

# Systematics of the genus *Daubenya* (Hyacinthaceae: Massonieae)

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**Keywords:** *Amphisiphon* W.F.Barker, *Androsiphon* Schltr., *Daubenya* Lindl., Hyacinthaceae, Massonieae Baker, *Neobakeria* Schltr., South Africa, taxonomy

## ABSTRACT

*Daubenya* Lindl. was until recently thought to comprise the single species *D. aurea* Lindl. but is now considered to include the monotypic genera *Androsiphon* Schltr. and *Amphisiphon* W.F.Barker, as well as the species previously referred to the genus *Neobakeria* Schltr. Eight species are now recognized in the genus, including the new combinations *Daubenya comata* (Burch. ex Baker) J.C.Manning & A.M.van der Merwe and *D. zeyheri* (Kunth) J.C.Manning & A.M.van der Merwe. Each species is fully described and illustrated in black-and-white and in colour. A key to the species, and distribution maps are provided.

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## INTRODUCTION

The Hyacinthaceae (excluding the North American chlorogaloid genera) are now well established as a monophyletic lineage within the order Asparagales (Fay & Chase 1996; Pfosser & Speta 1999; Fay *et al.* 2000). The family is distributed through Africa, across most of Europe and central Asia to India, and in Andean South America, with centres of diversity in southern Africa and the Mediterranean (Speta 1998). The plants prefer open,

sunny habitats in seasonal climates and are correspondingly rare in heavily wooded, tropical regions. Although it has long proved difficult to devise a natural infrafamilial classification of the Hyacinthaceae, recent molecular analysis of the chloroplast DNA region *trnL-F* provides strong support for the division of the family into four subfamilies, Oziroëoideae, Urgineoideae, Ornithogaloideae and Hyacinthoideae (Pfosser & Speta 1999). Within the subfamily Hyacinthoideae two clades are retrieved. The first combines the Indian and African genera south of the Sahara, and largely coincides with the delimitation of the tribe Massonieae Baker (with the significant inclusion of the sub-Saharan species previously placed in the genus *Scilla* L.). The second clade includes the Mediterranean and Asian genera, corresponding to the tribe Hyacintheae Dumort (Pfosser & Speta 1999). Despite the strong molecular support for the recognition of these two tribes, few corroborative morphological characters are available. Further division of tribe Massonieae into the subtribes Ledebouriinae and Massoniinae (Müller-Doblies & Müller-Doblies 1997) is not supported by the molecular data. The poor congruence between morphological and other characters within Hyacinthaceae has also made generic circumscriptions very difficult. One of the consequences of this has been the recognition of a large number of genera that are poorly defined morphologically (Speta 1998).

Within the tribe Massonieae the relationships between the species traditionally placed in the genera *Amphisiphon* W.F.Barker (1 sp.), *Androsiphon* Schltr. (1 sp.), *Daubenya* Lindl. (1 sp.), *Neobakeria* Schltr. (1–3 spp.) and *Massonia* Houtt. (± 6 spp.) have been especially controversial (Jessop 1976; Müller-Doblies & Müller-Doblies 1997; Goldblatt & Manning 2000). These genera share some morphological characters, in particular two prostrate or spreading leaves and a condensed inflorescence of more or less tubular flowers but differ greatly from one another in floral details. Traditional morphological methods have not been useful in resolving the relationships between the species but molecular analysis has proven extremely informative. Analysis of chloroplast DNA (Van der Merwe *et al.* in prep.) includes *Amphisiphon*, *Androsiphon*, *Daubenya*, *Neobakeria* and one species of *Massonia* in a strongly supported monophyletic clade. This clade is resistant to further segregation at the generic level and the cir-

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MS. received: 2002-01-09.





PLATE 1.—A, *Daubenya comata*; B, *D. namaquensis*; C, *D. marginata*; D, *D. zeyheri*; E, *D. alba*; F, *D. capensis*; G, *D. stylosa*; H, *D. aurea*. Photographer: John Manning.



cumscription of the genus *Daubenia* is therefore broadened to circumscribe the whole clade. The genus *Daubenia* in this broader sense is characterized by a tunicated bulb with the older tunics leathery and dark brown and extending as a short papery neck, two  $\pm$  glossy leaves with impressed longitudinal striations on the upper surface, and a racemose, corymbose or subspicate inflorescence of white, red or yellow flowers with a slender, cylindrical perianth tube. Species of *Massonia* s. str. are characterized by their soft, fleshy leaves, corymbose inflorescences with large, leaflike bracts, white to pink flowers with the tepals typically sharply recurved from the base and then incurved in a characteristic sigmoid fold, and tumbleweed-like infructescences.

*Daubenia* is centred along the western edge of the southern African central plateau and all of the species are winter-growing. Most are highly localized endemics restricted to pockets of doleritic clays. The vegetative similarity between the species contrasts sharply with the unusual diversity of floral form evident in the genus. This floral radiation represents adaptations to a variety of pollinating agents, including insects such as bees, butterflies, moths and monkey beetles and sunbirds. Most of the species exhibit adaptations to anemochory, especially in the development of large, winged capsules. These winged, dehiscent capsules contrast markedly with the indehiscent, ovoid capsules present in two of the species. Eight species are recognized within this expanded concept of *Daubenia*, some of them well established in horticulture but others very poorly known. This revision provides full descriptions of all species as well as notes on their history, ecology and distribution. All of the species were studied in the field and each is fully illustrated in black-and-white and in colour.

#### MATERIALS AND METHODS

Herbarium specimens in BOL, K, NBG, PRE and SAM were studied to gather data on morphology, flowering time and distribution. Extensive fieldwork was also undertaken and all species were visited in their natural habitat. All observations on pollinators were made in the field. Conservation status for each species was assessed according to the new IUCN categories and criteria (Victor 2000).

#### MORPHOLOGICAL CHARACTERS OF TAXONOMIC SIGNIFICANCE

**Bulb:** the bulbs in *Daubenia* are turbinate to globose or ovoid in shape and between 20–35 mm diam. The outer tunics become leathery and dark brown on drying, and split at the top into narrow, flat, papery segments that form a characteristic neck. This papery neck is particularly conspicuous in species or individuals with deeply buried bulbs. A similar neck is found in some species of *Lachenalia* but not in any species of *Massonia* s. str.

**Leaves:** all species have paired leaves that are prostrate or spreading. The leaf bases are subterranean and long or short depending on the depth of the bulb. The blades are glabrous and rather glossy above with impressed longitudinal striations along the main veins.

They are lanceolate to ovate in shape and measure 40–150  $\times$  25–50 mm.

**Leaf anatomy:** leaves in *Daubenia* are amphistomatic with a thick cuticle. The marginal epidermal cells are columnar with slightly thickened walls and a unicellular hypodermis is present at the leaf margin. The mesophyll typically comprises three rows of palisade parenchyma adaxially and three rows of spongy parenchyma abaxially. The vascular bundles are surrounded by parenchymatous bundle sheaths. Slight indentations correlating with the impressed longitudinal striations on the upper leaf surface occur above the main veins. In these indentations the epidermal cells are smaller than elsewhere with thicker outer periclinal walls and they overlie two rows of palisade parenchyma instead of three.

**Inflorescence:** is borne at ground level between the leaves on a subterranean peduncle. It is essentially racemose but varies in shape from conical to capitate. Shortening of the rachis in several species results in a corymbose, rather capitate inflorescence, whereas suppression of the pedicels results in a subspicate inflorescence, accompanied in some species by shortening of the axis. Well-developed pedicels and a corymbose inflorescence are found in *Daubenia aurea*, *D. alba*, *D. capensis* and *D. zeyheri* but the remaining species are characterized by a subspicate inflorescence. This is usually conical, protruding for up to 90 mm above the leaves in *D. marginata* and *D. namaquensis*, but is  $\pm$  capitate in *D. comata* and *D. stylosa*. The inflorescence bracts are usually inconspicuous and pale in colour except in *D. aurea*, which is characterized by large, green bracts. The bracts typically increase in size acropetally but the degree of this increase varies. In *D. comata*, *D. stylosa* and *D. zeyheri* the upper bracts are only slightly larger than the lower ones and form an inconspicuous greenish coma at the top of the inflorescence. In *D. namaquensis* and *D. marginata*, however, the increase in bract size is marked and the inflorescences are topped by a more conspicuous coma of greenish or pinkish to orange bracts. The inflorescence remains at ground level until the fruits are mature, at which stage the peduncle elongates rapidly from the base, pushing the infructescence well above the ground as a prelude to dispersal of the seeds.

**Flowers:** there is great variation in the morphology of the flowers in *Daubenia* but all species are characterized by a slender, cylindrical perianth tube. The tepals are usually free and spreading from the level of the stamen insertion but in *D. stylosa* they are fused well beyond this level into a narrow tube around the staminal column. Tepal colour ranges from white or pinkish in *D. alba*, *D. comata*, *D. marginata* and *D. zeyheri*, to bright yellow in *D. capensis*, *D. namaquensis* and *D. stylosa*, or brilliant red in most populations of *D. aurea*. The flowers in most species are actinomorphic but some degree of zygomorphy is evident in the lowermost flowers in *D. comata* and *D. namaquensis*, and reaches an extreme degree in *D. aurea*. In *D. comata* and *D. namaquensis* the outer flowers are at most weakly bilabiate through a slight asymmetry in the perianth tube, with the adaxial side slightly longer than the abaxial side. An analogous situation is also sometimes evident in the filament column in the lowermost flowers of *D. alba*. In *D. aurea*, however, the



zygomorphy is extremely marked and results from the great enlargement of the lowermost tepals of the lower flowers, accompanied by an elongation of the perianth tube on this side rather than on the adaxial side. The stamens in most species of *Daubenya* are  $\pm$  fused at the base into a staminal column or tube. This is most marked in *D. alba*, *D. aurea*, *D. capensis* and *D. stylosa*. In the bilabiate, lower flowers of *D. aurea*, the abaxial tepals are actually fused to the staminal column and as a consequence of this the abaxial filaments are inserted much higher up the perianth than the adaxial and appear to be free from one another. In *D. capensis* a thick, convex disc occludes the top of the staminal tube with the style protruding through a small pore in the disc. The staminal column is very short in *D. marginata* and *D. zeyheri*, and is lacking or only slightly evident in *D. comata* and *D. namaquensis*.

**Fruit and seeds:** the fruit in *Daubenya* is a papery capsule, typically dehiscent loculicidally in the upper portion. In *D. comata* the capsule is obovoid and rounded but in most of the other species it is  $\pm$  inflated and three-angled. These angles are particularly well developed in the upper part of the capsules in *D. alba* and *D. capensis*, and the capsules in these two species are decidedly cuneate in shape. The species *D. marginata*, *D. namaquensis* and *D. zeyheri* are distinctive in their deciduous capsules that fall free of the pedicels at maturity and are dispersed individually. In other species of *Daubenya* the capsules remain attached to the pedicel and rachis and the entire infructescence functions as the dispersal unit. Unique capsules with a persistent, horn-like style characterize *D. stylosa*. The capsules in this species are essentially indehiscent although the locules eventually separate along the septa. The seeds in all species are globose and black in colour with a smooth testa. They range in size from 2–3 mm diam.

#### DISTRIBUTION AND ECOLOGY

*Daubenya* is a small genus of eight species that is endemic to South Africa. It is largely restricted to the fringes of the winter rainfall region along the Bokkeveld and Roggeveld Escarpments, which mark the western margin of the South African central plateau. Five of the eight species occur here, at altitudes of 1 000–1 500 m. Most of the species of *Daubenya* are highly local endemics and only *D. comata* is more widespread, occurring over much of the South African central plateau. All of the species are winter-growing, despite the fact that not all are restricted to the winter rainfall region. Plants typically leaf and flower in the autumn or winter, between April and July, with only one species, *D. aurea*, flowering in the spring, in early September. Five of the species, *D. alba*, *D. aurea*, *D. capensis*, *D. stylosa* and *D. zeyheri* are restricted to the winter rainfall region and respond largely to frontal rain that falls between April and August. Apart from *D. zeyheri*, which is a coastal species confined to calcareous sands near Saldanha, the remaining four winter rainfall species occur along the edge of the Bokkeveld and Roggeveld Escarpments from Nieuwoudtville and Calvinia in the north southwards to Sutherland. The remaining three species occur partially or wholly within the summer rainfall region. *Daubenya*

*marginata* is distributed along the Roggeveld Escarpment but extends inland to Fraserburg, where it enters the summer rainfall region; *D. namaquensis* occurs at the edge of the summer rainfall region in Bushmanland, east of Springbok; and *D. comata* is widespread across the central parts of the summer rainfall region. Despite their distribution, these three species respond to autumn thundershowers and begin to grow slightly before the winter rainfall species.

Most species of *Daubenya* are highly localized endemics known only from a few populations. They typically occur in small colonies, sometimes in large numbers, in heavy clay soils, and are invariably restricted to low-lying washes or drainage lines where the soil becomes seasonally waterlogged. The majority of the species occur on the South African central plateau, where they are largely restricted to clays derived from dolerite. The particular nature of doleritic clays ensures that these soils retain moisture for longer than the surrounding clays derived from shales of the Karoo series. The two remaining species occur on more sandy substrates, *D. namaquensis* in deep red sands and *D. zeyheri* in calcareous coastal sands.

All of the species of *Daubenya* are vulnerable to disturbance or transformation of their habitat, particularly through agriculture. Although predation of the bulbs by porcupines is common among the species growing on the Roggeveld Escarpment, its impact on the populations is unknown. The numbers of these rodents can be expected to have increased as a result of the reduction in their natural predators, particularly leopard. Most species of *Daubenya* still appear to set large quantities of seed in the wild to replace the adult plants consumed by herbivores. An additional pressure on populations comes from sheep and baboon, which eat the leaves and inflorescences, resulting in a drastic reduction in seed set in some instances. A recent initiative aims at the protection of a population of the yellow-flowered form of *D. aurea* from overgrazing through co-operation of the landowner and the local bulb growers' association. There is, however, no formal conservation of this population and its survival thus remains uncertain. In another encouraging development, cultivated bulbs of *D. aurea* have become available in commercial nurseries. All of the species of *Daubenya* are worth cultivating for their compact habit and brilliantly coloured, often fragrant flowers.

#### POLLINATION AND SEED DISPERSAL

The floral diversity evident in the genus *Daubenya* is exceptional in the family Hyacinthaceae and reflects a corresponding diversity in pollination strategies. These include several strategies that, although well developed in the Western Cape, are rare or absent elsewhere. Most of the species produce fragrant, white or yellow flowers that are visited for nectar or pollen by a variety of diurnal and nocturnal insects, including pollen- and nectar-collecting bees, butterflies and moths in the family Noctuidae. The species with generalist flowers include *D. namaquensis*, *D. comata*, *D. alba* and *D. stylosa*. In these species the nectar collects either in the perianth tube only or also in the staminal tube above this. Both the



perianth and staminal tubes are narrow and the nectar is thus accessible only to long-tongued insects.

Two species, *D. marginata* and *D. zeyheri*, are adapted to pollination by sunbirds. The adaptations to ornithophily in these species include a reduced and widened staminal tube that forms a shallow reservoir in which significant quantities of nectar accumulates, orange or red filaments (with purple bases in *D. zeyheri*) and a lack of fragrance. Ornithophily occurs in several other genera of Hyacinthaceae in the Western Cape, especially *Lachenalia* and *Veltheimia*. *Daubenya aurea* is adapted to pollination by monkey beetles (Scarabidae-Rutellinae), a pollination strategy that appears to be unique among the Hyacinthaceae, although well represented among Western Cape Iridaceae. These active, hairy beetles utilize various brightly coloured, open or bowl-shaped flowers as sites for reproduction and are often encountered on various species of Asteraceae and Iridaceae (Goldblatt *et al.* 1998). Flowers adapted to these beetles are typically ornamented with dark markings that act as beetle mimics, decoying the insects through their resemblance to potential mates. Adaptations for this type of beetle pollination in *D. aurea* are the asymmetric enlargement of the lower or peripheral flowers in the inflorescence to imitate the ray florets of Asteraceae like *Arctotis* and *Gazania*, the lack of nectar, with associated vestigial staminal tube, and the absence of floral fragrance. Although the pollination biology of the remaining species, *D. capensis*, has not been studied, the peculiar structure of the flowers and their yeasty odour suggest that the species might be adapted to pollination by rodents. This strategy is also evident in one or two species of *Massonia* (Hyacinthaceae) (Johnson *et al.* 2001) as well as several species of *Androcymbium* Willd. (Colchicaceae) among the geophytes in Western and Northern Cape.

In all species of *Daubenya* the fruiting peduncle elongates at maturity, raising the infructescence above the ground, and then abscises to release it. Thereafter, the species differ markedly in seed dispersal strategies. In *D. comata* and *D. stylosa* no particular adaptations for seed dispersal appear to be developed and the relatively small capsules remain attached to the axis, shedding the seeds immediately around the plants. These autochorous species have short or vestigial pedicels that do not elongate at maturity and  $\pm$  ovoid capsules that are indehiscent, although the locules do eventually separate along the septa to release the seeds over time as they disintegrate. The remaining species exhibit a suite of adaptations to anemogeochoy or wind dispersal through tumbling (Van der Pijl 1982; Snijman & Linder 1996). The most prominent of these adaptations are the large, three-angled or -winged, loculicidally dehiscent capsule and the frequent detachment of the entire inflorescence as a single unit before seed release. In *D. marginata*, *D. namaquensis* and *D. zeyheri* the capsules abscise readily from the pedicels at maturity and are dispersed individually but in the remaining species they remain attached to the peduncle and the infructescence is dispersed as an entire unit. The surface area of the dispersal unit in these species is further increased by the prominent wings on the capsules in *D. alba* and *D. capensis*, giving them a kite-like appearance and by the large papery bracts in *D.*

*aurea*, which act as sails. The conversion of the infructescence into a tumbleweed is enhanced in *D. alba* and *D. capensis* through the elongation of the pedicels, increasing the size of the infructescence and giving it a rounded, balloon-like form. There is a remarkable similarity in the adaptations to wind dispersal of the fruits developed in these latter species and in the genus *Massonia*, particularly the obtriangular, winged capsules borne on relatively long pedicels to form a rounded, balloon-like structure that is readily dispersed by the wind. In *Massonia*, however, the pedicels are invariably subtended by large, sail-like bracts resembling those found in *D. aurea*. The smooth, globose seeds in the anemochorous species are easily shaken out of the capsules but do not appear to disperse significantly thereafter.

Anemogeochoy is well known in the family Amaryllidaceae: subtribe Amaryllideae (Snijman & Linder 1996) but has not been studied in the Hyacinthaceae. In both of these families, however, this mode of seed dispersal is more common in South Africa than elsewhere in the continent, and is best developed in the semi-arid, winter rainfall region.

## EVOLUTION

Sequence analysis of the *trnL-trnF* region of the chloroplast genome (Van der Merwe *et al.* in prep.) offers little resolution within the genus apart from indicating a close relationship between the species *D. alba* and *D. capensis*. This species pair is well defined morphologically by the cuneate, winged capsules borne on long pedicels. Their relationship to the remaining species as well as the relationships between these species remain unresolved. Although the similarity in floral form and capsules in *D. marginata* and *D. zeyheri* suggests that these two species are closely allied, further morphological assessment of relationships within the genus is confounded by the high degree of autapomorphies displayed by each species. Until further genetic analysis is complete, little more can be said about possible relationships between the species.

The genus *Daubenya* is essentially restricted to seasonally moist, usually clay depressions and all of the species respond to autumn rains, whether they occur in the winter or summer rainfall regions. There is thus little ecological diversification within the genus in response to climate or soils, which is probably not surprising given that all species are vegetatively indistinguishable. Apart from *D. comata* and *D. marginata*, species of *Daubenya* are local endemics that are rarely sympatric. Exceptions are the species pairs *D. aurea* and *D. marginata* in one or two localities, and *D. stylosa* and *D. capensis*. It is perhaps significant that the members of these pairs flower at different times, suggesting that flowering time operates as a prezygotic isolating mechanism between them. While there may be little diversification within the genus in response to climate or soil, *Daubenya* is unparalleled in the Hyacinthaceae in its floral radiation. This extreme variation can be linked to differences in pollination strategy and is accompanied by some variation in capsule morphology and seed dispersal mechanisms. Most species are anemochorous to some degree and adapta-



tions to wind dispersal of the seeds include both elaboration of the capsules themselves as well as enlargement of the inflorescence bracts. Exceptions are *D. stylosa* and possibly *D. comata*, which have indehiscent capsules with no apparent adaptations for seed dispersal. Although the anemochorous species are more diverse than those lacking obvious seed dispersal mechanisms, the individual species adapted to anemochory are not more widespread than the autochorous species. This suggests that anemochory in *Daubenya* has facilitated saltational speciation, whereby the occasional colonization of suitable new habitats through seed dispersal has favoured speciation through founder-effects and subsequent genetic drift.

#### TAXONOMIC HISTORY

The taxonomic history of the genus *Daubenya* reflects the significance that has traditionally been attached to floral differences among the Hyacinthaceae, resulting in the establishment of several monotypic genera between 1835 and 1936 for newly discovered species with distinctive flowers. The first of these genera, *Daubenya*, was established in 1835 by Lindley to accommodate the species *D. aurea*, which is characterized by extremely zygomorphic lower flowers. Floral zygomorphy is uncommon in the family Hyacinthaceae and this degree of zygomorphy does not occur elsewhere in the family. In his treatment of the sympetalous genera of the family Hyacinthaceae, Baker (1871) allied *Daubenya* with the genus *Massonia* in his tribe Massonieae on the basis of the reduced peduncle. Benthams (1883), however, included these two genera in his tribe Allieae because their congested inflorescences in which the flowers are subtended by large bracts suggested the umbel-like inflorescences of Alliaceae. Species related to *D. aurea* but with less well-developed bracts were placed by Baker (1871) first in section *Astemma* of *Massonia* and later in subgenus *Astemma* of *Polyxena* (Baker 1897). The species recognized by Baker (1871) in subgenus *Astemma* are those that are currently recognized as *D. comata*, *D. marginata* and *D. zeyheri* and he remarked at the time on the similarity between them and certain species of *Massonia*, with the suggestion that the two groups were best combined. This opinion was followed in recent treatments of the group (Jessop 1976; Müller-Doblies & Müller-Doblies 1997) but was not the view of Rudolf Schlechter (1924), who segregated the taxa placed by Baker in *Polyxena* subgenus *Astemma* as a distinct genus, *Neobakeria*, nor of Phillips (1951) or Dyer (1976). At the same time that Schlechter described *Neobakeria*, he also established another genus, *Androsiphon*, for a florally unusual species discovered a few years previously by his brother. Following this, yet another monotypic genus was established by Barker (1936), for the species *Amphisiphon stylosa*. These two genera were combined by Phillips (1951) but have been retained as distinct by subsequent workers, starting with Dyer (1976) and Jessop (1976). Recent studies on the molecular systematics of the group reject the recognition of these genera. The characters on which these various genera were based are best seen as extreme adaptations to a variety of pollination and seed dispersal strategies (Goldblatt & Manning 2000). Those species with more conventional

flowers that were previously placed in *Neobakeria* are now also confirmed to be closely allied to these florally more unusual species. Although all of these genera were included in an expanded concept of the genus *Daubenya* (Goldblatt & Manning 2000), not all of the species were transferred to that genus and this is accordingly done here.

#### SYSTEMATIC TREATMENT

***Daubenya* Lindl.** in Botanical Register 21: t. 1813 (1835); Baker: 394 (1871); Baker: 417 (1897); E. Phillips: 193 (1951); R.A. Dyer: 940 (1976); Jessop: 431 (1976); U. Müll.-Doblies & D. Müll.-Doblies: 91 (1997). Type: *D. aurea* Lindl.

*Polyxena* Kunth subgenus *Astemma* sensu Baker: 419 (1897) non *Massonia* Thunb. section *Astemma* Endl.: 145 (1836).

*Androsiphon* Schltr.: 148 (1924); Jessop: 432 (1976); U. Müll.-Doblies & D. Müll.-Doblies: 86 (1997). Type: *A. capense* Schltr.

*Neobakeria* Schltr.: 150 (1924); U. Müll.-Doblies & D. Müll.-Doblies: 86 (1997). Type: *N. namaquensis* Schltr.

*Amphisiphon* W.F. Barker: 19 (1936); Jessop: 432 (1976); U. Müll.-Doblies & D. Müll.-Doblies: 86 (1997). Type: *A. stylosa* W.F. Barker.

Deciduous geophytes. *Bulb* turbinate to globose, sometimes deeply buried; outermost tunics leathery, dark brown, extending in a neck as narrow, flat, papery segments. *Leaves* 2, spreading to prostrate, lanceolate to ovate, longitudinally striate, glossy green, bases clasping peduncle for some distance. *Inflorescence* corymbose or racemose to subsapicate, congested and capitate to conical; peduncle subterranean in flower but elongating from base in fruit and then well-exserted; bracts usually small, rarely large, usually increasing in size acropetally, the uppermost sterile, often forming a coma; pedicels suberect, vestigial to well developed in lower flowers but decreasing in length acropetally, sometimes elongating slightly in fruit. *Flowers* white to lilac, greenish yellow or red, strongly scented or unscented, actinomorphic or sometimes dimorphic with lower flowers slightly or strongly bilabiate, sympetalous; perianth tube cylindrical or somewhat dorsoventrally compressed, shorter in upper flowers, sometimes either adaxial or abaxial part of tube longer than opposing part in lower flowers; tepals spreading to suberect or recurved, rarely erect and connate, linear to oblanceolate, usually subsimilar but sometimes lower three much enlarged. *Stamens* erect or slightly spreading; filaments subequal or adaxial ones slightly longer, free or fused below into short or long tube, inserted on base of tepals but sometimes tepals fused above filament insertion and then filaments apparently arising within perianth tube; anthers dorsifixed. *Ovary* ovoid; style usually between two-thirds and as long as filaments; stigma penicillate; ovules 6–8 in two series per locule. *Infructescence* toppling over at maturity through elongation of lower part of peduncle. *Capsule* papery, obovoid, and 3-angled or sometimes somewhat inflated and 3-winged, acute or retuse at apex, usually dehiscent loculicidally from top, rarely indehiscent, style rarely persistent as a beak. *Seeds* globose, smooth and glossy, black.



Species eight, South Africa, mainly the more arid winter rainfall parts.

Key to species

- 1a Lower flowers strongly zygomorphic with lower three tepals much enlarged, oblanceolate and several times longer than upper tepals; perianth red or yellow; lower bracts large, 25–35 mm long ..... 8. *D. aurea*
- 1b Lower flowers not or weakly zygomorphic with tepals sub-similar; perianth yellow to white or pinkish; lower bracts small or large, 1–30 mm long:
  - 2a Filaments united into narrow tube 8–12 mm long:
    - 3a Pedicels 1–3 mm long; tepals ± connate into a narrow tube above stamen insertion ..... 7. *D. stylosa*
    - 3b Pedicels 12–25 mm long; tepals spreading and free above stamen insertion:
      - 4a Flowers white; perianth tube 12–27 × 1.2–2.0 mm; tepals linear-oblanceolate ..... 5. *D. alba*
      - 4b Flowers yellow; perianth tube 6–10 × 3–4 mm; tepals oblong to ovate ..... 6. *D. capensis*
  - 2b Filaments free or shortly united into wide-mouthed tube up to 3 mm long:
    - 5a Perianth tube of lower flowers 25–45 mm long; tepals recurved; filaments free, white or flushed lilac ..... 1. *D. comata*
    - 5b Perianth tube of lower flowers 10–25 mm long; tepals spreading or suberect; filaments free or shortly united into tube, yellow to red:
      - 6a Lowermost flowers zygomorphic through basal fusion of upper tepals; tepals linear; flowers fragrant ..... 2. *D. namaquensis*
      - 6b Lowermost flowers actinomorphic; tepals ovate to lanceolate; flowers unscented:
        - 7a Inflorescence conical, topped with conspicuous coma of coloured bracts; perianth tube compressed-cylindrical, 2–3 mm diam.; stamens uniformly yellow to red ..... 3. *D. marginata*
        - 7b Inflorescence capitate, sometimes with inconspicuous coma of green bracts; perianth tube cylindrical, 1–2 mm diam.; stamens orange to red with basal collar flushed deep purple ..... 4. *D. zeyheri*

1. *Daubenya comata* (Burch. ex Baker) J.C.Manning & A.M.van der Merwe, comb. nov.

*Massonia comata* Burch. ex Baker in Journal of the Linnean Society, Botany 11: 392 (1871); Jessop: 421 (1976); U.Müll.-Doblies & D.Müll.-Doblies: 68 (1997). *Polyxena comata* (Burch. ex Baker) Baker: 419 (1897). *Neobakeria comata* (Burch. ex Baker) Schltr.: 150 (1924). Type: Northern Cape, Noupoot Dist., Carolus Poort, 19 March 1813, Burchell 2751 (K, holo.).

Bulb subglobose, 20–35 mm diam., deeply buried; outer tunics leathery, dark brown, extending in a papery neck up to 30 mm long. *Leaves* 2, spreading to prostrate, ovate to lanceolate, 60–150 × 30–90 mm, bases clasping peduncle for up to 80 mm, dark green or flushed maroon. *Inflorescence* subspicate, capitate, exerted up to 20 mm above leaves; bracts increasing in size acropetally, lowermost linear or awl-shaped, white, 7–12 mm long, those above gradually becoming broader, ovate to lanceolate, up to 10 × 2 mm, uppermost sterile, forming a coma, green or flushed pinkish, up to 8 × 3 mm; pedicels vestigial, lowermost up to 1 mm long, flowers subsessile. *Flowers* white or flushed pink, strongly scented during the day and night, fragrance sweet and spicy; weakly dimorphic, lower flowers slightly bilabiate, upper flowers actinomorphic; perianth tube cylindrical or abaxial surface flattened, lightly curved outwards, (25–)30–35(–45) mm long in lower flowers, ± 15 mm long in upper flowers, 2–3 mm diam.; in lower flowers adaxial half of tube ± 1 mm longer than abaxial half, with short sinus between upper three and lower three tepals; tepals spreading from base and then recurved or coiling downwards, linear-oblong to narrowly oblanceolate, up to 7 × 1.5–2.0 mm. *Stamens* erect at anthesis, later spreading slightly above; filaments subequal or adaxial ones slightly longer, free, inserted on or up to 1 mm above base of tepals, (7–)10–15 mm long; anthers pink, 2.5–3.0 mm long before dehiscence. *Ovary* ovoid, ± 3 mm long; style reaching to just below or slightly above filaments, 20–40 mm long. *Capsule* obovoid, 3-angled but rounded on angles, 10–12 × 7–8 mm. *Seeds* globose, ± 2 mm diam. *Flowering time*: mid April to mid May. Figure 1; Plate 1A.

*Distribution and ecology*: *Daubenya comata* is scattered across the western portion of the South African

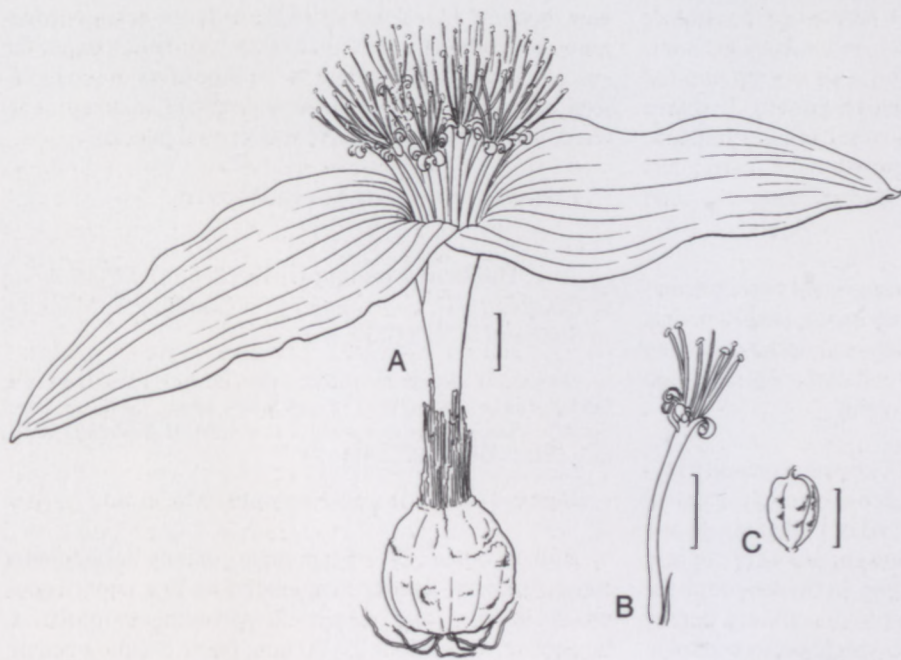


FIGURE 1.—*Daubenya comata*. A, whole plant; B, lower flower and bract; C, capsule. Scale bars: A–C, 10 mm. Artist: John Manning.



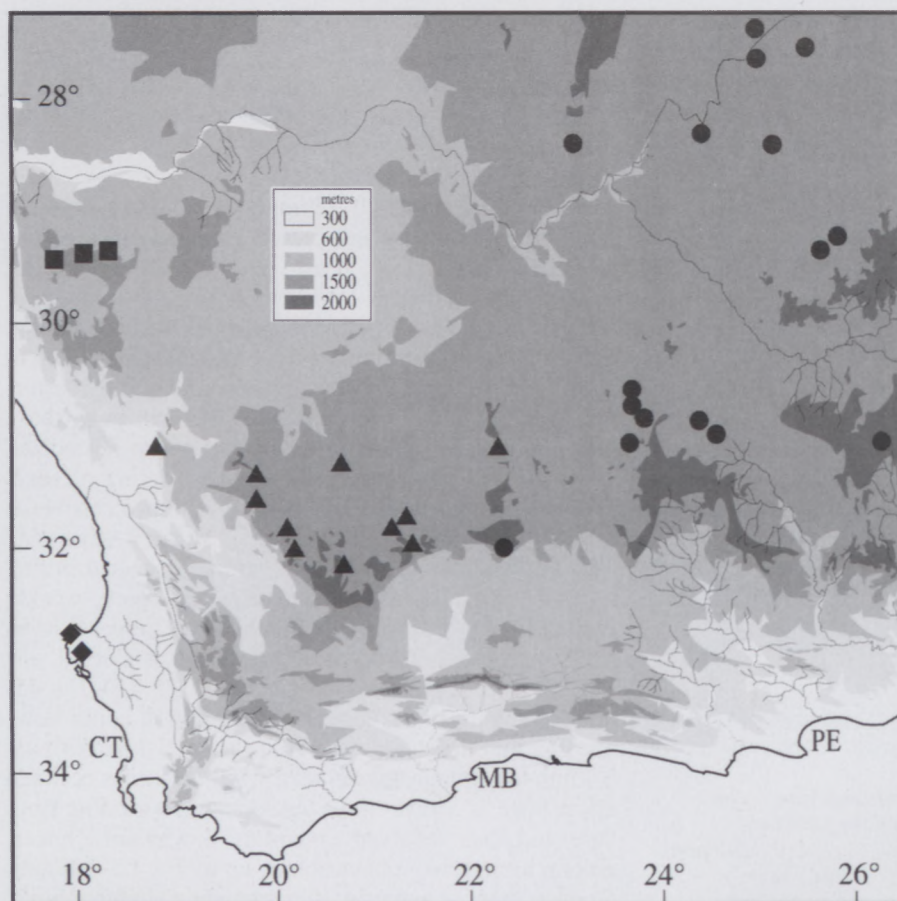


FIGURE 2.—Distribution of *Daubenya comata*, ●; *D. namaquensis*, ■; *D. marginata*, ▲; *D. zeyheri*, ◆.

central plateau where it is largely restricted to altitudes between 1 200–1 500 m, bordering the western rim of the drainage basin of the Orange/Gariep and Vaal Rivers (Figure 2). It has been recorded from Beaufort West near the northern border of the Western Cape, eastwards to Molteno in the Eastern Cape, through the Free State and eastern parts of the North-West as far north as Barberspan near Delareyville. Plants grow in colonies in seasonally waterlogged loam or clay, particularly the red, glutinous clays derived from the doleritic sills that are frequently exposed across the interior plateau. These soils retain moisture and remain damp for longer than the surrounding karoo shales. Like *D. namaquensis*, another early flowering species, *D. comata* responds to late summer showers, flowering before the soils dry up and the temperatures drop too low for active growth. It shares this strategy and habitat with several other sympatric dwarf geophytes with a similar growth habit, particularly *Androcymbium asteroides*, *Moraea falcifolia* and *Polyxena ensifolia*.

The white or pink flowers are strongly and sweetly scented throughout the day and night. They secrete small amounts of nectar and are pollinated by pollen- and nectar-collecting bees during the day (*Apis mellifera* and *Anthophora* sp.) and by small noctuid moths during the night.

**Diagnosis and relationships:** *D. comata* is readily recognized by the capitate inflorescence of strongly scented, white flowers with narrow, recurved or coiled tepals and free filaments. The lowermost flowers are very slightly bilabiate through a slight asymmetry in the length of the perianth tube, in the same way but to much less a degree than in *D. namaquensis*. The two species also resemble

one another in their free filaments but they differ in inflorescence shape, flower colour and in the form and size of the capsules. The small, sessile capsules in *D. comata* are rounded on the sides and quite unlike the inflated and angled or winged capsules that characterize the other species in the genus.

**History:** *D. comata* was first collected on the Farm Caroluspoort, just south of the Free State border near Noupoot, on 19 March 1813 (McKay 1943) by the naturalist and traveller William John Burchell. Fifty years were to elapse before the species was formally published by the Kew botanist J.G. Baker in 1871, with due acknowledgement to Burchell, who had sketched and named the species in his field notebook at the time of its original collection. It is now known to be widespread, although scattered, across the southern African central plateau.

**Conservation status:** Not endangered.

**2. *Daubenya namaquensis* (Schltr.) J.C.Manning & Goldblatt** [*'D. namaquana'*], in Goldblatt & Manning in *Strelitzia* 9: 713 (2000).

*Neobakeria namaquensis* Schltr.: 150 (1924); U.Müll.-Doblies & D.Müll.-Doblies: 86 (1997). Type: South Africa, Northern Cape, Springbok Dist., Zabies (= Sabies), 4 June 1896, M. Schlechter 90 (B, holo.; BOL!, GRA, PRE, SAM!, Z).

*Massonia angustifolia* sensu Jessop: 419 (1976) in part.

Bulb turbinate, 20–35 mm diam., deeply buried; outer tunics leathery, dark brown, extending in a papery neck up to 30 mm long. *Leaves* 2, spreading to prostrate, lanceolate, 100–150 × 25–70 mm, bases clasping pedun-



cle for up to 100 mm, dark green. *Inflorescence* subspicate, conical, exerted up to 90 mm above leaves; bracts increasing in size acropetally, lowermost awl-shaped, white, 1–2 mm long, those above gradually becoming longer and oblanceolate, up to  $6 \times 3$  mm, uppermost sterile, forming a coma, spatulate, green or flushed pinkish, up to  $8 \times 3$  mm; pedicels suberect, decreasing in length acropetally, lowermost up to 5 mm long, uppermost up to 0.5 mm long, flowers subsessile. *Flowers* greenish yellow, strongly scented during the day and night, fragrance sweet and spicy, carnation-like; dimorphic, lower flowers slightly bilabiate, upper flowers actinomorphic; perianth tube cylindrical or abaxial surface flattened, lightly curved outwards, 13–15 mm long in lower flowers, 9–10 mm long in upper flowers,  $\pm 2$  mm diam.; in lower flowers adaxial half of tube  $\pm 2$  mm longer than abaxial half with pronounced sinus between upper three and lower three tepals; tepals spreading from base and curving upwards in outer half, linear-oblanceolate,  $9\text{--}10 \times 1\text{--}1.5$  mm, apices weakly cucullate. *Stamens* erect at anthesis, later spreading slightly above; filaments subequal or adaxial ones slightly longer, 13–15 mm long, free, inserted on base of tepals; anthers yellow, up to 2.5 mm long before dehiscence. *Ovary* ovoid,  $\pm 3$  mm long; style reaching to between two-thirds and as long as filaments, 15–25 mm long. *Capsule* abscising at maturity, obovoid,  $20\text{--}23 \times 15$  mm, somewhat inflated, 3-angled and introrse at base but 3-winged and obtuse at apex, dehiscing loculicidally from top. *Seeds* globose,  $\pm 2$  mm diam. *Flowering time*: mid May to mid June. Figure 3; Plate 1B.

*Distribution and ecology*: *Daubenia namaquensis* is known from a few collections made in the semi-arid flats east of Okiep and Springbok at an altitude of 1 000 m (Figure 2). This region, just east of Namaqualand proper and on the extreme western edge of Bushmanland, lies on the boundary between winter and summer rainfall regions

and in consequence receives both erratic late summer showers as well as some rain from the occasional winter frontal system that extends inland from Namaqualand. The species responds rapidly to autumn rains and flowers in early winter before temperatures drop too low for active growth. Plants of *D. namaquensis* occur in small colonies in deep red sands in a vegetation dominated by the willowy shrub, *Sisymbrium sparteum* (Zygophyllaceae) and the tussock grass, *Stipagrostis namaquensis*. The colonies are restricted to lower-lying drainage areas in which the water table remains nearer the surface. The very deeply seated bulbs are an obvious adaptation enabling the plants to make use of this soil moisture.

The greenish yellow flowers are strongly and sweetly clove-scented throughout the day and night. They secrete small amounts of nectar and are probably pollinated by a variety of diurnal and nocturnal insects, including bees and moths.

*Diagnosis and relationships*: *D. namaquensis* is distinguished by the well-exserted conical inflorescence of strongly scented, yellow flowers with linear tepals and free filaments. Although confused by Jessop (1976) with *D. marginata*, the resemblance between the two species is very superficial, encompassing nothing more than the prominent inflorescence topped by a coma of sterile bracts. The flowers of *D. marginata* are unscented, with ovate, whitish or pale yellow tepals and golden yellow or orange filaments that are fused at the base into a short collar. A distinct feature of *D. namaquensis* is the bilabiate lower flowers in which the upper side of the perianth tube is prolonged for  $\pm 2$  mm beyond the lower side, resulting in a distinct sinus between the three upper and three lower tepals. This differential in the tube length rapidly becomes less evident higher up the inflorescence and the upper flowers are quite actinomorphic. This asymmetry

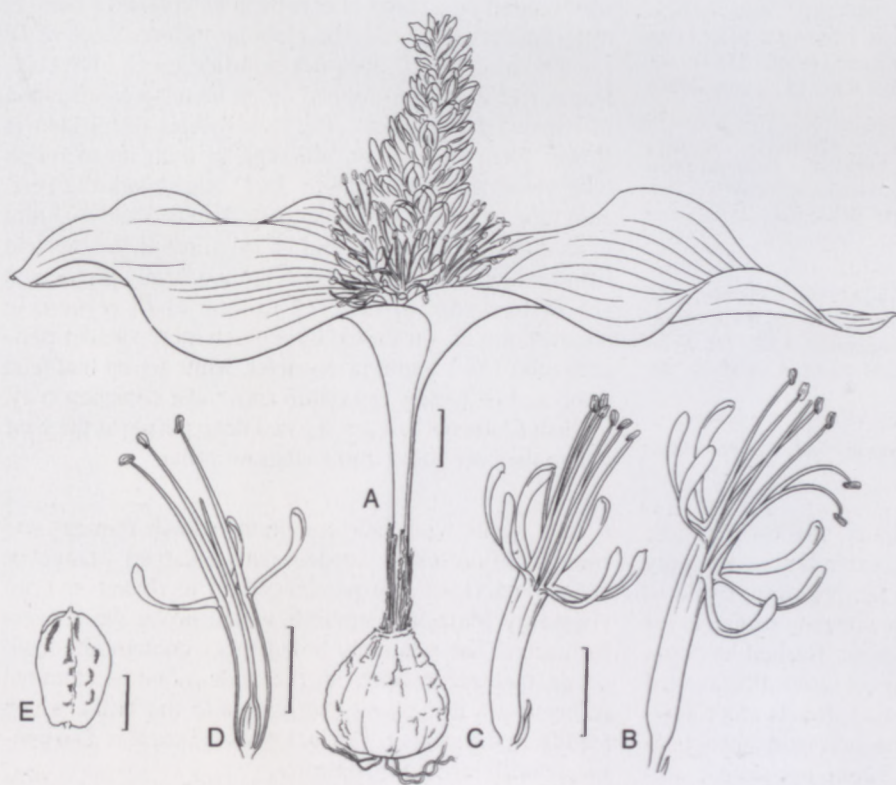


FIGURE 3.—*Daubenia namaquensis*. A, whole plant; B, lower flower and bract. C, D, upper flower: D, l/s. E, capsule. Scale bars: A–E, 10 mm. Artist: John Manning.



in the lower flowers is not very evident without careful examination, especially in pressed material. It occurs also, although to a lesser degree, in some other species of *Daubenya*, particularly *D. comata* and *D. stylosa*.

**History:** *D. namaquensis* was first collected by Max Schlechter during a trip to Namaqualand with his brother, the botanist Friedrich Richard Rudolf Schlechter, soon after his arrival in South Africa in May 1896. Two decades were to pass before it was described, when it formed the basis of the genus *Neobakeria*, established by Rudolf Schlechter to accommodate the group of species until then treated as *Polyxena* subgenus *Astemma*. These seven species were distinguished from *Polyxena* s. str. by their uniseriate stamens, and from *Massonia* by their inconspicuous bracts. Although struck by the well-exserted, foxtail-like inflorescence of *D. namaquensis*, Schlechter ironically overlooked the even more diagnostic zygomorphy of the lower flowers through dissecting only the more accessible upper flowers, which are perfectly actinomorphic. This characteristic was also overlooked by Jessop (1976), who confused the species with *D. marginata*. The curious zygomorphy of the lower flowers of *D. namaquensis* was only recently highlighted by Müller-Doblies & Müller-Doblies (1997). They used it as the basis for restricting the circumscription of the genus *Neobakeria* to this species alone, while in turn overlooking the fact that floral zygomorphy of the same type occurs, albeit to a lesser extent, in both *D. comata* and *D. stylosa*. Over a century was to pass before the species was collected for the second time and it is still known from only a handful of specimens.

**Conservation status:** Endangered (B1+2c, D).

### 3. *Daubenya marginata* (Willd. ex Kunth) J.C. Manning & A.M. van der Merwe in Bothalia 32: 65 (2002).

*Massonia marginata* Willd. ex Kunth: 299 (1843). *Polyxena marginata* (Willd. ex Kunth) Benth. & Hook. ex T. Durand & Schinz: 366 (1895). *Neobakeria marginata* (Willd. ex Kunth) Schltr.: 150 (1924). Type: South Africa, Caput Bonae Spei (B-WILLD 6373, holo.-NBG, photo!).

*Massonia rugulosa* Licht. ex Kunth: 299 (1843). *Polyxena rugulosa* (Licht. ex Kunth) Baker: 420 (1897). *Neobakeria rugulosa* (Licht. ex Kunth) Schltr.: 150 (1924). Type: Caput Bonae Spei, Lichtenstein 224 (B, holo., ?destroyed).

*Polyxena haemanthoides* Baker: t. 1727 (1888); E. Phillips: t. 56 (1922a). *Neobakeria haemanthoides* (Baker) Schltr.: 150 (1924). Type: South Africa, Nuweveld Mountains near Fraserburg, April 1886, Bolus 5493 [BOL, lecto!., designated by J.C. Manning & A.M. van der Merwe: 65 (2002); G, SAM!].

*Massonia angustifolia* auct. non *M. angustifolia* L.f. (= *M. echinata* L.).

Bulb subglobose, 20–30 mm diam., shallowly buried; outer tunics leathery, dark brown, extending as a papery neck up to 40 mm long. *Leaves* 2, spreading, ovate to elliptic, 50–100 × 25–50 mm, base clasping peduncle for 20–30 mm, apiculate, dark green or flushed maroon. *Inflorescence* subspicate, capitate or conical, exserted 20–60 mm above leaves at flowering; bracts erect, lowermost triangular, 2–5 mm long, becoming oblanceolate-spathulate acropetally, up to 8 × 3 mm, uppermost ster-

ile, imbricate, forming a short or elongate coma flushed orange, up to 10 × 5 mm; pedicels 1.0–2.5 mm long. *Flowers* greenish yellow with yellow or orange stamens, unscented; perianth tube compressed-cylindrical, 10–15(–20) × 2–3 mm; tepals suberect, inner three connate for 0.5–1.0 mm beyond outer three, lanceolate, conduplicate, 6–8 × 2.5 mm. *Stamens* connate for 1.5–2.5 mm in a wide-mouthed, slightly flaring staminal collar; filaments suberect and lightly incurved, 10–15(–22) mm long; anthers yellow, 2.0–2.5 mm long before anthesis. *Ovary* ovoid, ± 6 mm long; style lightly deflexed, 11–20 mm long. *Capsule* abscising at maturity, ellipsoid to obovoid, 12–15 × 15–20 mm, somewhat inflated, introrse at base, obtuse at apex, 3-angled below but 3-winged at apex. *Seeds* globose, ± 2.5 mm diam., glossy black. *Flowering time:* May to July, rarely to August. Figure 4; Plate 1C.

**Distribution and ecology:** *Daubenya marginata* is widespread across the Roggeveld Escarpment and western karoo at altitudes of 1 000–1 500 m, from near Calvinia and Williston southwards to Sutherland, thence eastwards along the Nuweveld scarp as far inland as Fraserburg and Loxton (Figure 2). A few isolated populations occur to the west, below the Bokkeveld Escarpment, at an altitude of 200 m in the Knersvlakte north of Vanrhynsdorp. Populations occur on silt or gritty clay, more rarely red clays derived from dolerite, in seasonally moist depressions or washlines. *D. marginata* grows sympatrically with *D. aurea* in some colonies but flowers several months earlier.

**Diagnosis and relationships:** *D. marginata* is morphologically very close to *D. zeyheri* and the two were regarded as conspecific by Jessop (1976). There are, however, several differences between them, some rather subtle. In *D. marginata* the inflorescence is typically conical and protrudes above the leaves, and is invariably surmounted by a coma of conspicuous yellow or orange, often spatulate bracts. The globular inflorescence of *D. zeyheri*, in contrast, does not protrude much above the leaves and is at most topped by an inconspicuous coma of narrow, green bracts. The two species differ also in flower form and colour, although in both the perianth tube varies greatly in length. In *D. marginata* the perianth tube is always conspicuously flattened and 2–3 mm in diameter, the tepals tend to be flushed yellow and firm-textured and the filaments are uniformly pigmented yellow to orange or red. The flowers of *D. zeyheri*, in contrast, are characterized by a much more slender perianth tube 1.0–1.5 mm in diameter, white tepals that tend to be almost papery in texture and, most conspicuously, reddish filaments that are flushed deep purple at the base where they are fused into a shallow collar.

The plants with their orange to reddish stamens and conical inflorescence topped with enlarged orange or yellow bracts are conspicuous when in flower and are visited by Malachite sunbirds which probe the flowers for nectar. The relatively broad tubes contain abundant nectar that accumulates in the wide-mouthed staminal collar where it is readily accessible to the birds, which feed from the ground. The lack of floral scent is also consistent with bird pollination.



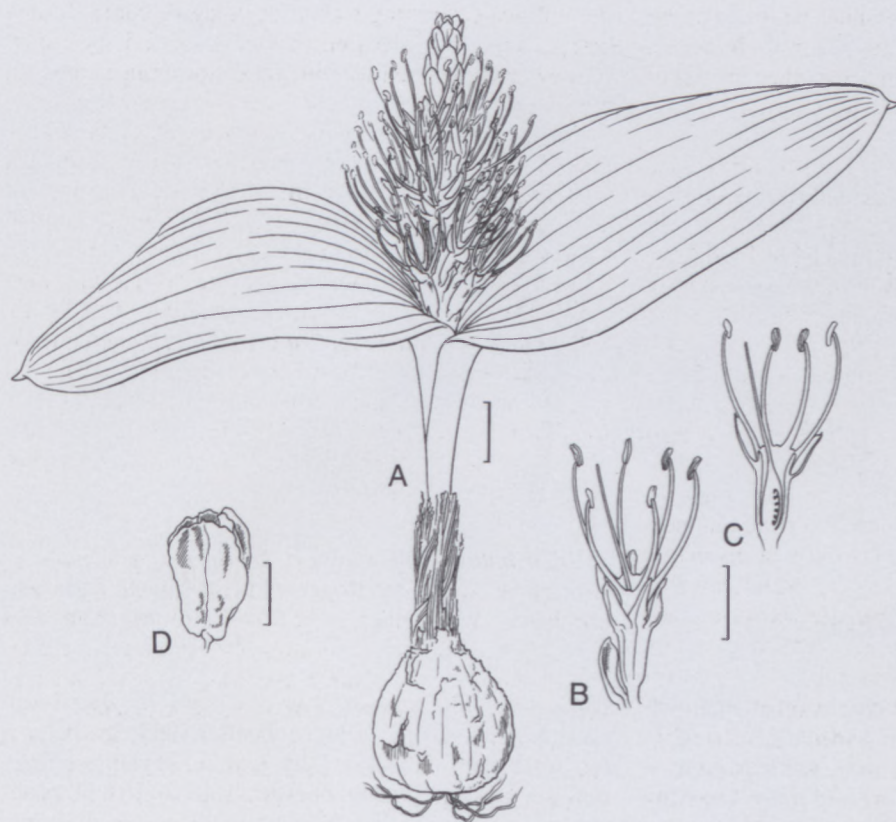


FIGURE 4.—*Daubenya marginata*. A, whole plant. B, C, flower: B, with bract; C, l/s. D, capsule. Scale bars: A–D, 10 mm. Artist: John Manning.

**History:** the true identity of this species has been misunderstood ever since the Kew botanist J.G. Baker confused it with *Massonia angustifolia* L.f., possibly as early as 1871 but certainly by 1897. This mistake was perpetuated by subsequent authors until recently, when it was shown that *M. angustifolia* is actually conspecific with *Massonia echinata* L. (Manning & Van der Merwe 2002). The species known by all authors after Baker as *M. angustifolia* is in fact properly known as *Daubenya marginata*, first described as *Massonia marginata* by the Berlin Botanist Carl Kunth. Although known to his predecessor, Carl Willdenow, it was not formally named until Kunth (1843) published the name that had earlier been suggested for it by Willdenow. The collector and place of collection of the type specimen are unknown. The species was later described as *Polyxena haemanthoides* by Baker in 1888, based on a plant collected by the Cape Town stockbroker and botanist, Harry Bolus, on the Nuweveld Mountains near Fraserburg in April 1886. It seems that Bolus intended describing the species himself, as *Haemantholirion capense*, but Baker must have dissuaded him from this step. Baker did, however, retain the reference to the genus *Haemanthus* (Amaryllidaceae) that the appearance of the plant had suggested to Bolus. Baker, although suspecting that his species was similar to Kunth's, had not seen material of *M. marginata* and thus described it as new. The species was recognized until Jessop (1976) revised the genus. Unconvinced that the apparent differences between it and *D. zeyheri* were significant, he combined the two taxa under the misapplied name *M. angustifolia*.

**Conservation status:** Not endangered.

4. *Daubenya zeyheri* (Kunth) J.C.Manning & A.M.van der Merwe, comb. nov.

*Massonia zeyheri* Kunth in *Enumeratio plantarum* 4: 298 (1843); U.Müll.-Doblies & D.Müll.-Doblies: 77 (1997). *Polyxena zeyheri* (Kunth) Benth. & Hook. ex T.Durand & Schinz: 367 (1895). Type: without locality or date, *Zeyher* 298 [†B, holo. destroyed; K, lecto!., designated by Jessop: 419 (1976)].

*Massonia pedunculata* Baker: 8 (1892). Type: South Africa, Malmesbury Dist., near Hopefield, Schaapplaatsfontein, June 1887, *Bachmann* 2043 (K, lecto!., here designated; B.–BOL, drawing!).

*Massonia burchellii* Baker: 393 (1871). *Polyxena burchellii* (Baker) Baker: 420 (1897). *Neobakeria burchellii* (Baker) Schltr.: 150 (1924). Type: South Africa, Caput Bonae Spei, *Burchell* s.n. (K, holo!., –BOL, drawing!).

*Massonia angustifolia* auct. non *M. angustifolia* L.f. (= *M. echinata* L.).

Bulb subglobose, 20–30 mm diam., outer tunics leathery, dark brown, extending as a papery neck up to 10 mm long. *Leaves* 2, spreading, elliptic to lanceolate, 60–150 × (10–)30–80 mm, bases clasping peduncle for 10–100 mm, apiculate, dark green. *Inflorescence* corymbose, capitate, exserted 20–40 mm above leaves; bracts erect, lowermost triangular, 2–3 mm long, becoming lanceolate acropetally and increasing in size, up to 8 × 2 mm, uppermost sometimes sterile and forming inconspicuous coma; pedicels 2–10 mm long, lowermost sometimes longer than upper. *Flowers* translucent, whitish tinged pink on tube, stamens reddish tinged purple at the base, papery in texture, unscented; perianth tube cylindrical, lightly constricted at mouth, 12–20 mm long in lower flowers but rarely more than 13 mm in upper flowers, 1.5–2.0 mm diam, inner tepals connate for 0.5–1.0 mm beyond outer ones; tepals spreading at base then suberect, lanceolate, conduplicate, 6–10 × 2.5–3.0 mm. *Stamens* reddish but staminal collar purple, connate for 1.0–1.5 mm in a flaring staminal collar; filaments suberect, 12–19 mm long; anthers yellow or reddish, 2–3 mm long before anthesis. *Ovary* ovoid, ± 4 mm long;



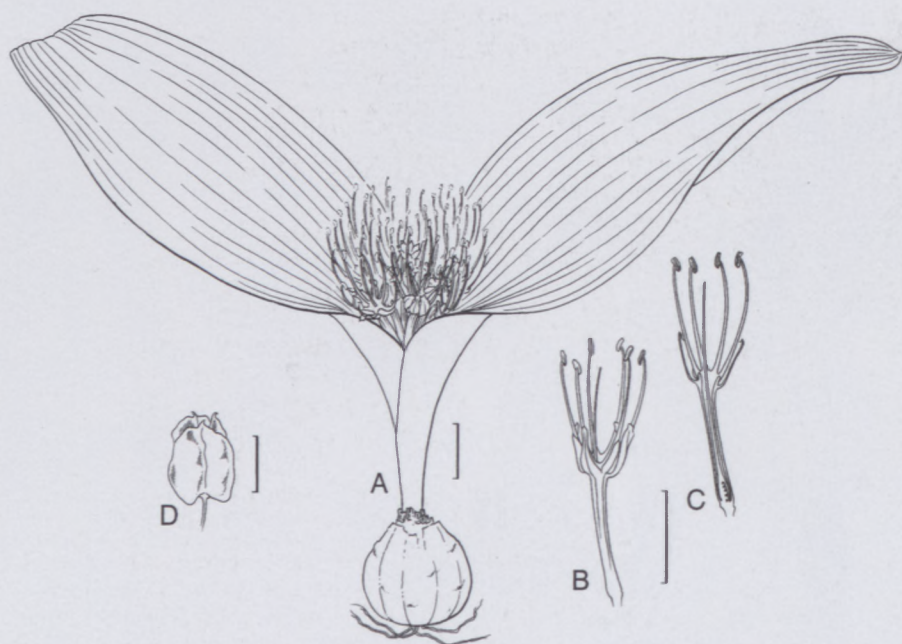


FIGURE 5.—*Daubenya zeyheri*. A, whole plant. B, C, flower: C, l/s. D, capsule. Scale bars: A–D, 10 mm. Artist: John Manning.

style 15–30 mm long. *Capsule* abscising at maturity, broadly ovoid, 10–15 × 9–13 mm, somewhat inflated, 3-angled, introrse at base, obtuse at apex. *Seeds* globose, ± 2.5 mm diam., glossy black. *Flowering time*: late May and June to early July. Figure 5; Plate 1D.

**Distribution and ecology:** *Daubenya zeyheri* is a coastal species occurring near sea level, unlike the other species in the genus, which occur at higher altitudes inland. It is restricted to the west coast of Western Cape, where it is now known from only three locations, one at Paternoster and Cape Columbine and the others less than 20 km to the south, near Saldanha (Figure 2). The material that formed the type of *M. pedunculata* was collected 10 km southeast of Hopefield on the Farm Schaapplaatsfontein but no further collections have been made from here and this population has presumably disappeared under wheat. *D. zeyheri* grows on sandy calcareous soils overlying limestone, sometimes in dense colonies.

The flowers, with their reddish filaments and contrasting glistening purple centres attract the attention of Lesser double-collared sunbirds, which probe the flowers for the copious nectar that is held in the wells formed by the staminal collars. The lack of floral fragrance is typical of bird-pollinated flowers.

**Diagnosis and relationships:** although closely related to *D. marginata* and sometimes difficult to separate from it in the dry state, living plants of *D. zeyheri* are readily recognized by the conspicuous purple centres to the flowers. The pigmentation is restricted to the staminal collar and when this is filled with nectar the flowers appear to have a glistening black centre that is quite lacking in *D. marginata*, in which the stamens are uniformly yellow or orange to reddish. Other more subtle differences between the two species are discussed under *D. marginata*. The two were treated as conspecific by Jessop (1976).

**History:** *D. zeyheri* has been described several times under different names but the earliest name dates from

1843, when the species was described by the Berlin botanist, Carl Kunth, from a collection made by the professional plant collector, Carl Zeyher. Zeyher's collection was made sometime between 1829 and 1834, probably near Saldanha Bay, which is still one of only two sites where the species is known to occur. The species was redescribed twice, both times by the Kew botanist J.G. Baker. In 1892 he described *Massonia pedunculata* from a specimen collected near Hopefield by the German naturalist Frans Bachmann, who practised medicine in the village from 1886–1887. A few years later he named *Massonia burchellii* from a collection made by the naturalist and traveller William John Burchell. Baker was clearly unsure about the exact identity of several of his species because he later transferred *M. burchellii* to *Polyxena* while leaving *M. pedunculata* in *Massonia*, although noting that it lacked the large bracts that are so characteristic of the genus.

**Conservation status:** Endangered (B1+2c, C2).

5. ***Daubenya alba*** A.M.van der Merwe, in A.M.van der Merwe & Marais in South African Journal of Botany 68: 312 (2002). Type: South Africa, Northern Cape, 25 km SW Middelpos, Farm Botuin, June 2001, Van der Merwe 195 (NBG, holo.).

Bulb subglobose to turbinate, 10–15 mm diam., usually shallowly buried; outer tunics leathery, brown, extending in a short, papery neck up to 5 mm long. *Leaves* 2, suberect to spreading, ovate to lanceolate, 40–100 × 15–50 mm, bases flushed red and clasping peduncle for up to 30 mm, dark green. *Inflorescence* corymbose, capitate, exserted up to 20 mm above leaves; bracts ovate-lanceolate, 3–4 mm long; pedicels well developed, lowermost 12–19 mm long, elongating slightly in fruit and ultimately 20–25 mm long. *Flowers* mauve or white with tips of tepals, filaments and exposed portion of style flushed pale lilac or mauve, strongly scented during the day and night, fragrance sweet and spicy, actinomorphic; perianth tube cylindri-



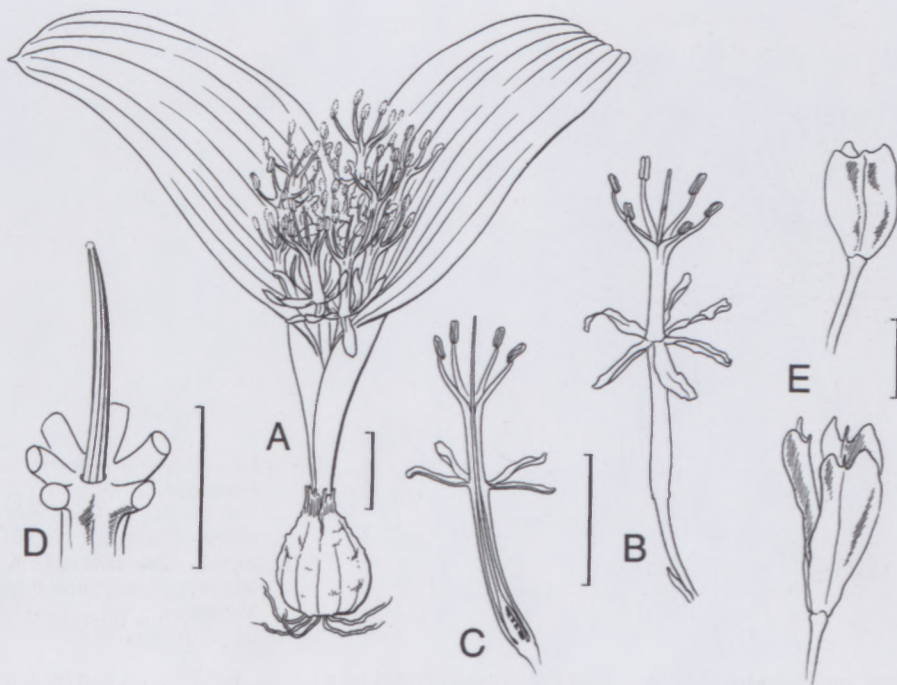


FIGURE 6.—*Daubenya alba*. A, whole plant. B–D, flower: B, with bract; C, l/s; D, detail of mouth of staminal tube. E, capsules. Scale bars: A–C, E, 10 mm; D, 5 mm. Artist: John Manning.

cal, (10–)12–25(–27) mm long, 1.5–2.0 mm diam.; tepals spreading from base, linear-oblong to narrowly oblanceolate, (8–)10–13 × 1.5–2.0 mm. *Stamens* connate below into cylindrical tube 8–10(–20) mm long, free parts suberect or lightly incurved at tips, (6–)8–15 mm long; anthers brown to purple, ± 2 mm long before dehiscence. *Ovary* ovoid, ± 4 mm long; style reaching up to 2 mm beyond anthers, 28–30(–50) mm long. *Capsule* ovoid-cuneate to obtriangular, (12–)20–25 × 10–12 mm, tapering below, deeply retuse above, three-winged. *Seeds* globose, 2.0–2.5 mm diam., glossy black. *Flowering time*: mid May to mid June. Figure 6; Plate 1E.

**Distribution and ecology:** *Daubenya alba* is known from a few scattered localities along the edge of the Roggeveld Escarpment between Calvinia and Middelpos at an altitude of 1 000–1 500 m (Figure 7). The plants

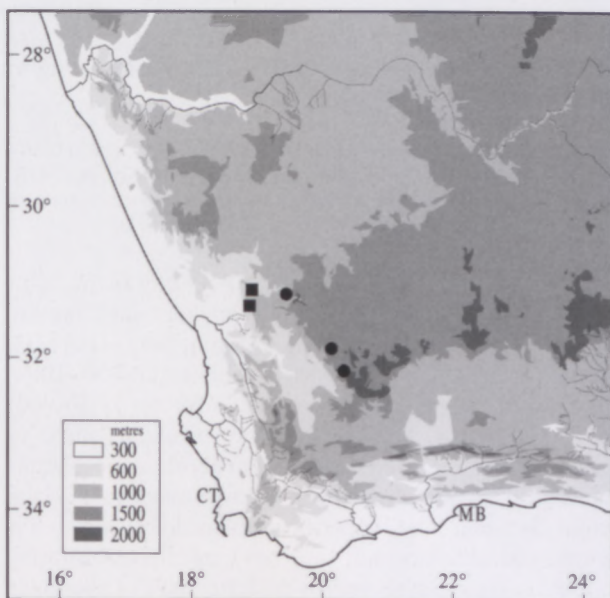


FIGURE 7.—Distribution of *Daubenya alba*, ●; *D. capensis*, ■.

grow in colonies in seasonally waterlogged doleritic clay, on low hills or at the foot of rocky dolerite outcrops.

**Diagnosis and relationships:** *D. alba* is readily recognized by its white to lilac flowers with the stamens fused below into a narrow tube 6–10 mm long. The slight zygomorphy of the lowermost flowers, resulting from a slight asymmetry in the staminal tube, that is mentioned in the original description, is not always evident. The relationships of *D. alba* appear to lie with *D. capensis*, which it resembles in several respects, particularly its relatively long pedicels, cylindrical staminal tube and large, obtriangular capsules that are deeply retuse at the apex. The two species are readily distinguished by their flowers. In *D. capensis* the firm-textured flowers are bright yellow with a shorter, broader tube, 6–10 mm long and ovate tepals. The flowers of *D. alba* are altogether more delicate, with a slender perianth tube, 12–20 mm long and narrowly oblanceolate tepals. In addition *D. alba* lacks the conspicuous disc occluding the mouth of the staminal tube that is characteristic of *D. capensis*.

**History:** the most recently discovered species in the genus, *D. alba* was in cultivation in a few specialist collections by the early 1990s, although the type material was only collected from the wild in June 2001.

**Conservation status:** Vulnerable (B1+2c, D).

**6. *Daubenya capensis* (Schltr.) A.M.van der Merwe & J.C.Manning**, in Goldblatt & J.C.Manning in *Strelitzia* 9: 713 (2000).

*Androsiphon capense* Schltr.: 148 (1924); Brandham: 124 (1990); U.Müll.-Doblies & D.Müll.-Doblies: 86 (1997). Type: South Africa, Northern Cape, Calvinia Dist., Onder-Bokkeveld, Oorlogskloof, 2500 ft, July 1897, R. Schlechter 10969 (B, holo.; BOL<sup>1</sup>, G, GRA, PRE, Z).

Bulb subglobose, 20–30 mm diam., outer tunics leathery, dark brown, extending as a very short, papery neck up to 5 mm long. *Leaves* 2, spreading, ovate to elliptic,



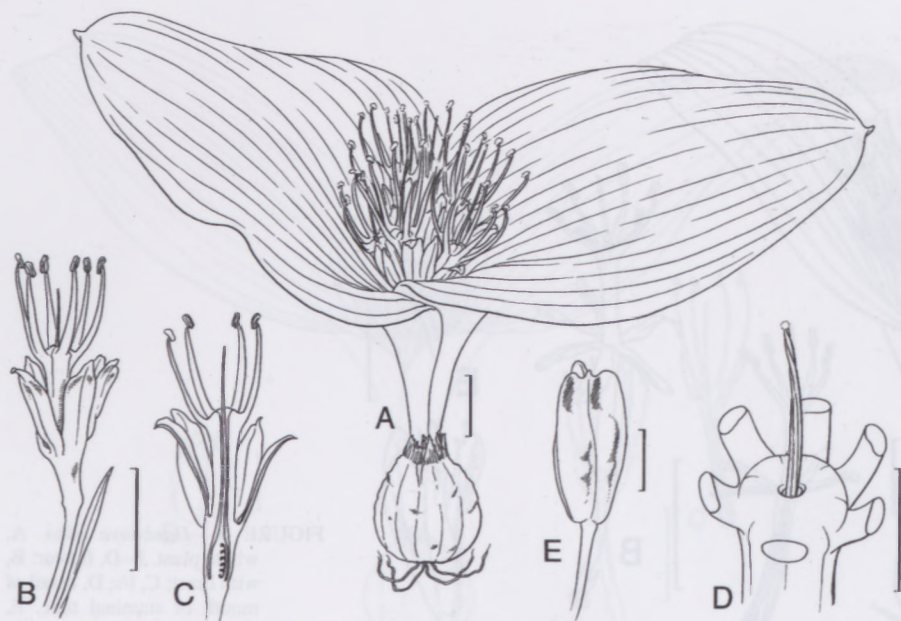


FIGURE 8.—*Daubenya capensis*. A, whole plant. B–D, flower: B, with bract; C, l/s; D, detail of mouth of staminal tube. E, capsule. Scale bars: A–C, E, 10 mm; D, 5 mm. Artist: John Manning.

50–150 × 25–90 mm, bases clasping peduncle for 20–80 mm, apiculate, dark green. *Inflorescence* corymbose, capitate, 30 × 40 mm; bracts erect, linear-oblongate, lowermost 25–30 × 2–3 mm, becoming shorter acropetally, uppermost oblanceolate-spathulate; pedicels 15–25 mm long, elongating slightly in fruit and ultimately 20–30 mm long. *Flowers* firm-textured, golden yellow with staminal column and operculum flushed red-dish orange and style streaked with red, yeast-scented; perianth tube subcylindrical, widening slightly upwards, 6–10 × 3–4 mm; tepals suberect, inner three sometimes connate for up to 1 mm beyond outer three, oblong to oblanceolate, 11–15 × 3–4 mm. *Stamens* connate in a stiff, thick-walled cylinder for 9–12 mm, top of tube occluded by convex disc or operculum through which style protrudes, upper portion of filaments suberect and lightly incurved, 10–14 mm long; anthers yellow, 2.0–2.5 mm long before anthesis. *Ovary* ovoid, ± 6 mm long; style erect, 20–25 mm long. *Capsule* ovoid-cuneate to obtriangular, 20–30 × 10–12 mm, tapering below, three-winged with apex deeply retuse. *Seeds* globose, ± 2.5 mm diam., glossy black. *Flowering time*: late June and July, rarely early August. Figure 8; Plate 1F.

**Distribution and ecology:** *Daubenya capensis* is endemic to the immediate vicinity of Nieuwoudtville, where it is known from several populations around the village at an altitude of 800 m (Figure 7). It is restricted to seasonally moist dolerite flats in red clay. The large, prominently three-winged capsules borne on relatively long pedicels form a rounded, balloon-like infructescence that is readily dispersed by the wind.

The curious disc that occludes the mouth of the tube is glossy and has the appearance of being wet even when dry, although nectar does in fact ooze out of the pore in the staminal disc and accumulate on it. Nothing is known about the pollination biology of the species but the firm texture of the flowers and their yeasty odour suggest rodent pollination.

**Diagnosis and relationships:** *D. capensis* is readily distinguished from other species of *Daubenya* in which

the filaments are fused into a long, narrow column by the peculiar disc that occludes the mouth of the column and through which the style protrudes via a narrow pore. *D. capensis* is most similar in floral form to *D. alba*, which it also resembles in its distinctly pedicellate flowers and large, obtriangular capsules that are deeply retuse at the apex. The fruits in these two species are among the largest in the genus. *D. capensis* is readily distinguished from *D. alba* by its more robust, yellow flowers with shorter perianth tube, 6–10 mm long and by the conspicuous disc that occludes the mouth of the staminal tube.

**History:** *D. capensis* was first collected in July 1897 by the German botanist, Friedrich Richard Rudolf Schlechter and was described by him some years later, when it formed the basis of his monotypic genus *Androsiphon*. Here it remained until recently, when that genus was included in *Daubenya* (Goldblatt & Manning 2000).

**Conservation status:** Vulnerable (B1+2c, D).

**7. *Daubenya stylosa* (W.F.Barker) A.M.van der Merwe & J.C.Manning**, in Goldblatt & J.C.Manning in *Strelitzia* 9: 713 (2000).

*Amphisiphon stylosum* ['stylosa'] W.F.Barker: 19 (1936); Brandham: 58 (1989); U.Müll.-Doblies & D.Müll.-Doblies: 86 (1997). Type: South Africa, Northern Cape, Calvinia Dist., 3 miles north of Nieuwoudtville, 21 June 1934, Salter 4552 (BOL, holo.!).

Bulb subglobose to turbinate, 20–35 mm diam., usually shallowly buried; outer tunics leathery, dark brown, extending in a papery neck up to 5 mm long. *Leaves* 2, suberect to spreading, ovate to lanceolate, (20–)50–100 × 15–50 mm, bases clasping peduncle for up to 30(–60) mm, dark green. *Inflorescence* subspicate, capitate or rarely conical, exerted up to 50 mm above leaves; bracts increasing in size acropetally, lowermost lanceolate, white, 3–5 mm long, uppermost oblanceolate, up to 8 × 3 mm; pedicels suberect, 1–3 mm long, flowers subsessile. *Flowers* greenish yellow with free part of filaments and style golden yellow, honey-scented; perianth tube cylindrical, 8–14 mm long in lower flowers with portion



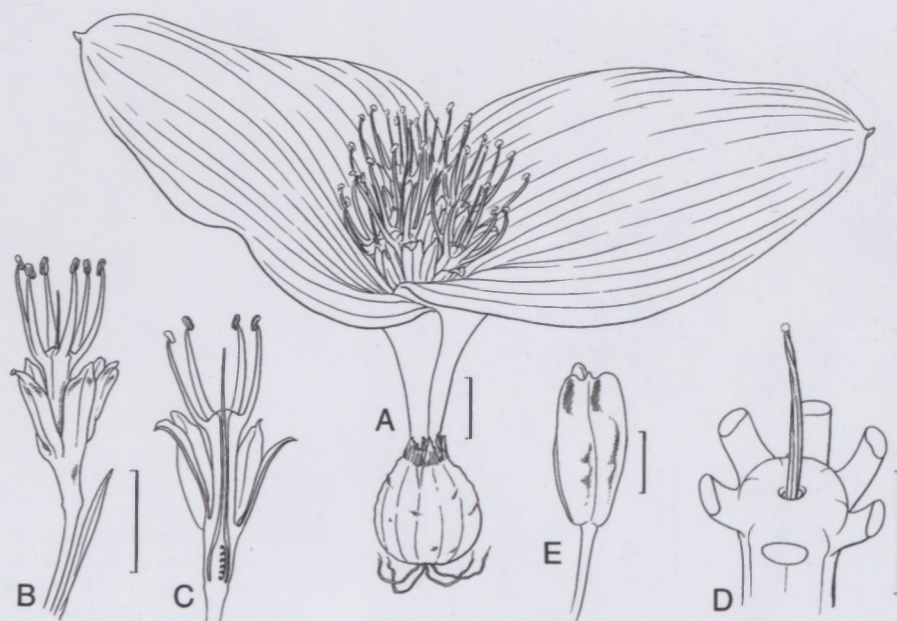


FIGURE 8.—*Daubenya capensis*. A, whole plant. B–D, flower: B, with bract; C, l/s; D, detail of mouth of staminal tube. E, capsule. Scale bars: A–C, E, 10 mm; D, 5 mm. Artist: John Manning.

50–150 × 25–90 mm, bases clasping peduncle for 20–80 mm, apiculate, dark green. *Inflorescence* corymbose, capitate, 30 × 40 mm; bracts erect, linear-oblongate, lowermost 25–30 × 2–3 mm, becoming shorter acropetally, uppermost oblanceolate-spathulate; pedicels 15–25 mm long, elongating slightly in fruit and ultimately 20–30 mm long. *Flowers* firm-textured, golden yellow with staminal column and operculum flushed red-dish orange and style streaked with red, yeast-scented; perianth tube subcylindrical, widening slightly upwards, 6–10 × 3–4 mm; tepals suberect, inner three sometimes connate for up to 1 mm beyond outer three, oblong to oblanceolate, 11–15 × 3–4 mm. *Stamens* connate in a stiff, thick-walled cylinder for 9–12 mm, top of tube occluded by convex disc or operculum through which style protrudes, upper portion of filaments suberect and lightly incurved, 10–14 mm long; anthers yellow, 2.0–2.5 mm long before anthesis. *Ovary* ovoid, ± 6 mm long; style erect, 20–25 mm long. *Capsule* ovoid-cuneate to obtriangular, 20–30 × 10–12 mm, tapering below, three-winged with apex deeply retuse. *Seeds* globose, ± 2.5 mm diam., glossy black. *Flowering time*: late June and July, rarely early August. Figure 8; Plate 1F.

*Distribution and ecology*: *Daubenya capensis* is endemic to the immediate vicinity of Nieuwoudtville, where it is known from several populations around the village at an altitude of 800 m (Figure 7). It is restricted to seasonally moist dolerite flats in red clay. The large, prominently three-winged capsules borne on relatively long pedicels form a rounded, balloon-like infructescence that is readily dispersed by the wind.

The curious disc that occludes the mouth of the tube is glossy and has the appearance of being wet even when dry, although nectar does in fact ooze out of the pore in the staminal disc and accumulate on it. Nothing is known about the pollination biology of the species but the firm texture of the flowers and their yeasty odour suggest rodent pollination.

*Diagnosis and relationships*: *D. capensis* is readily distinguished from other species of *Daubenya* in which

the filaments are fused into a long, narrow column by the peculiar disc that occludes the mouth of the column and through which the style protrudes via a narrow pore. *D. capensis* is most similar in floral form to *D. alba*, which it also resembles in its distinctly pedicellate flowers and large, obtriangular capsules that are deeply retuse at the apex. The fruits in these two species are among the largest in the genus. *D. capensis* is readily distinguished from *D. alba* by its more robust, yellow flowers with shorter perianth tube, 6–10 mm long and by the conspicuous disc that occludes the mouth of the staminal tube.

*History*: *D. capensis* was first collected in July 1897 by the German botanist, Friedrich Richard Rudolf Schlechter and was described by him some years later, when it formed the basis of his monotypic genus *Androsiphon*. Here it remained until recently, when that genus was included in *Daubenya* (Goldblatt & Manning 2000).

*Conservation status*: Vulnerable (B1+2c, D).

7. *Daubenya stylosa* (W.F.Barker) A.M.van der Merwe & J.C.Manning, in Goldblatt & J.C.Manning in *Strelitzia* 9: 713 (2000).

*Amphisiphon stylosum* ['stylosa'] W.F.Barker: 19 (1936); Brandham: 58 (1989); U.Müll.-Doblies & D.Müll.-Doblies: 86 (1997). Type: South Africa, Northern Cape, Calvinia Dist., 3 miles north of Nieuwoudtville, 21 June 1934, Salter 4552 (BOL, holo!).

Bulb subglobose to turbinate, 20–35 mm diam., usually shallowly buried; outer tunics leathery, dark brown, extending in a papery neck up to 5 mm long. *Leaves* 2, suberect to spreading, ovate to lanceolate, (20–)50–100 × 15–50 mm, bases clasping peduncle for up to 30(–60) mm, dark green. *Inflorescence* subspicate, capitate or rarely conical, exserted up to 50 mm above leaves; bracts increasing in size acropetally, lowermost lanceolate, white, 3–5 mm long, uppermost oblanceolate, up to 8 × 3 mm; pedicels suberect, 1–3 mm long, flowers subsessile. *Flowers* greenish yellow with free part of filaments and style golden yellow, honey-scented; perianth tube cylindrical, 8–14 mm long in lower flowers with portion



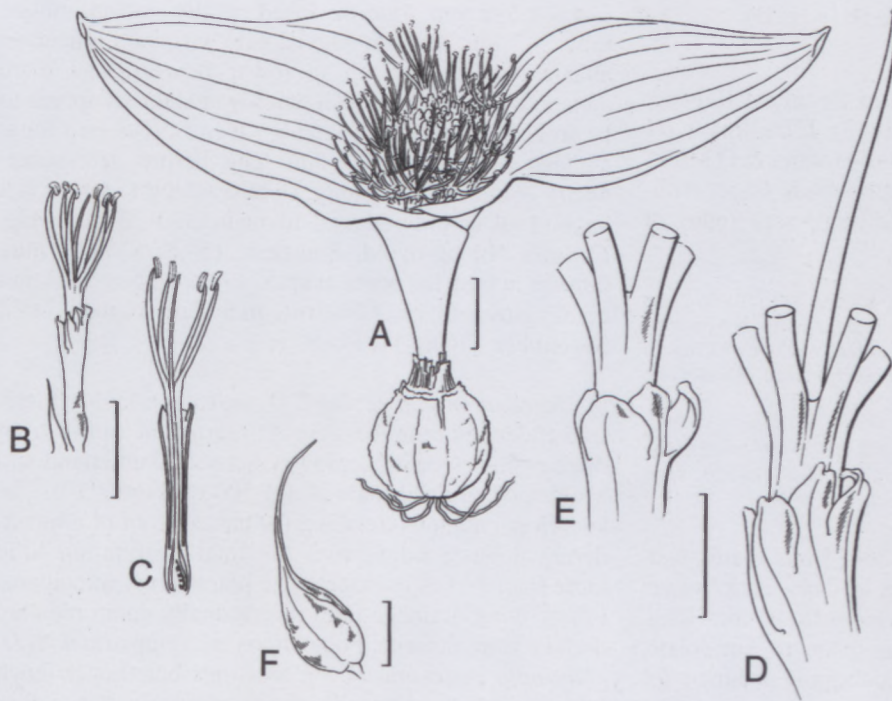


FIGURE 9.—*Daubenya stylosa*. A, whole plant. B–E, flower: B, with bract; C, lvs; D, tepal detail of lower part; E, tepal detail of upper part. F, capsule. Scale bars: A–C, F, 10 mm; D, E, 5 mm. Artist: John Manning.

below level of filament insertion 4–7 mm long but 6–8 mm long in upper flowers with portion below level of filament insertion 2–3 mm long, 2.0–2.5 mm diam.; lower flowers lightly bilabiate with adaxial portion of tube  $\pm$  3 mm longer than abaxial half through a greater degree of fusion of upper three tepals; tepals connate into tube above level of filament insertion, free parts oblong to ovate, 2–5 mm  $\times$  2.0–2.5 mm. *Stamens* fused below into tube 10–15 mm long, free parts of filaments suberect, 9–10 mm long; anthers yellow, up to 2.5 mm long before dehiscence. *Ovary* ovoid,  $\pm$  3 mm long; style reaching to top or just beyond filaments, 17–28 mm long. *Capsule* depressed-ovoid, 10–12  $\times$  7–10 mm, lightly retuse at base and tapering above into persistent style which forms slender beak  $\pm$  20 mm long, indehiscent but eventually separating along septa. *Seeds* globose,  $\pm$  2 mm diam., glossy black. *Flowering time*: mid May to mid June. Figure 9; Plate 1G.

**Distribution and ecology:** *Daubenya stylosa* is a highly local endemic around Nieuwoudtville where it is known from a few populations in the immediate vicinity of the town, especially along the trekpath that passes the Farm Glenlyon, at an altitude of 800 m (Figure 10). The populations here are extremely dense. The plants typically grow in lower-lying drainage areas in red doleritic clays. Scattered plants occur along the foot of dolerite outcrops on the Wildflower Reserve and on Glenlyon itself. The species is more or less sympatric with *D. capensis* but the two cannot be confused, either in flower or fruit. The compact infructescence in *D. stylosa* lacks the adaptations for wind dispersal typically found in most other species in the genus and the seeds are mainly shed immediately around the parent plants.

The sweetly scented, greenish yellow flowers secrete small amounts of nectar that ooze out of the mouth of the staminal column. They are visited avidly for the nectar by honeybees (*Apis mellifera*) and the Painted lady butterfly (*Cynthia cardui*) during the day and by several species of noctuid moth at dusk.

**Diagnosis and relationships:** the species is readily recognized by its almost completely fused tepals, which form a tube around the staminal column, and by the persistent styles that remain attached to the capsule. These stiff, prong-like beaks are a conspicuous feature of the subsessile fruits. In addition, unlike most other species in the genus, which have loculicidally dehiscent capsules, the fruits in *D. stylosa* are essentially indehiscent although the locules eventually separate along the septa to release the seeds.

**History:** *D. stylosa* was first collected relatively recently, in June 1934, by retired Royal Navy Paymaster, T.M. Salter, best known for his work on the genus *Oxalis*. It was described soon thereafter in the monotypic genus *Amphisiphon* by the Cape Town botanist W.F. Barker. Included in *Amphisiphon* by Phillips (1951), the genus was recently transferred to *Daubenya* (Goldblatt & Manning 2000).

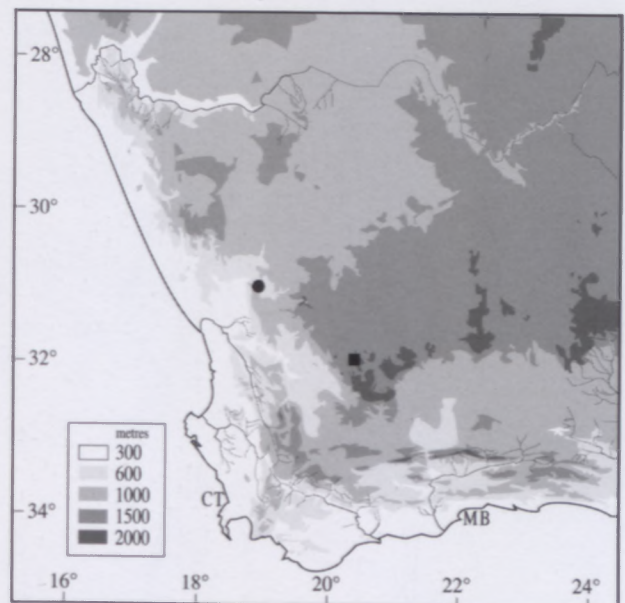


FIGURE 10.—Distribution of *Daubenya stylosa*, ●; *D. aurea*, ■.



*Conservation status:* Vulnerable (B1+2c, D).

8. *Daubenya aurea* Lindl. in Botanical Register 21: t. 1813 (1835); Kunth: 301 (1843); E. Phillips: t. 71 (1922b); Jessop: 431 (1976); U. Müll.-Doblies & D. Müll.-Doblies: 91–95 (1997). Type: South Africa, Cape, without locality or collector, cultivated by Messrs Young of Epsom (icono!).

*Daubenya fulva* Lindl.: t. 53 (1839); Kunth: 300 (1843). Type: received from the Cape of Good Hope, with other bulbs, but [mistakenly] believed to have been collected somewhere on the East Coast of Africa or in Madagascar, cultivated by Robert Barchard, Wandsworth (CGE, holo.).

*Daubenya coccinea* Harv. ex Baker: 395 (1871). *D. aurea* Lindl. var. *coccinea* (Harv. ex Baker) Marloth in E. Phillips (1922b). Type: Caput Bonei Spei, Harvey s.n. (TCD, holo.).

Bulb subglobose to turbinate, 20–35 mm diam., usually shallowly buried; outer tunics leathery, dark brown, extending in a short, papery neck up to 10 mm long. *Leaves* 2, suberect to spreading, ovate to lanceolate, 50–100(–140) × 20–75 mm, bases clasping peduncle for 5–50 mm, dark green. *Inflorescence* corymbose, capitate, exserted up to 50 mm above leaves; bracts decreasing in size acropetally, greenish, lowermost obovate to oblanceolate, 25–35 × 10–15(–20) mm long, uppermost up to 20 × 10 mm; pedicels suberect, lowermost 5–10 long, uppermost up to 3 mm long. *Flowers* brilliant red or canary yellow, rarely flushed reddish at tips of tepals, at most lightly scented, ± zygomorphic and bilabiate; lower flowers strongly bilabiate with abaxial or lower half of tube much prolonged and adnate to filament column and lower three tepals forming conspicuous lip separated from upper tepals by pronounced sinus, sometimes dorsal or uppermost tepal arising very much below remaining tepals, perianth tube obliquely cylindrical, 15–25 mm long on upper side but 20–40 mm long on lower side, 3–4 mm diam., upper tepals oblong-ovate, laterals obliquely so, 2–4 × 1.5–2.0 mm, lower tepals oblanceolate to obovate, subequal or median larger, 20–40 × 5–15 mm; upper flowers weakly zygomorphic or actinomorphic, perianth tube 13–20 × 2.5–3.5 mm, tepals oblong,

2–4 × 1.5–2 mm. *Stamens* fused basally into an oblique tube, 5–7 mm long on adaxial side but much longer on abaxial side, especially in lower flowers, and there adnate to lower tepals such that lower stamens appear to be free, free parts of filaments suberect, 4–8 mm long; anthers yellow, 2.5–3.0 mm long before dehiscence. *Ovary* ovoid, 7–8 mm long; style reaching to top or just beyond all or only adaxial filaments, 20–25 mm long. *Capsule* oblong-ovoid, 3-angled, 15–20 × 7–10 mm, introrse at base but acute at apex. *Seeds* globose, ± 3 mm diam., glossy black. *Flowering time*: late August to mid September. Figure 11; Plate 1H.

*Distribution and ecology:* *D. aurea* is a highly localized endemic of the Roggeveld Escarpment known from three or four localities midway between Sutherland and Middelpos, at an altitude of ± 1 500 m (Figure 10). The known populations lie along the eastern foot of a meandering dolerite ridge, with the total distribution little more than 10 km in extent. The plants grow in colonies in low-lying drainage lines in seasonally damp red clay derived from dolerite. Populations are sympatric with *D. marginata* in several of the localities but flower much later than that species. *D. aurea* occurs in two colour forms, the more common one a brilliant red and the other canary yellow. Populations are typically uniformly coloured, although red populations will often contain occasional yellow morphs, whereas yellow populations may include a few plants in which the tepals are flushed reddish at the tips. The yellow populations consistently come into flower one or two weeks before the red but the fruits appear to take much longer to ripen. The prominent papery bracts that are characteristic of the species are particularly conspicuous in fruit, serving as sails that assist in the wind dispersal of the infructescences.

The inflorescence resembles a large daisy capitulum in the genus *Arctotis* or *Gazania* due to the enlargement of the lower florets, and the species is adapted to pollination by monkey beetles (Scarabidae: Holpiinae) that congregate on the large flower heads to mate. The flowers, unlike those of the other species in the genus, do not produce nectar and are also unscented or at most weakly



FIGURE 11.—*Daubenya aurea*. A, whole plant; B, lower flower and bract. C, D, upper flower; D, l/s. E, capsule. Scale bars: A–E, 10 mm. Artist: John Manning.



scented. Both of these characteristics are typical adaptations to pollination by monkey beetles.

**Diagnosis and relationships:** *D. aurea* is a highly distinctive species that cannot be confused with any other species in the genus. The highly zygomorphic lower flowers in which the outer tepals are greatly exaggerated in size make this species instantly recognizable. It is also characterized by large floral bracts that are persistent and papery in fruit.

**History:** it is ironic that the source of the original material of the best known species of *Daubenya* remained obscure for so long. *D. aurea* was described in 1835 by John Lindley, Professor of Botany at the University College, London and head of the Chelsea Physic Garden, from a yellow-flowered plant cultivated by the nurserymen, Messrs Young of Epsom. Nothing is known of its origin beyond that the Youngs obtained their plant from the Cape of Good Hope under the name *Massonia lutea*. Three years later a reddish-flowered variant of the species came to Lindley's attention through the agency of John Royle, then Professor of Materia Medica at King's College, London, from the collection of Robert Barchard of East Hill, Wandsworth. Lindley was struck by the apparently more extreme zygomorphy evident in the flowers of the red form and he recognized this collection as a different species, *D. fulva*, on this basis. The name is an allusion to the tawny colour of the plant, but this, along with the rather etiolated appearance of the plant, was probably the result of cultivation in less than ideal light. From the illustration it is clear that this plant was in fresher flower than the first one that Lindley had seen and he presumably examined only the lowest, most zygomorphic flowers in the inflorescence. This plant had been received from the Cape of Good Hope with other bulbs but was believed to have been collected somewhere along the East Coast of Africa or in Madagascar. This was, of course, not the case but it is possible that Barchard received his plant from the same source as did the Youngs. A dried plant of *D. fulva* was later seen by Baker (1897) in the herbarium of William Wilson Saunders, who had a notable garden at East Hill from 1857 to 1874 and was a neighbour of Barchard. It is thus probable that his specimen came from Barchard himself and is possibly even the one illustrated in the protologue. At the same time that Lindley was describing his two species of *Daubenya*, a specimen appears to have been in the possession of William Henry Harvey in Cape Town. Harvey, although nominally Colonial Treasurer, occupied most of the four years that he spent in Cape Town between 1835 and 1842 on botany. Harvey's specimen formed the basis of *D. coccinea*, described by Baker (1871), which was distinguished from *D. fulva* by its compact inflorescence and more robust flowers. Although the provenance of the plant is unknown, its appearance is typical of wild collected material or that grown under good light, such as would have been experienced in Cape Town. It is impossible to be certain on this point but the more or less coincidental appearance of material in three different hands strongly suggests that it all originated from the same source. Circumstantial evidence favours Capt Walter Synnot as this source. Synnot spent four years in Clanwilliam as deputy landdrost, returning to Ireland in 1825 with numerous bulbs and

seeds. These were disposed of in England to various nurseries and included various species from the Bokkeveld and Roggeveld Escarpments, some of which only flowered in the 1830s. It is thus quite possible that among them were seeds or plants of *D. aurea*.

Almost a century was to pass without further information until, in 1920, Rudolph Marloth came upon *Daubenya aurea* in the wild on the Roggeveld Escarpment. Marloth, a retired chemist with a passionate interest in South African botany, sent plants and exact details of the locality and habitat to the Pretoria botanist, E.P. Phillips, who published the story of the rediscovery in 1922. At the same time it became evident that no significant structural differences existed between the three species hitherto known and they were consequently reduced to one. Although further plants were sent to Kirstenbosch gardens by a Mr Metelerkamp in 1936 (Hall 1970), they soon languished and it was left to Harry Hall, then Senior Horticulturalist at the Gardens, to locate Marloth's collecting site in 1968 and bring the species into cultivation once more. He has provided a lively account of his search, illustrated with fine photographs of the plants in the wild (Hall 1970).

**Conservation status:** Vulnerable (B1+2c, D).

#### Specimens examined

- Acocks 16344, 22097 (1) PRE. Archibald 3066, 3118 (1) PRE.  
 Barker 9736, 10179, 10237, 10244 (4) NBG; 6703 (2) NBG; 9366, 9389 (6) NBG; 9390, 10545 (7) NBG. Boucher 5153 (3) NBG.  
 Cloete & Haselau 96 (8) NBG. Coetzer 67 (3) NBG. Compton 702/28, 7470 (3) NBG; NBG1531/26 (6) NBG.  
 Hall 225, 3242, 4253 (3) NBG; 3240, s.n. (8) NBG; 3269 (8) NBG. PRE; 3276 (8) PRE. Harrower 305 (5) NBG. Henrici 3983 (1) PRE. Herman 530 (1) PRE.  
 Leipoldt 796 (6) NBG. Leistner 1900 (1) PRE; 2508 (2) KMG, M. PRE. Louw 1828 (1) BOL. PRE.  
 Manning 2175 (4) NBG; 2250 (2) NBG; 2263, 2343, s.n. (3) NBG; 2327, 2329 (1) NBG; 2345 (5) NBG; Marloth 10346 (8) PRE; 10415 (8) BOL; 10415 (8) NBG. PRE. McCarthy SAM23080 (1) SAM. Meiring BOL2775/15 (8) BOL. F.W. Meterlekamp 355/37 (8) NBG. Mostert 819 (1) PRE. Muller sub Marloth 9550 (8) PRE.  
 Oliver 4423, 9464 (3) NBG; 4412, 8932, 8972 (8) NBG.  
 Perry 3511 (8) NBG. Perry & Snijman 2132, 2143 (7) NBG.  
 Rossouw s.n. (3) NBG.  
 Saaijan 125 (1) PRE. Salter 1558/34 (7) NBG; 4452 (3) BOL. Schlechter 90 (2) SAM. BOL. Schlieben 9017 (2) BOL, BM, BR, M. PRE, Z. Snijman 1228, 1705 (7) NBG. Stayner s.n. (3) NBG. Steytler s.n. (4) NBG.  
 Thompson 2439, 3011, 3093 (3) NBG.  
 Van der Merwe 195 (5) NBG. Van Wyk 934 (1) PRE; 2578 (6) BOL; 2579 (7) BOL. Vlok 633 (6) NBG.  
 Wilman s.n. (1) BOL.  
 Zambatis 202 (1) PRE. Zietsman & Zietsman 1700 (1) PRE.

#### ACKNOWLEDGEMENTS

We are grateful to A. Horstmann and G. Summerfield for providing material for illustration and to the curators and staff of the cited herbaria, particularly Clare Archer. The colour illustrations were kindly sponsored by Rachel and Rod Saunders of Silverhill Seeds.



## REFERENCES

- BAKER, J.G. 1871. A revision of the genera and species of herbaceous capsular gamophyllous Liliaceae. *Journal of the Linnean Society, Botany* 11: 349–436.
- BAKER, J.G. 1888. *Polyxena haemanthoides*. *Hooker's Icones Plantarum* sér. 3, 8: t. 1727.
- BAKER, J.G. 1892. Liliaceae novae Africae australis barbarii regii Berolinensis. *Botanische Jahrbücher* 15, Beiblatt 25, Heft 3: 5–8.
- BAKER, J.G. 1897. Liliaceae. In W.T. Thiselton-Dyer, *Flora capensis* 6: 253–528.
- BARKER, W.F. 1936. *Amphisiphon*, a new genus of Liliaceae. *Journal of South African Botany* 2: 19–23.
- BENTHAM, G. 1883. Liliaceae. In G. Bentham & J.D. Hooker, *Genera plantarum* 3. Reeve, London.
- BRANDHAM, P.E. 1989. *Amphisiphon stylosa*. *Kew Magazine* 6: 58–61.
- BRANDHAM, P.E. 1990. *Androsiphon capense*. *Kew Magazine* 7: 124–128.
- DURAND, T. & SCHINZ, H. 1895. *Conspectus florae africae V. Monocotyledoneae et Gymnospermeae*. Jardin Botanique de l'État, Brussels.
- DYER, R.A. 1976. *The genera of southern African flowering plants*, vol. 2. Department of Agriculture, Pretoria.
- ENDLICHER, S.L. 1836. Liliaceae. *Genera plantarum* 1: 139–153. Beck, Vienna.
- FAY, M.F. & CHASE, M.W. 1996. Resurrection of Themidaceae for the *Brodiaea* alliance, and recircumscription of Alliaceae, Amaryllidaceae and Agapanthoideae. *Taxon* 45: 441–451.
- FAY, M.F., RUDALL, P.J., SULLIVAN, S., STOBART, K.L., DE BRUIJN, A.Y., REEVES, G., QAMARUZ-ZAMAN, F., HONG, W.-P., JOSEPH, J., HAHN, W.J., CONRAN, J.G. & CHASE, M.W. 2000. Phylogenetic studies of Asparagales based on four plastid DNA regions. In K.L. Wilson & D.A. Morrison, *Monocots: systematics and evolution*: 360–371. CSIRO Publishing, Collingwood, Australia.
- GOLDBLATT, P. & MANNING, J. 2000. Cape plants: a conspectus of the Cape flora of South Africa. *Strelitzia* 9.
- GOLDBLATT, P., BERNHARDT, P. & MANNING, J.C. 1998. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelilinae: Hopliini) in southern Africa. *Annals of the Missouri Botanical Garden* 85: 215–230.
- HALL, H. 1970. *Daubenya* Lindley. *Journal of the Botanical Society of South Africa* 56: 13–16.
- JESSOP, J.P. 1976. Studies in the bulbous Liliaceae in South Africa: 6. The taxonomy of *Massonia* and allied genera. *Journal of South African Botany* 42: 401–437.
- JOHNSON, S.D., PAUW, A. & MIDGLEY, J. 2001. Rodent pollination in the African lily *Massonia depressa* (Hyacinthaceae). *American Journal of Botany* 88: 1768–1773.
- KUNTH, C. S. 1843. *Enumeratio plantarum* 4. Stuttgart, Tübingen.
- LINDLEY, J. 1835. *Daubenya aurea*. *Botanical Register* 21: t. 1813.
- LINDLEY, J. 1839. *Daubenya fulva*. *Botanical Register* 25: t. 53.
- MANNING, J.C. & VAN DER MERWE, A.M. 2002. A new combination in *Daubenya* (Hyacinthaceae). *Bothalia* 32: 63–65.
- MÜLLER-DOBLIES, U. & MÜLLER-DOBLIES, D. 1997. A partial revision of the tribe Massonieae (Hyacinthaceae). *Feddes Repertorium* 108: 49–96.
- PHILLIPS, E.P. 1922a. *Polyxena haemanthoides*. *The Flowering Plants of South Africa* 2: t. 56.
- PHILLIPS, E.P. 1922b. *Daubenya aurea*. *The Flowering Plants of South Africa* 2: t. 71.
- PHILLIPS, E. P. 1951. The genera of South African flowering plants. *Memoirs of the Botanical Survey of South Africa* No. 25.
- PFOSSER, M. & SPETA, F. 1999. Phylogenetics of Hyacinthaceae based on plastid DNA sequences. *Annals of the Missouri Botanical Garden* 86: 852–875.
- SCHLECHTER, R. 1924. Drei neue Gattungen der Liliaceen aus Südafrika. *Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin* 9: 145–151.
- SNIJMAN, D.A. & LINDER, P. 1996. Phylogenetic relationships, seed characters, and dispersal system evolution in Amaryllideae (Amaryllidaceae). *Annals of the Missouri Botanical Garden* 83: 362–386.
- SPETA, F. 1998. Hyacinthaceae. In K. Kubitzki, *The families and genera of vascular plants*, vol. 3: 261–285. Springer-Verlag: Berlin.
- VAN DER MERWE, A.M. & MARAIS, E.M. 2002. *Daubenya alba* (Hyacinthaceae, tribe Massonieae), a new species from the Roggeveld, Northern Cape Province. *South African Journal of Botany* 68: 312–315.
- VAN DER MERWE, A., BELLSTEDT, D.U., MARAIS, E.M. & HARLEY, E.H. in prep. Phylogenetic relationships in subtribe Massoniinae of tribe Massonieae (Hyacinthaceae) based on non-coding *trnL-trnF* chloroplast sequences.
- VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. Springer-Verlag, Berlin.
- VICTOR, J. 2000. *Red Data List Workshop*. National Botanical Institute, Pretoria.