage are present within *Scadoxus* Raf. Furthermore, Haemantheae is the only group within Amaryllidaceae s.s. in which baccate fruits have evolved. Meerow and Clayton (2004) proposed, therefore, that the evolution of these features within low-light habitats was the primary event that separated the early Haemantheae from the rest of the family, probably facilitated later by a reduction in the base chromosome number within the lineage recognised as subtribe Haemanthinae. Meerow and Clayton (2004) inferred an eastern South African origin for the lineage, unlike Conrad (2008) who inferred a generalised origin in southern Africa.

Although contemporary woodlands occur predominantly in the east of the subcontinent, data from pollen deposits indicate that the vegetation within the southwestern Cape northwards to the Orange River was characterised predominantly by subtropical forest patches and woodland during the early to middle Miocene (Coetzee & Rogers 1982; Coetzee & Muller 1984; Scholtz 1985; De Villiers & Cadman 2001; Neumann & Bamford 2015). For the area north of the Orange River, however, the data show that there was a shift towards dry to mesic woodland, and that the coastal regions of central and northern Namibia were arid to hyper-arid since the early Miocene (Neumann & Bamford 2015). Cowling et al. (2005) suggest, however, that a more realistic reconstruction of the Oligocene-Eocene vegetation might be an admixture of forest and thicket formations, the former being limited to localised, high-moisture sites.

Within this context, and using the results of Conrad (2008), the divergence of *Haemanthus* from *Scadoxus* within the early Miocene suggests that these lineages benefited from different niches; shady, subtropical habitats for *Scadoxus* and newly available, open niches within woodland, possibly resembling thicket *sensu* Cowling et al. (2005), for *Haemanthus*. Several independent studies from Miocene fossil data and global climatic data infer that such vegetation was present in the lower Orange River valley (Hendey 1983), Bushmanland (De Wit & Bamford 1993) and the Olifants River

valley (Bamford 2000) under nonseasonal-rainfall conditions across the Cape in the early to middle Miocene (Zachos et al. 2001).

During the subsequent onset of a seasonal, temperate climate and the associated decline of woodland throughout the subcontinent, it is conceivable that the evolutionary trajectory of *Haemanthus* trended further towards open, warm habitats, facilitated by its bulbous habit and a reduction to $x = 8$ base chromosome number.

The earliest dichotomy of *Haemanthus* into two major sublineages, represented by subg. *Serena* and subg. *Haemanthus*, is estimated as having occurred within the late Miocene (Conrad 2008), following the increased upwelling of the Benguela Upwelling System along the western coastline, which established an increasing aridity gradient from east to west (McCarthy & Rubidge 2005; Linder & Verboom 2015), as well as a shift in rainfall seasonality similar to the modern balance of a summer-versus winter-rainfall climate around the middle Miocene (Linder & Verboom 2015).

This major dichotomy thus suggests an early disjunction between eastern and western ancestral populations, which subsequently followed divergent radiation patterns. Through the late Miocene-Pliocene, ± 14 million years ago, the western sublineage diversified rapidly into several taxa under a winter-rainfall climate (Conrad 2008), whereas the eastern sublineage diversified into fewer, highly variable taxa that became dominant over a large part of the summer-rainfall area.

The climate-induced fragmentation of these sublineages to the east and west of southern Africa likely also reflects the change, from the late Miocene onwards, to a colder and drier climate due to the growth of the Antarctic ice sheet. Thus, by the end of the Pliocene, woodlands and thicket patches had contracted to the warmer, frost-free northeastern, eastern and southeastern rim of the subcontinent, largely in fire-protected areas, as part of a mosaic with evolving savanna and grassland (Cowling et al. 2005). Given the berry-fruit's short-dispersal ability, it is reasonable to invoke vicariance rather than more recent dispersal in either direction as the cause of the sublineages' largely mutually exclusive distribution patterns.

All extant descendants of the lineage encompassing subg. *Haemanthus* remain restricted within the Greater Cape Floristic Region, where they have become adapted to winter rain and cool growing conditions. Radiation within the clade indicates an origin within the north, in the present day semi-arid Succulent Karoo, where most diversification has taken place. The only clade endemic to the Fynbos Biome in the south, comprising the three lowland species *H. canaliculatus*, *H. pumilio* and *H. sanguineus*, is estimated to have an origin ± 2.05 million years ago, thus representing some of the younger elements present within the Core Cape Floristic Region (Conrad 2008; Verboom et al. 2009). A reasonable assumption is that the recent and limited radiation of *Haemanthus* within fynbos was perhaps due to the early ancestors' inability to occupy dense heathland prior to the emergence of new habitats on the coastal forelands and the advent of fire.

The *Serena* sublineage, centred in the eastern half of southern Africa, is comparatively species poor. It resolves as two small radiations that are inferred to have responded differently to colder periods

during the Miocene when grasslands were being established (Jacobs et al. 1999), and when new habitats were emerging following the Miocene-Pliocene Drakensberg uplift (Partridge & Maud 2000; Carbutt & Edwards 2006). The minor subclade, comprising *H. albiflos*, *H. carneus*, *H. deformis* and *H. pauculifolius*, is inferred to have persisted within patches of thicket and open woodland, mainly along the equable east coast and the deeply incised valleys of the northeast where the lineage remained protected from frost and fire. Populations of *H. albiflos* within the Great Fish River drainage area became remarkably diverse, possibly as an adaptation to the numerous new habitats that emerged there when sediments were scoured from the extensive drainage basin.

In contrast to the east-coast subclade within subg. *Serena*, the other members of the lineage are inferred to have diverged into the colder, high-lying, fire-prone temperate grasslands that were developing in the eastern interior and sub-escarpment areas. Here they either escaped fire by occupying rocky habitats, or they adapted to fire by flowering early, thus enabling seedling establishment in open habitats before the onset of frost.

Adding to the pattern of biogeographical fragmentation and the hypothesis of speciation due to vicariance, as proposed above, is the unusual distribution of *H. avasimontanus*, a notable outlier on the central Namibian escarpment, where it inhabits deeply incised, shady kloofs. The large distance between this isolated species near Windhoek and its widespread putative sister species, *H. montanus*, in the eastern grasslands suggests that these species are perhaps relicts of an ancestor that once straddled the subcontinent from east to west.

Further phylogenetic analyses, focusing on the rare *H. avasimontanus* from Namibia and the imperfectly known *Haemanthus* taxon from the prominent Bushmanland inselbergs along the lower Orange River valley, are yet to assess the hypothesis proposed above, and in so doing they may contribute to the ongoing broader enquiry into the evolutionary history of taxa that have radiated transversely across southern Africa.

Key evolutionary traits

Fundamental to the evolutionary success of *Haemanthus* is the means by which populations have become established and maintained, which is primarily via seedlings. The seeds are large, non-dormant, invariably chlorophyll-rich and metabolically active, thus comprising a suite of derived features that maximise seedling survival in climates with a short or cool growing period. A feature unique to the seeds of the winter-rainfall lineage is the subepidermal layer of anthocyanin, which perhaps serves as protection from incoming radiation while the seeds are exposed above ground during the dry autumn.

Within the summer-rainfall subclade, *H. montanus* is remarkable among the entirely green-seeded taxa in having particularly large seeds, an inferred adaptation to the short growing season and early frosts within its high-lying, grassland habitat. In contrast, the almost chlorophyll-free seed (apart from the green embryo), which is shared with *Scadoxus* and *Clivia*, and is inferred to be plesiomorphic, is

restricted to the small east-coast subclade, comprising *H. albiflos*, *H. deformis* and *H. pauculifolius*, that occupies the non-seasonal rainfall region of southern Africa.

The possession of a bulb, which is inferred to be a derived state within *Haemanthus* (Meerow et al. 1999; Meerow & Clayton 2004), is unquestionably key to the lineage's success. Its stored underground reserves are inferred to have enabled shifts in both leafing and flowering periodicity that allowed the release of the non-dormant seeds to be finely tuned with the early onset of the growing season, thus maximising opportunities for seedlings to flourish under optimal conditions.

Specialisations of the bulb within the summer-rainfall *Serena* sublineage are limited to the photosynthetic bulb habit within the shade-loving east-coast subclade, whereas they are more advanced within the winter-rainfall sublineage which became subject to prolonged summer aridity. These adaptations manifest as a deeply buried bulb habit, which is correlated with the development of an elongated bulb neck, and the shift in tunic arrangement to a markedly two-ranked form that allows a lateral expansion in bulb size.

It is reasonable to infer that the evolution of large, biseriate bulbs within the winter-rainfall species is tightly coupled with the evolution of autumn flowering and the hysteranthous-leaved habit, as this flowering phenology is entirely reliant upon underground stored reserves. Likewise, it is probable that the biseriate bulbs' increased storage capacity was key to allowing the sublineage to bridge the barrier posed by the Cape's infertile acid sands, thereby enabling a small number of taxa to colonise new habitats in lowland fynbos.

Morphological specialisations of the foliage have evolved almost exclusively within the winter-rainfall *Haemanthus* sublineage. These include the prostrate-leaved habit, as well as an upright-leaved habit correlated with a reduction in leaf number, the enlargement of the photosynthetic area by means of leaf undulations, and the speckling and barring in red or dark green on the leaf blade. In many ways these reflect responses to the low-energy growth conditions of the Greater Cape Floristic Region's winter-wet climate. Further novelties are psammophorous leaves, which may have evolved to counter the effects of wind abrasion, as well as the evolution of bristle-like trichomes that may contribute to the thermal and evapotranspiration regulation of the leaves. The evolution of leaf pubescence, which is unusual in the tribe, apart from within *Gethyllis* L., is well-developed in both winter- and summer-rainfall sublineages.

Based on the phylogenetic analyses of Meerow and Clayton (2004) and Conrad (2008), the ancestral flower colour within *Haemanthus* remains equivocal. Nevertheless, the association of red colours with the persistent, upright orientation of the spathe bracts and flowers during anthesis represents a suite of characters unique to the majority of winter-rainfall *Haemanthus*. Together they create a stiff, tight, brightly coloured, brush-like flower cluster that appears to have evolved to attract nectarivorous birds and the specialised, large brown satyrid butterfly, *Aeropetes tulbaghia*. Notable developments within this group of taxa are the gibbosities at the base of the tepals and the swollen tepal tips, which are inferred to provide extra support for probing birds. The sequence in which these features have been acquired is not apparent, but the characteristic succulence and bright colouring contrasts sharply

with the less specialised inflorescences that have evolved elsewhere in the genus, which are softly spreading, delicate pink- to white-flowered, and are well suited to small-bodied pollinators.

These evolutionary inferences still await more rigorous analysis, particularly with a view to examining the early drivers of speciation among plants that have limited dispersal abilities, small allopatric distributions and strong habitat associations within the Greater Cape Floristic Region. It is significant in this regard that the key morphological features of the bulbs and seeds that have evolved within these clades are either unique within *Haemanthus* or are unusual within the tribe, which lends weight to their use in delimiting the subgeneric taxa recognised in this account of *Haemanthus*.

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Addendum

Molecular phylogenetics of **Haemanthus** (Amaryllidaceae: Haemantheae)

Authors

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Introduction

Haemantheae, the only baccate-fruited tribe within Amaryllidaceae, has formed part of several molecular phylogenetic studies on the family in the recent past (Meerow & Clayton 2004; Conrad et al. 2006; Conrad 2008; Bay-Smidt et al. 2011; Rønsted et al. 2012). Members of the tribe comprise *Clivia* Lindl., *Cryptostephanus* Welw., *Gethyllis* L., *Apodolirion* Baker, which is doubtfully distinct from *Gethyllis* (Traub 1963; Meerow & Clayton 2004), *Haemanthus* L. and *Scadoxus* Raf. Of these genera only *Cryptostephanus* and *Scadoxus* extend beyond southern Africa into tropical Africa, with the latter reaching as far north as the Arabian Peninsula.

The earliest molecular study to investigate generic relationships within tribe Haemantheae (Meerow & Clayton 2004) made use of two DNA regions: *trnL-F* and nrITS sequences. All genera of the tribe were represented, including four species of *Haemanthus* (*H. albiflos* Jacq., *H. graniticus* Snijman, *H. humilis* Jacq. and *H. pumilio* Jacq.). In the single most parsimonious tree, based on the combined plastid and nuclear sequences, *Haemanthus* resolved as sister to *Scadoxus* and within *Haemanthus* the synanthous-leaved species (*H. humilis* and *H. albiflos*) from the summer-rainfall region of southern Africa resolved as sister to the hysteroanthous-leaved species from the winter-rainfall region (*H. graniticus* and *H. pumilio*).

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Thereafter, the study of generic relationships within Haemantheae by Conrad et al. (2006) used four plastid DNA regions (*rpoB-trnC* intergenic spacer, *trnL-F* intron, *rps16* intron and *psbA-trnH* intergenic spacer) and an increased sample of 19 taxa within *Haemanthus*. The parsimony analysis retrieved further support for the sister relationship between the synanthous-leaved, summer-rainfall taxa, *H. humilis* subsp. *humilis*, *H. humilis* subsp. *hirsutus* (Baker) Snijman and *H. carneus* Ker Gawl., and the hysternanthous-leaved winter-rainfall taxa represented by *H. pubescens* L.f. subsp. *pubescens sensu* Snijman (1984), *H. canaliculatus* Levyns, *H. sanguineus* Jacq. and *H. pumilio*.

Conrad (2008) later expanded her studies on the tribe by analysing 24 taxa within *Haemanthus* with the addition of one nuclear region (ITS) to the four plastid DNA regions used previously (Conrad et al. 2006). Her parsimony analysis, based on combined nuclear and plastid data, generated a strict consensus tree that resolved a strongly supported dichotomy within *Haemanthus*, a topology that closely resembles the tree generated by ITS nuclear data alone. As in earlier studies the strict consensus tree resolves a strongly supported summer-rainfall clade of *H. montanus* Baker, *H. humilis* subsp. *humilis*, *H. humilis* subsp. *hirsutus*, *H. carneus*, *H. albiflos*, *H. deformis* Hook.f. and *H. pauculifolius* Snijman & A.E.van Wyk, which is sister to the more diverse winter-rainfall clade, thus supporting the dichotomy between the synanthous-leaved species and hysternanthous-leaved species within *Haemanthus*. More recently this topology has been supported by a maximum likelihood tree generated by Madzivire (2021) using nrITS, mitochondrial *nad1i477* intron and plastid *trnL-F* sequence data from the 24 *Haemanthus* taxa previously used by Conrad (2008), plus 26 new *H. pumilio* samples, with *Scadoxus* as the outgroup.

Due to the importance of tribe Haemantheae for medical research, Bay-Smidt et al. (2011) undertook parsimony analysis of the tribe using sequences from ITS and the plastid *trnL-F* region, with *Amaryllis belladonna* L. as the outgroup. The primary aim was to use the phylogenetic hypothesis to evaluate the distribution of alkaloids within the group. The consensus trees showed a well-supported clade within *Haemanthus* corresponding to a summer-rainfall group of *H. albiflos*, *H. deformis*, *H. humilis* and *H. hirsutus* Baker (considered by the authors to warrant species rank). The placement of *H. montanus*, a near-synanthous-leaved species from the summer-rainfall region, however, resolved as sister to the winter-rainfall group of *H. amarylloides* Jacq., *H. coccineus* L., *H. graniticus*, *H. pumilio* and *H. sanguineus*, thus differing from its position in the strict consensus tree of Conrad (2008). The sample of just 10 taxa within *Haemanthus*, however, was low compared with the 24 taxa analysed by Conrad (2008).

With the focus on how phylogeny can predict chemical diversity for medical use, Rønsted et al. (2012) generated a further phylogeny of Amaryllidaceae *sensu stricto* using ITS, *trnL-F* and *matK* sequences. Their Bayesian consensus tree retrieved a similar topology to that of Bay-Smidt et al. (2011) in which *H. montanus* resolved as sister to the winter-rainfall group within *Haemanthus*. The sample of seven *Haemanthus* taxa is, nevertheless, extremely low.

As the submission to GenBank of the DNA sequences associated with Conrad's work has remained pending until now, her studies (Conrad et al. 2006; Conrad 2008) have largely remained overlooked,

despite being the most extensively sampled studies to date, namely 19 and 24 taxa respectively, of the 27 *Haemanthus* taxa recognised at the time. The purpose of the present study is to bring Conrad's preliminary studies to completion to help establish baseline infrageneric relationships of the taxa within *Haemanthus*, for use in the systematic account of *Haemanthus* presented here (pp. 43–155). Due to the differing results obtained by Bay-Smidt et al. (2011) and Rønsted et al. (2012) from those of Conrad (2008), a particular aim of the present study is to re-evaluate the relationship of *H. montanus* to other taxa within *Haemanthus*. Our analyses, in addition, include the recently described *H. humanii* G.D.Duncan, a narrowly endemic habitat specialist from Namaqualand, South Africa, characterised by two autapomorphies not previously known within Haemantheae, namely long bristle-like trichomes, arranged in regular rows on the adaxial leaf surface, and flowers with proximally thickened and minutely hooked inner filaments.

Materials and methods

Taxonomic sampling

All recently published molecular phylogenetic studies involving *Haemanthus* included no more than 10 taxa from the genus (Meerow & Clayton 2004; Bay-Smidt et al. 2011; Rønsted et al. 2012). The present study includes 23 of the 25 currently recognised species of *Haemanthus* and uses the molecular sequences associated with the work of Conrad et al. (2006) and Conrad (2008) (Appendix 1). Only *H. arenicola* (Snijman) Snijman from the northern Namaqualand sandveld (for change in taxonomic rank see pp. 130–133) and *H. avasimontanus* Dinter, a rare species from central Namibia, are still to be analysed. Representatives from all three subtribes, recognised by Meerow and Clayton (2004), within the tribe Haemantheae were included in the analyses, viz., *Haemanthus* and *Scadoxus* within Haemanthinae Pax., *Gethyllis* within Gethyllidinae (Dumort.) Meerow, and *Clivia* and *Cryptostephanus* within Cliviinae D.Müll.-Doblies & U.Müll.-Doblies. Species of *Apodolirion* were omitted from our analyses since the question as to whether or not *Apodolirion* should be maintained as distinct from *Gethyllis* warrants an adequately sampled separate study. The tribe Calostemmataceae, which Meerow et al. (1999) reported as sister to Haemantheae, was represented by *Calostemma purpureum* R.Br. and the monogeneric tribe Cyrtantheae, which Rønsted et al. (2012) showed was sister to the Haemantheae was represented by *Cyrtanthus sanguineus* Hook.f. subsp. *sanguineus* in our analyses (Snijman & Meerow 2010). The trees were rooted with *Pancratium illyricum* L.

Phylogenetic data

DNA extraction, amplification and sequencing

Total DNA was extracted from herbarium or silica material using either the 2x CTAB method of Doyle and Doyle (1987), or the DNeasy Plant Mini Kit (Qiagen Inc., Valencia, CA, USA) according

to the manufacturer's instructions. The voucher specimen information and GenBank accession numbers for the material used in the analyses are given in Appendix 1.

The internal transcribed spacers (ITS) of nuclear ribosomal DNA were amplified using the primer combinations of Sun et al. (1994). The *trnL-F* region (consisting of the adjacent *trnL* intron and *trnL-F* intergenic spacer) was amplified using the exon primers c and f (Taberlet et al. 1991). The *rps16* region was amplified using the primers *rps16F* and *rps16R2* (Oxelman et al. 1997). Successfully amplified PCR products were purified using either a QIAquick PCR purification kit (Qiagen Inc.) according to the manufacturer's instructions, or according to the ExoSAP protocol of Werle et al. (1994).

Phylogenetic analyses

The 68 new sequences, together with published sequences from GenBank, were manually aligned, with gaps positioned to minimise nucleotide mismatches. *Pancratium illyricum* was used to root the trees. The ITS (45 taxa and 772 characters), combined plastid (48 taxa and 1 771 characters), and combined nuclear-plastid dataset (48 taxa and 2 493 characters) were analysed using Maximum Parsimony (MP) and Bayesian inference (BI).

The MP algorithm was implemented in PAUP* version 4.0b4 (Swofford 2000). Character transformations were unordered and equally weighted (Fitch 1971). A heuristic search with 1 000 random sequence additions, tree bisection reconnection (TBR) branch-swapping, and the MULPARS option selected, was performed. All character transformations were treated with equal likelihood and a maximum of 10 trees were saved in each replicate to minimise swapping on local minima. Trees of the shortest length were saved and used as starting trees for a second round of TBR swapping with no limit on the number of trees saved, to ensure the shortest trees were recovered in the analysis. Node support was evaluated using the bootstrap function in PAUP, with a full search, 1 000 replicates and a limit of 1 000 trees per replicate (Farris et al. 1996). Only bootstrap support (BS) values greater than 50% were retained, and the following scale was used to evaluate support percentages: 50–74%, weak; 75–84%, moderate; and 85–100%, strong.

BI analyses were performed on the three datasets using MrBayes 3.2.3 (Ronquist & Huelsenbeck 2003). Data from each region, where relevant, were partitioned in each dataset and all parameters were unlinked (statfreq, revmat, shape, pinvar) between partitions. The nuclear substitution model GTR + G + I, found by jModeltest v. 0.1.1 (Posada 2008), was implemented in all three BI analyses. Two simultaneous runs were completed for 1 million generations with a sampling frequency of 100. The standard deviation between the split frequencies stabilised below 0.01 and suboptimal trees, estimated using Tracer version 1.5. (Rambaut & Drummond 2009), were discarded as the 'burn-in' phase. The remaining trees were used to construct a 50% majority rule consensus tree with posterior probabilities (PP). Support values greater than 0.5 were retained, and the following scale was used to evaluate support values: 0.50–0.94, weak; and 0.95–1.00, strong.

Results

Nuclear dataset

In the nrITS MP analysis, 186 trees were retained with a tree length of 424 steps (consistency index (CI) = 0.74; retention index (RI) = 0.90). The topologies of both the BI (Figure S1) and MP (Figure S1) analyses were consistent with one another, although the trees produced in the BI analyses were, as expected, better resolved, with strong support values for almost all of the clades within *Haemanthus* (Figure S1). Almost all of the genera within the Haemantheae were recovered to be monophyletic with strong support in both analyses, except for *Clivia* that was unresolved in both analyses. *Haemanthus* was recovered as monophyletic in all analyses, with strong support in both the MP (BP 98) and BI (PP 1.0) analyses and sister to *Scadoxus* in the BI analysis, with moderate support (PP 0.95), although this relationship was unresolved in the MP analysis. Within *Haemanthus*, a clade corresponding to the newly recognised subg. *Serena* (Raf.) Snijman (BP 100, PP 1.0) was recovered as sister to the larger clade corresponding to subg. *Haemanthus* (BP 99, PP 1.0). Within subg. *Haemanthus* two strongly supported subclades were recovered, a subclade which comprised the Core Cape Floristic group (*H. sanguineus*, *H. pumilio* and *H. canaliculatus*) together with the Knersvlakte endemic *H. humanii* (BP 96, PP 0.99) and a more species-rich subclade, the *H. coccineus*–*H. unifolius* subclade (BP 100, PP 1.0).

Plastid dataset

In the combined plastid MP analysis, 2 879 trees were retained with a tree length of 213 steps (CI = 0.89; RI = 0.91). The phylogenies produced in the BI (Figure S2) and MP (Figure S2) analyses were consistent with one another in topology, with the BI analyses slightly better resolved and supported. Within the tribe Haemantheae, *Scadoxus*, *Gethyllis* and *Cryptostephanus* were recovered as monophyletic, with strong support in both analyses. Both *Clivia* and *Haemanthus* were unresolved, although as in the nuclear dataset the two clades of *Haemanthus* were recovered in a clade together with *Scadoxus* (BP 76, PP 0.99). Two main clades within *Haemanthus* were recovered, a clade corresponding to subg. *Serena* (although excluding *H. montanus*) (BP 98, PP 1.0) and a clade corresponding to subg. *Haemanthus* including *H. montanus* (BP 60, PP 0.95). These two main clades largely correspond with those in the nuclear analyses, differing only in the placement of *H. montanus* within the subg. *Haemanthus* clade and not with the other species of subg. *Serena*. Within the subg. *Haemanthus* clade, the placement of *H. humanii* also differed with *H. humanii* recovered with *H. pubescens* and *H. amarylloides*, although with strong support only in the BI analyses (BP 63, PP 1.0), and not within a subclade comprising the Core Cape Floristic species (*H. sanguineus*, *H. pumilio* and *H. canaliculatus*) as recovered in the nuclear analyses (Figure S1). The placement of *H. sanguineus*, *H. pumilio* and *H. canaliculatus* was unresolved in both the plastid BI and MP analyses.

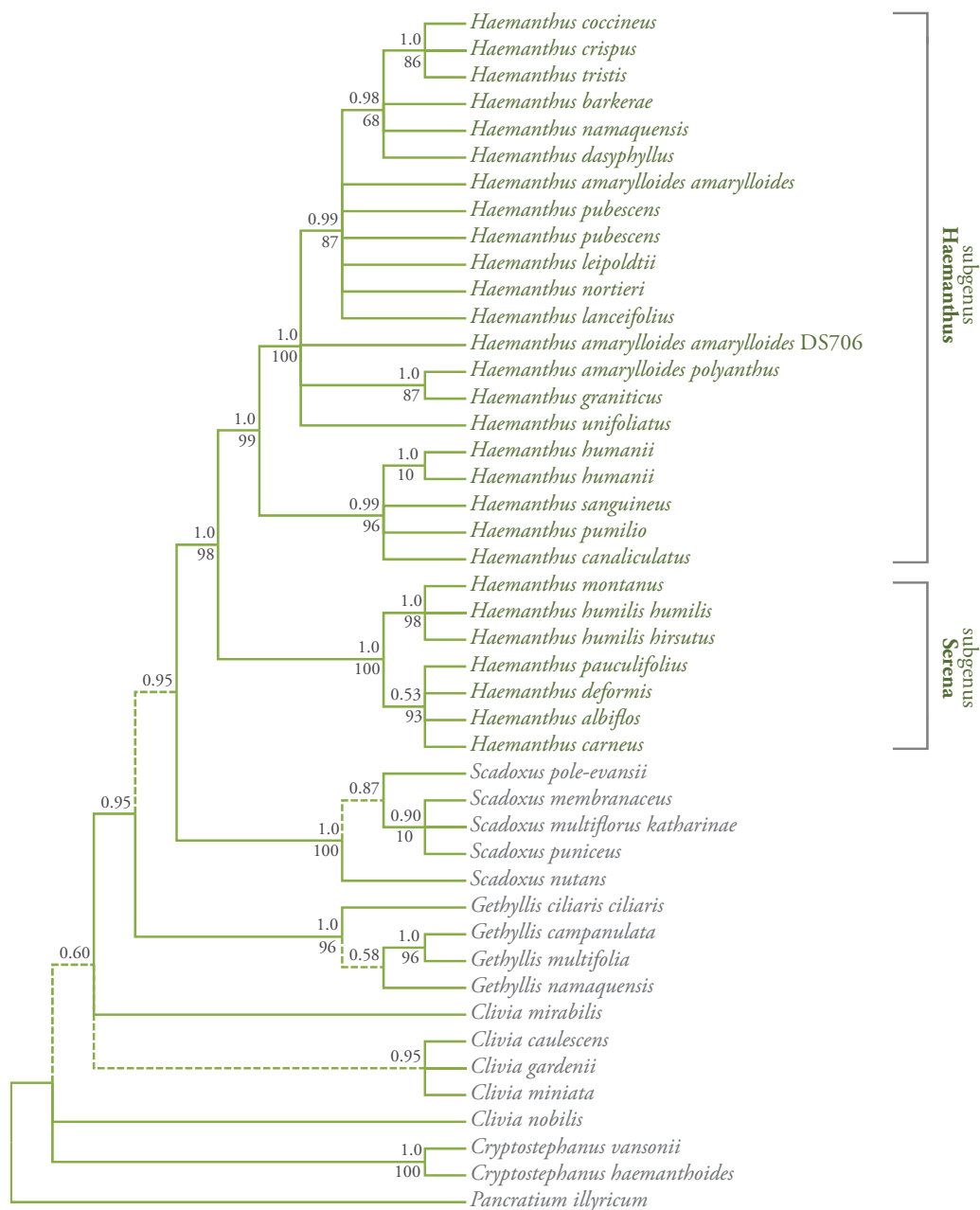


Figure S1. Bayesian inference (BI) tree of nrITS sequence data, with the subgeneric circumscriptions within *Haemanthus* indicated alongside. Posterior probability values above 0.5 are indicated above the branches and Bootstrap support values above 50% are indicated below the branches. Branches not recovered on the strict consensus tree of the Maximum Parsimony analysis are indicated by dashed lines.

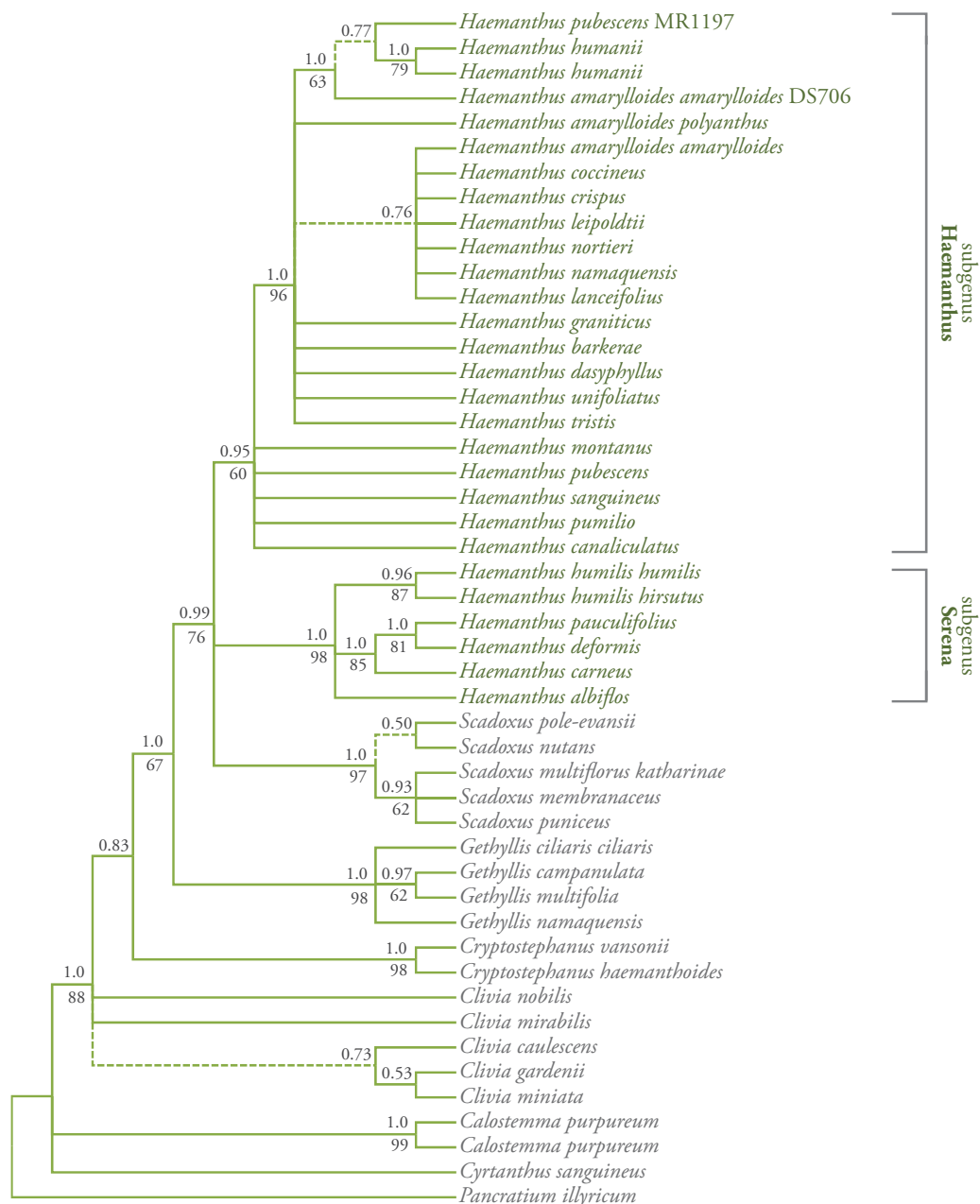


Figure S2. Bayesian inference (BI) tree of *rps16* and *trnL-F* sequence data, with the subgeneric circumscriptions within *Haemanthus* indicated alongside. Posterior probability values above 0.5 are indicated above the branches and Bootstrap support values above 50% are indicated below the branches. Branches not recovered on the strict consensus tree of the Maximum Parsimony analysis are indicated by dashed lines.

Combined nuclear and plastid dataset

In the combined nuclear and plastid MP analysis, 650 trees were retained with a tree length of 760 steps (CI = 0.74; RI = 0.88). The topologies of the BI (Figure S3) and MP (Figure S4) analyses were largely consistent with one another, although differing markedly in the placement of *H. humanii*. With the exception of *Clivia*, which forms a clade with poor support, the other genera within the Haemantheae were recovered as monophyletic with strong support in both the MP and BI analyses (BP 100, PP 1.0). *Haemanthus* was recovered as monophyletic in both analyses, with strong support in both the MP (BP 99) and BI (PP 1.0) analyses. The sister relationship with *Scadoxus* was strongly supported in the BI analyses (PP 1.0) but less so in the MP analyses (BP 86). The two main clades corresponding to subg. *Serena* (including *H. montanus*) and subg. *Haemanthus* were strongly supported (BP 100 and PP 1.0 for both clades). Within subg. *Haemanthus*, two strongly supported subclades were again recovered, although differing between the MP and BI analyses in the placement of *H. humanii*. In the BI analyses (Figure S3), *H. humanii* was recovered, with weak support (PP 0.73), together with *H. pubescens* and *H. amarylloides* within a weakly supported subclade (PP 0.85), as also recovered in the plastid analyses (Figure S2). In the MP analyses (Figure S4) *H. humanii* was weakly recovered in a subclade (BP 67) together with the Core Cape Floristic group (*H. sanguineus*, *H. pumilio* and *H. canaliculatus*) and not in the larger and more species-rich subclade, which was moderately supported (BP 88). The latter placement corresponds to that recovered in the nuclear analyses (Figure S1).

Discussion

In our study, based on Bayesian and parsimony analyses of nuclear ribosomal ITS and plastid *trnL-F* and *rps16* regions for eight genera of Amaryllidaceae and 25 taxa of *Haemanthus*, the combined analyses are the most highly resolved of the resultant ITS and plastid trees. In both the BI and MP trees from the combined nuclear and plastid analyses, the baccate-fruited Haemantheae resolve as monophyletic but with weak support. The monophyly of both subtribe Haemanthinae and Gethyllidinae is strongly supported, although the support for the Cliviinae clade is low (Figures S3 and S4). Within subtribe Haemanthinae the sister relationship of *Scadoxus* and *Haemanthus*, which were once treated as a single genus by several authors (Baker 1888, 1896; Bjørnstad & Friis 1972), receives strong to moderate support. Subtribe Gethyllidinae resolves as sister to subtribe Haemanthinae, and Cliviinae is sister to Haemanthinae–Gethyllidinae, an alliance that is also supported in the earlier study by Meerow and Clayton (2004).

The southern African genus *Haemanthus*, which is the primary focus of the present analyses, resolves into two well supported major clades that differ notably with respect to phytogeography and ecology. Subgenus *Serena*, newly recognised by Snijman in this volume, includes summer-rainfall, synanthous- or near synanthous-leaved taxa that occupy mesic to dry grasslands, coastal scrub and subtropical thicket ecosystems. In contrast, the second clade, corresponding to subg. *Haemanthus sensu stricto* (not the broadly circumscribed subgenus of Bjørnstad and Friis, 1972) consists of hysteroanthous-leaved species from the winter-rainfall Succulent Karoo and Fynbos biomes. The limits of these

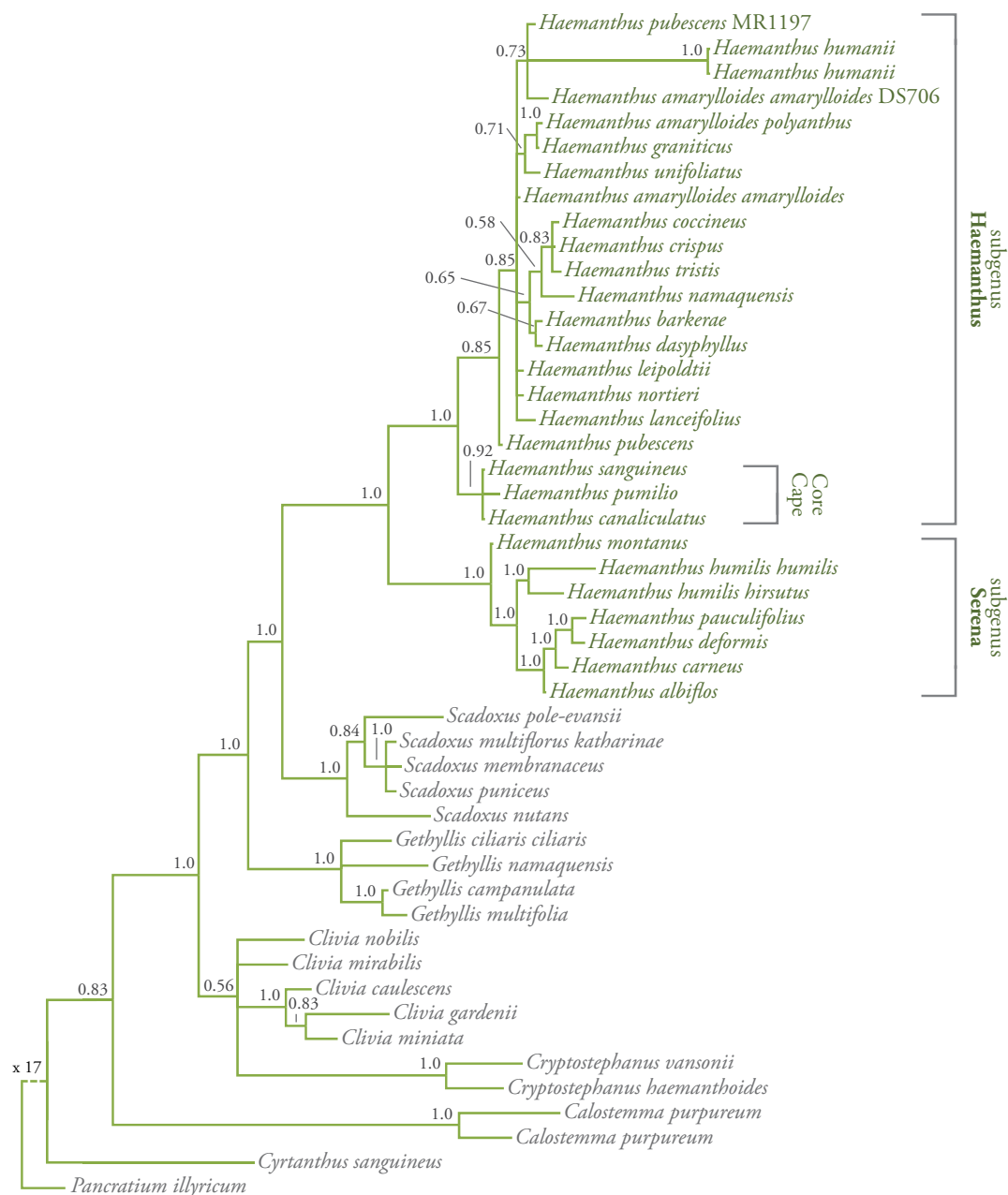


Figure S3. Bayesian inference phylogram of nrITS, *rps16* and *trnL-F* sequence data, with the subgeneric circumscriptions within *Haemanthus* indicated alongside. Posterior probability values above 0.5 are indicated above the branches. The scale indicates the number of expected substitutions per site.

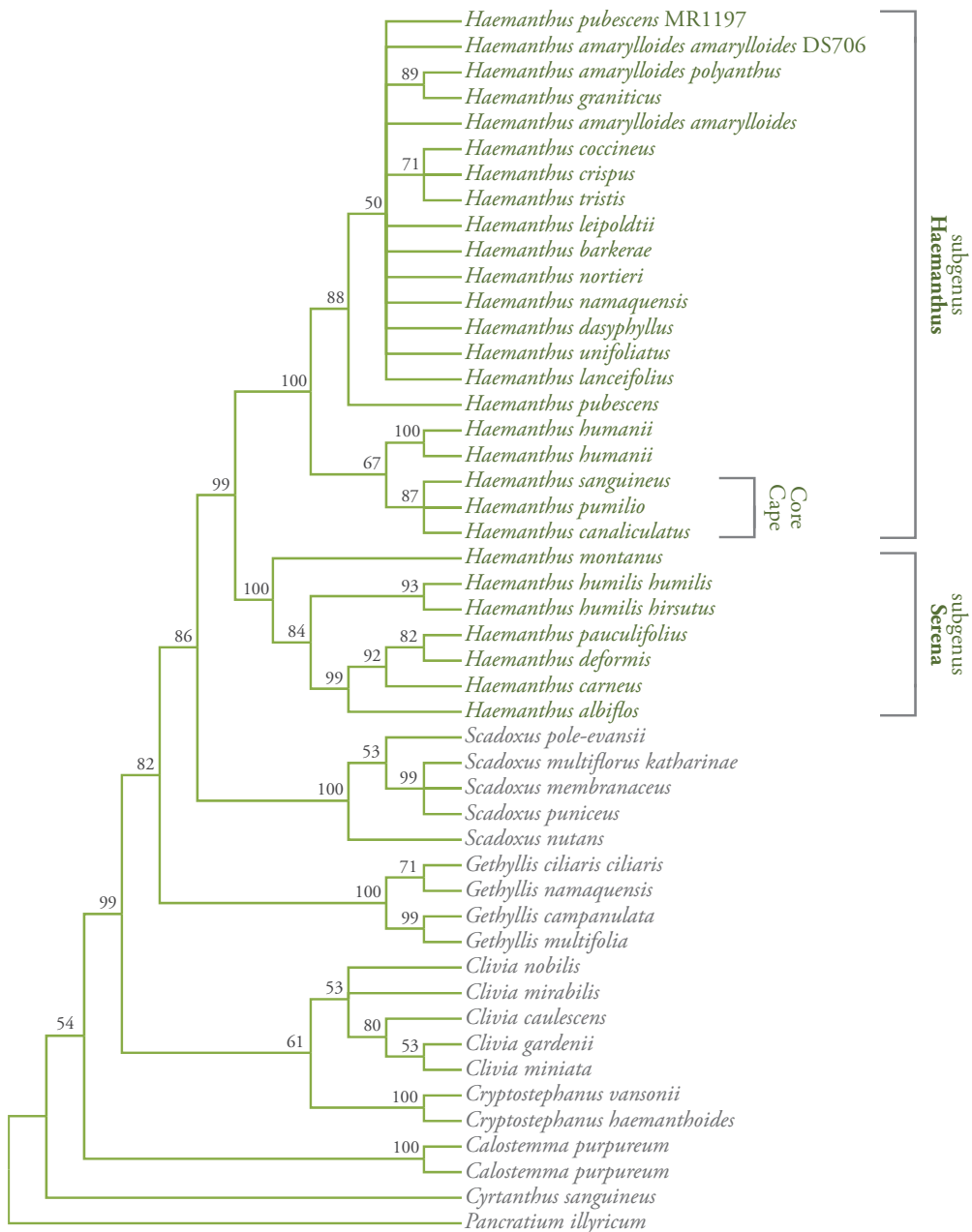


Figure S4. Strict Consensus tree of the 650 equally most parsimonious trees with a length of 760 steps, based on the Maximum Parsimony analysis of nrITS, *rps16* and *trnL-F* sequence data, with the subgeneric circumscriptions within *Haemanthus* indicated alongside. Bootstrap support values above 50% are indicated above the branches.

subclades, however, have been controversial, given that the analyses of Bay-Smidt et al. (2011) and Rønsted et al. (2012) rendered the widespread grassland species *H. montanus*, from the summer-rainfall region, as sister to the winter-rainfall subclade. The basis for uniting this species within the latter, however, is considered to be weak, since these studies sampled less than half the taxa recognised within *Haemanthus* and the provenances of the samples used are largely unknown. In contrast, the inclusion of *H. montanus* within the summer-rainfall subclade in our analyses is strongly supported in both the ITS trees (Figure S1) and the combined ITS and chloroplast trees (Figures S3 and S4). *Haemanthus montanus* is retrieved within the winter-rainfall clade (subg. *Haemanthus*) only in the poorly resolved chloroplast trees (Figure S2). Analysing the combined dataset with *H. montanus* excluded due to the observed incongruence between the nuclear and chloroplast trees did not affect the overall topology and so this taxon was retained in the final combined analyses.

Diagnostic characters thus far used to support the distinction between *Haemanthus sensu stricto* and *Scadoxus* (Müller-Doblies & Müller-Doblies 1975; Friis & Nordal 1976) continue to be stable. Arising from our study, the most notable correlation between the topology resolved by the DNA sequences and the known morphological synapomorphies within *Haemanthus* is at subgeneric level. Thus, the winter-rainfall subclade (subg. *Haemanthus*) is characterised by hysteranthous leaves and wine-red to reddish brown seeds. In contrast, the summer-rainfall subclade (subg. *Serena*) is morphologically characterised by synanthous or near-synanthous leaves and green or white seeds. Furthermore, most taxa in subg. *Haemanthus* have bulbs with unequally long tunics arranged in two opposite rows. Otherwise, Conrad's (2008) analyses revealed extensive homoplasy within *Haemanthus* for both vegetative and floral characters, a factor that accounts for the difficulty in developing a character state matrix for the genus (see Nordal & Duncan 1984).

The position of the spathe bracts at anthesis, a character used by Baker (1888, 1896) and Bjørnstad and Friis (1972) to delimit the infrageneric classification within *Haemanthus*, is particularly homoplasious. For example, *H. carneus*, which has membranous, early descending spathe bracts, is embedded within a clade in which the species (*H. albiflos*, *H. deformis* and *H. pauculifolius*) have leathery, upright spathe bracts, and this clade is sister to the remaining species within subg. *Serena* that all have early descending spathe bracts (Figures S1–S4). Flower colour is similarly homoplasious. Although red-flowered species are confined within subg. *Haemanthus*, flower colour varies from red to pink, and cream-coloured to white within the subgenus. For the Core Cape Floristic group alone (*H. canaliculatus*–*H. sanguineus* clade), which is sister to all the remaining members of the subg. *Haemanthus* (Figures S3 and S4), red or pink flowers are present within *H. sanguineus*, red flowers are typical of *H. canaliculatus*, and pink flowers characterise *H. pumilio*. Likewise, the presence of pubescence within *Haemanthus*, although uncommon within the family, is inferred to have arisen four times within subg. *Haemanthus* (Conrad 2008), whereas the reduction in leaf number from two to one each season, as in *H. pauculifolius*, *H. nortieri* Isaac and *H. unifolius* Snijman, has evolved independently within the genus at least twice.

Lastly, the low internal branch lengths that have been revealed in our study, except for *H. humanii*, could mean that a great deal of the diversity within *Haemanthus* is of relatively recent occurrence. Meerow et al. (1999) have noted this as a feature throughout the Amaryllidaceae *sensu stricto*, in

striking contrast to other asparagalean families included in their analyses. However, they also consider the possibility that the base substitution rates in the chloroplast genome are lower within Amaryllidaceae than within other Asparagales. The equivocal position of *H. humanii* either as sister to the Core Cape clade in the ITS (Figure S1) and combined BI tree (Figure S3) or embedded in a clade with *H. amarylloides* and *H. pubescens* in the plastid (Figure S2) and combined MP tree (Figure S4) may be the result of biological processes such as hybridisation or incomplete lineage sorting. Excluding *H. humanii* from the combined analyses did not alter the overall topology and so this taxon was retained in the analyses despite the incongruence.

Conclusion

In conclusion, our combined analyses, augmented by additional sampling for *Haemanthus*, results in a well-resolved, reasonably supported phylogeny for tribe Haemantheae, in agreement with that of Meerow and Clayton (2004). The combined analyses are sufficiently robust to enable the recognition of two subgenera within *Haemanthus sensu stricto* (excluding *Scadoxus*, as circumscribed by Friis & Nordal, 1976), thus facilitating the delimitation by Snijman (this volume) of a small summer-rainfall clade of synanthous- or near synanthous-leaved species and a larger winter-rainfall clade of species with hysternanthous leaves under the names subg. *Serena* and subg. *Haemanthus*, respectively.

Acknowledgements

The authors wish to acknowledge Ms Tasha Lyner who assisted with laboratory work and Dr Kenneth Oberlander who suggested several improvements to the manuscript.

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Appendices

Appendix 1.

Accessions for DNA sequence data, with corresponding voucher information and GenBank accession numbers. GenBank numbers lacking superscripts are published here for the first time.

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae					
<i>Clivia caulescens</i> R.A.Dyer	Winter s.n. (hort. NBG 573/99)	Songimvelo Reserve, Mpumalanga, SA	OR499778; -	OR391488 ^a	OR424479 ^a
<i>Clivia gardenii</i> Hook.	Rourke 2160 (NBG0167018)	Eshowe, KwaZulu-Natal, SA	AY280357 ^b	AY278960 ^b , AY278974 ^b	OR436498
<i>Clivia miniata</i> (Lindl.) Bosse	Rourke 2143 (NBG0167035)	Umtamvuma Gorge, KwaZulu-Natal, SA	AY280348 ^b	AY278961 ^b , AY278975 ^b	OR532449
<i>Clivia mirabilis</i> Rourke	Rourke 2220 (NBG0184720)	Oorlogskloof, Northern Cape, SA	OR499777; OR378330	OR391489 ^a	OR424480 ^a
<i>Clivia nobilis</i> Lindl.	Winter s.n. (hort. NBG 735/96)	Kei River mouth, Eastern Cape, SA	OR499776; OR378331	OR391490 ^a	OR424481 ^a
<i>Cryptostephanus haemanthoides</i> Pax	Luke & Luke 6398 (hort. NBG)	Hort. Quentin Luke, Kenya	OR499784; -	OR391491 ^a	OR424482 ^a
<i>Cryptostephanus vansonii</i> I. Verd.	Duncan s.n. (NBG0196209)	Unknown	OR499783; OR378332	OR391492 ^a	OR424483 ^a
<i>Gethyllis campanulata</i> L. Bolus	Manning 22427 (NBG0176780)	Nieuwoudtville, Northern Cape, SA	OR499780; -	OR391493 ^a	OR424484 ^a
<i>Gethyllis ciliaris</i> (Thunb.) Thunb. subsp. <i>ciliaris</i>	Duncan 364 (hort. NBG 74/93)	Mamre, Western Cape, SA	OR499779; OR378333	OR391494 ^a	OR424485 ^a

^aConrad et al. (2006)

^bMeerow & Clayton (2004)

^cSnijman & Meerow (2010)

^dRønsted et al. (2012)

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae (continued)					
<i>Grthyllis multifolia</i> L. Bolus	Townsend 130 (NBG0191659)	De Doorns, Western Cape, SA	OR499781; -	OR391495 ^a	OR424486 ^a
<i>Grthyllis namaquensis</i> (Schönland) Oberm.	Manning s.n. (NBG0191661)	Spitzkop farm, Namibia	OR499782; OR378334	OR391496 ^a	OR424487 ^a
<i>Haemanthus albiflos</i> Jacq.	Winter 498 (hort. NBG 571/97)	Dwesa Reserve, Eastern Cape, SA	OR499789; OR364889	OR391486	OR424476
<i>Haemanthus</i> <i>amarylloides</i> Jacq. subsp. <i>amarylloides</i>	Snijman 706 (NBG0126821)	Grootvlei, Northern Cape, SA	OR357723	OR391483	OR424474
<i>Haemanthus</i> <i>amarylloides</i> Jacq. subsp. <i>amarylloides</i>	Snijman 599 (NBG0122774)	Nieuwoudtville, Northern Cape, SA	OR499758; OR378335	OR391497 ^a	OR424488 ^a
<i>Haemanthus</i> <i>amarylloides</i> subsp. <i>polyanthus</i> Snijman	Snijman 1784 (NBG0176726)	Kamiesberg, Northern Cape, SA	OR499757; OR378336	OR391498 ^a	OR424489 ^a
<i>Haemanthus barkerae</i> Snijman	Perry & Snijman 2252 (NBG0133554)	Nieuwoudtville, Northern Cape, SA	OR499764; OR378337	OR391499 ^a	OR424490 ^a
<i>Haemanthus</i> <i>candiculatus</i> Levyns	Snijman 1266 (NBG0167551)	Bettys Bay, Western Cape, SA	OR499773; OR378338	OR391500 ^a	OR424491 ^a

^aConrad et al. (2006)^bMeerow & Clayton (2004)^cSnijman & Meerow (2010)^dRønsted et al. (2012)

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae (continued)					
<i>Haemanthus carneus</i> Ker-Gawl.	<i>Wisura 1063</i> (NBG0089911)	Somerset East, Eastern Cape, SA	OR499771; OR378339	OR391501 ^a	OR424492 ^a
<i>Haemanthus coccineus</i> L.	<i>Snijman 1792</i> (NBG0176727)	Bulshoek Dam, Western Cape, SA	OR499759; OR378340	OR391502 ^a	OR424493 ^a
<i>Haemanthus crispus</i> Snijman	<i>Snijman 1771</i> (NBG0176725)	Vanhyns Pass, Northern Cape, SA	OR499760; OR378341	OR391503 ^a	OR424494 ^a
<i>Haemanthus dasyphyllus</i> Snijman	<i>Snijman 1299</i> (NBG0151994)	NW of Loeriesfontein, Northern Cape, SA	OR499768; OR378342	OR391504 ^a	OR424495 ^a
<i>Haemanthus deformis</i> Hook.f.	<i>Nichols 800</i> (hort. NBG 1075/84)	Vernon Crookes Reserve, KwaZulu-Natal, SA	OR499788; OR364890	OR391485	OR424477
<i>Haemanthus graniticus</i> Snijman	<i>Snijman 1782</i> (NBG 176730)	Kamiesberg, Northern Cape, SA	OR531096; OR531098	OR532451	OR424496
<i>Haemanthus humanii</i> G.D.Duncan	[<i>Human sub</i>] <i>Duncan s.n.</i> (NBG1565121)	Bitterfontein, Western Cape, SA	OR357721	OR391481	OR424472
<i>Haemanthus humanii</i> G.D.Duncan	<i>Snijman & Manning 2041</i> (NBG1569058)	Bitterfontein, Western Cape, SA	OR357722	OR391482	OR424473
<i>Haemanthus humilis</i> Jacq. subsp. <i>humilis</i>	<i>Van Jaarsveld 3325</i> (NBG0120280)	Matlabas, Limpopo Province, SA	OR499763; OR378344	OR391506 ^a	OR424498 ^a

^aConrad et al. (2006)

^bMeerow & Clayton (2004)

^cSnijman & Meerow (2010)

^dRønsted et al. (2012)

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae (continued)					
<i>Haemanthus humilis</i> subsp. <i>hirsutus</i> (Baker) Snijman	<i>Van Jaarsveld</i> 1834 (NBG0125072)	NW of Johannesburg, Gauteng, SA	OR499766; OR378343	OR391505 ^a	OR424497 ^a
<i>Haemanthus lanceifolius</i> Jacq.	<i>Snijman</i> 1797a (NBG0179724)	Vanrhynsdorp, Western Cape, SA	OR499772; OR378345	OR391507 ^a	OR424499 ^a
<i>Haemanthus leipoldtii</i> (Snijman) Snijman	<i>Snijman</i> 432 (NBG0121704)	Klawer, Western Cape, SA	OR499762; OR378346	OR391508 ^a	OR424500 ^a
<i>Haemanthus montanus</i> Baker	<i>Nichols</i> 999 (hort. NBG 672/88)	Itala Reserve, KwaZulu-Natal, SA	OR499785; OR364891	OR391487	OR424478
<i>Haemanthus namaquensis</i> R.A.Dyer	<i>Van Berkel</i> 294 (NBG0121548)	Karkams, Northern Cape, SA	OR499767; OR378347	OR391509 ^a	OR424501 ^a
<i>Haemanthus nortieri</i> Isaac	<i>Jangle</i> s.n. (hort. NBG 6/98)	Nardouwsberg, Western Cape, SA	OR499787; OR428340	OR436479	OR436496
<i>Haemanthus paucifolius</i> Snijman & A.E.van Wyk	<i>Symonds</i> s.n. (hort. NBG 3/98)	Strydom Tunnel, Mpumalanga, SA	OR531097; OR364888	OR391484	OR424475
<i>Haemanthus pubescens</i> L.f.	[<i>Manning</i> sub] <i>Rourke</i> 1197 (NBG0092730)	Mamre Road, Western Cape, SA	OR357720	OR391480	OR424471

^aConrad et al. (2006)^bMeerow & Clayton (2004)^cSnijman & Meerow (2010)^dRønsted et al. (2012)

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae (continued)					
<i>Haemanthus pubescens</i> L.f.	<i>Snijman</i> 1787 (NBG0176731)	Kalbaskraal, Western Cape, SA	OR499761; OR378348	OR391510 ^a	OR424502 ^a
<i>Haemanthus pumilio</i> Jacq.	<i>Snijman</i> 668 (NBG0126814)	Stellenbosch, Western Cape, SA	AY280358 ^b	AY278968 ^b , AY278982 ^b	OR532450
<i>Haemanthus sanguineus</i> Jacq.	<i>Snijman</i> 210 (NBG0120915)	near Robertson, Western Cape, SA	OR499765; OR378349	OR391511 ^a	OR424503 ^a
<i>Haemanthus tristis</i> Snijman	<i>Snijman</i> 1262 (NBG0151465)	Tanqua Karoo, Northern Cape, SA	OR499770; OR378350	OR391512 ^a	OR424504 ^a
<i>Haemanthus unifolius</i> Snijman	<i>Snijman</i> 181 (NBG0122498)	Spektakel Pass, Northern Cape, SA	OR499769; OR378351	OR391513 ^a	OR424505 ^a
<i>Scadoxus membranaceus</i> (Baker) Friis & Nordal	<i>Roux</i> 561 (hort. NBG 145/82)	Dwesa Forest, Eastern Cape, SA	OR499790; OR428341	OR436480	OR436497
<i>Scadoxus multiflorus</i> subsp. <i>katharinae</i> (Baker) Friis & Nordal	<i>Snijman & Manning</i> 1878 (NBG0182877)	Port St Johns, Eastern Cape, SA	OR499774; OR378352	OR391514 ^a	OR424506 ^a
<i>Scadoxus nutans</i> (Friis & I.Björnstad) Friis & Nordal	<i>Saunders</i> ex hort.	Uncertain, Ethiopia	OR557585; OR553409	OR567873	OR567875

^aConrad et al. (2006)

^bMeerow & Clayton (2004)

^cSnijman & Meerow (2010)

^dRønsted et al. (2012)

Taxon	Voucher information	Origin	ITS (ITS 1; ribosomal RNA and ITS 2)	<i>trnL</i>	<i>rps16</i>
Tribe Haemantheae (continued)					
<i>Scadoxus pole-evansii</i> (Oberm.) Friis & Nordal	Saunders ex hort.	Nyanga, Zimbabwe	OR557584; OR553408	OR567872	OR567874
<i>Scadoxus puniceus</i> (L.) Friis & Nordal	Wisura 1120 (hort. NBG 197/70)	Komga, Eastern Cape, SA	OR499775; OR553410	OR391515 ^a	OR436499 ^a
Tribe Cyrtantheae					
<i>Cyrtanthus sanguineus</i> Hook.f. subsp. <i>sanguineus</i>	Unknown s.n. (NBG0182888)	Uncertain, SA	GQ160851.1 ^c	EU523817.1 ^c	-
Tribe Pancratieae					
<i>Pancratium illyricum</i> L.	Rønsted 370 (C)	Unknown, 1288-2 (C)	JX464289.1 ^d	JX464371.1 ^d	FN594896.1 ^d
Tribe Calostemmateae					
<i>Calostemma purpureum</i> R.Br.	Rønsted 356 (C)	Telos Rare Bulbs, USA	JX464285.1 ^d	JX464367.1 ^d	-

^aConrad et al. (2006)^bMeerow & Clayton (2004)^cSnijman & Meerow (2010)^dRønsted et al. (2012)

Appendix 2.

Excluded taxa.

For full nomenclatural citations see Friis and Nordal (1976), Snijman (1984), POWO (2022) and WFO (2023).

- *Haemanthus abyssinicus* Herb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus allisoni* Baker, *nom. nud.*, probably *H. humilis* Jacq.
- *Haemanthus andrei* De Wild. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus angolensis* Welw. ex Baker = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus arabicus* M.Roem. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus arnoldianus* De Wild. & T.Durand = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus bequaerti* De Wild. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus bivalvis* Beck = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus brachyandrus* Baker = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus cabrae* De Wild. & T.Durand = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus ceciliae* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus cernuiflorus* J.Bell ex Drapeiz = *Clivia nobilis* Lindl.
- *Haemanthus ciliaris* L. = *Crossyne guttata* (L.) D.Müll.-Doblies & U.Müll.-Doblies
- *Haemanthus cinnabarinus* Decne. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus* × *clarkei* W.Watson, a garden hybrid between *H. coccineus* L. and *H. albiflos* Jacq.
- *Haemanthus coccineus* Forssk. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus coerulescens* Steud., *nom. nud.* = *Pauridia capensis* (L.) Snijman & Kocyan
- *Haemanthus colchicifolius* Salisb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus congolensis* De Wild. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus cruentatus* Schumach. & Thonn. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus cyrtanthiflorus* C.H.Wright = *Scadoxus cyrtanthiflorus* (C.H.Wright) Friis & Nordal
- *Haemanthus delagoensis* Herb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus demausei* De Wild. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus diadema* L.Linden = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus distichus* (L.f.) L.f. ex Savage = *Boophone disticha* (L.f.) Herb.
- *Haemanthus dubius* Kunth = *Phaedranassa dubia* (Kunth) J.F.Macbr.
- *Haemanthus eetveldeanus* De Wild. & T.Durand = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus euryisiphon* Harms = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus falcatus* Thunb. = *Ammocharis longifolia* (L.) Herb.
- *Haemanthus fascinator* Linden ex De Wild. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus fax-imperii* Cufod. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus fliflorus* Hiern ex Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus germanianus* J.Braun & K.Schum. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal

- *Haemanthus goetzei* Harms in Engler = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus grandifolius* Balf.f. = *Ledebouria grandifolia* (Balf.f.) A.G.Mill. & D.Alexander
- *Haemanthus guttatus* Banks ex Kunth = *Crossyne guttata* (L.) D.Müll.-Doblies & U.Müll.-Doblies
- *Haemanthus hookerianus* Herb., probably *H. coccineus* L. or *H. sanguineus* Jacq.
- *Haemanthus humilis* A.Chev., *nom. nud.* = *Scadoxus multiflorus* (Martyn) Raf.
- *Haemanthus hydrophilus* Thunb. = *Crinum campanulatum* Herb.
- *Haemanthus imperialis* hort. ex Laplace = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus insignis* Hook. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus kalbreyeri* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus katharinae* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *katharinae* (Baker) Friis & Nordal
- *Haemanthus kundianus* J.Braun & K.Schum. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus laurentii* De Wild. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus lescrauwaetii* De Wild. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus lindenii* N.E.Br. = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus longifolius* (De Wild. & T.Durand) Traub = *Scadoxus longifolius* (De Wild. & T.Durand) Friis & Nordal
- *Haemanthus longitubus* C.H.Wright = *Scadoxus multiflorus* (Martyn) Raf. subsp. *longitubus* (C.H.Wright) Friis & Nordal
- *Haemanthus lynesii* Stapf = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus maculatus* Jacq. ex Loudon, *nom. nud.* Identity unknown.
- *Haemanthus magnificus* (Herb.) Herb. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus magnificus* var. *gumbletonii* Baker = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus magnificus* var. *superbus* Baker = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus mannii* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *longitubus* (C.H.Wright) Friis & Nordal
- *Haemanthus membranaceus* Baker = *Scadoxus membranaceus* (Baker) Friis & Nordal
- *Haemanthus micrantherus* Pax = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus mildbraedii* Perkins = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus mirabilis* Perkins = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus multiflorus* Martyn = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus natalensis* Hook. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus nicholsonii* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus nutans* Friis & I.Bjørnstad = *Scadoxus nutans* (Friis & I.Bjørnstad) Friis & Nordal
- *Haemanthus obliquus* Donn, probably *H. coccineus* L. or *H. sanguineus* Jacq., description inadequate.
- *Haemanthus orbicularis* Donn, probably *H. coccineus* L. or *H. sanguineus* Jacq., description inadequate.
- *Haemanthus orchidifolius* Salisb. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus orientalis* (L.) Thunb. = *Brunsvigia orientalis* (L.) Aiton ex Ecklon
- *Haemanthus otaviensis* Dinter = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus pole-evansii* Oberm. = *Scadoxus pole-evansii* (Oberm.) Friis & Nordal

- *Haemanthus pseudocaulus* I.Bjørnstad & Friis = *Scadoxus pseudocaulus* (I.Bjørnstad & Friis) Friis & Nordal
- *Haemanthus pseudocaulus* subsp. *prorumpens* I.Bjørnstad & Friis = *Scadoxus pseudocaulus* (I.Bjørnstad & Friis) Friis & Nordal
- *Haemanthus pubescens* Blanco = *Crinum asiaticum* L. subsp. *asiaticum*
- *Haemanthus puniceus* L. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus puniceus* var. *fortuita* Herb. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus puniceus* var. *magnificus* Herb. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus puniceus* var. *membranaceus* (Baker) Baker = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus radcliffei* Rendle = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus redouteanus* M.Roem. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus redouteanus* M.Roem. var. *subalbus* M.Roem. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus roseus* Hort.Angl. ex Link, *H. humilis* Jacq. or *H. carneus* Ker Gawl.
- *Haemanthus rotularis* Baker = *Scadoxus cinnabarinus* (Decne.) Friis & Nordal
- *Haemanthus rouperi* hort. = *Scadoxus puniceus* (L.) Friis & Nordal
- *Haemanthus rupestris* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus sacculus* E.Phillips = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus sarniensis* (L.) Thunb. = *Nerine sarniensis* (L.) Herb.
- *Haemanthus seretii* De Wild. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus sessiliflorus* Dinter = *Massonia sessiliflorus* (Dinter) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig
- *Haemanthus sinuatus* Thunb. ex Schult.f. = *Boophone disticha* (L.f.) Herb.
- *Haemanthus somaliensis* Baker = *Scadoxus multiflorus* (Martyn) Raf., possibly subsp. *multiflorus*
- *Haemanthus spathulatus* hort. ex M.Roem., *nom. nud.*, the identity remains unknown.
- *Haemanthus speciosus* Colla, *nom. nud.*, the identity remains unknown.
- *Haemanthus spiralis* (L'Hér.) Aiton = *Strumaria spiralis* (L'Hér.) W.T.Aiton
- *Haemanthus stellatus* Steud., *nom. nud.* = *Pauridia capensis* (L.) Snijman & Kocyan
- *Haemanthus tenellus* Steud., *nom. nud.* = *Strumaria tenella* (L.f.) Snijman
- *Haemanthus tenuiflorus* Herb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus tenuiflorus* var. *coccineus* Hook.f. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus tenuiflorus* var. *delagoensis* (Herb.) Herb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
- *Haemanthus tenuiflorus* var. *mocambicensis* Herb. = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
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- *Haemanthus undulatus* (L.) Thunb. = *Nerine undulata* (L.) Herb.
- *Haemanthus vaginans* Thunb., probably *Strumaria truncata* Jacq. ex Willd.
- *Haemanthus vaginatus* Thunb. = *Strumaria truncata* Jacq. ex Willd.
- *Haemanthus zambesiacus* Baker = *Scadoxus multiflorus* (Martyn) Raf. subsp. *multiflorus*
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Website: www.sanbi.org



Haemanthus, a genus of 25 attractive bulbous plant species endemic to southern Africa, is a member of the sub-Saharan and Arabian Peninsula Haemantheae, the only tribe in Amaryllidaceae with baccate fruits. *Haemanthus* has a brush-type inflorescence of many small flowers surrounded by several large spathe bracts. This account provides a phylogeny-based subgeneric classification and two subgenera are recognised: *Haemanthus*, endemic to the winter-rainfall region, includes 18 species of hysteranthous-leaved plants with pink or red flowers; and *Serena*, restricted to regions of summer or nonseasonal rain, encompasses seven species of synanthous- or near synanthous-leaved plants with white or pink flowers. Radiation patterns suggest that speciation was likely due to vicariance, driven by the steady ecological and geographical isolation of the group's two major lineages under past climatic changes. This account gives the taxonomic history of the genus, describes character and species diversity and possible evolutionary pathways in the group. Keys are provided to the subgenera, species and subspecies. Each taxon is fully described with complete nomenclature and discussion on diagnostic characters, putative relationships and ecology. Species and subspecies are illustrated with colour plates of paintings and photographs, and maps show distribution ranges.

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